CHAPTER 42

Hormonal Control of Reproduction in Crocodilians

Valentine A. Lance[1]

CROCODILIANS have evolved a reproductive cycle closely synchronized with seasonal changes in the environment in which they live. This precise timing of reproduction ensures that embryos develop in the field when conditions are optimal for survival, and that the young are born at a time of year most likely to result in their continued survival. In temperate regions the most important environmental factor appears to be temperature. In equatorial regions, seasonal changes in rainfall, water levels in the rivers and lakes, or seasonal changes in food availability may be more important determinants of reproduction. What enables crocodilians to regulate their breeding cycles with such precision is their ability to sense these environmental changes and adapt their hormonal secretions accordingly.

Sound management of wild populations of crocodilians and successful breeding of crocodilians in captivity require thorough knowledge of reproductive physiology and an understanding of the environmental and nutritional factors regulating reproductive cycles. By raising crocodilians on farms, one hopes to obviate some of the environmental factors and thus exert control over breeding. Unfortunately, how environmental factors affect reproduction is still poorly understood.

This chapter reviews briefly what we have learnt of the reproductive cycle of American alligators (*Alligator mississippiensis*) and crocodilian reproduction in general. It also highlights major gaps in our knowledge — areas where a more intensive research effort is needed.

THE ANNUAL BREEDING CYCLE OF ALLIGATORS

The annual reproductive cycle of *A. mississippiensis* in Louisiana has been worked out in some detail using data collected from telemetry studies and from the examinations of reproductive tracts of animals killed throughout the year (Joanen and McNease 1970, 1972, 1979, 1980; McNease and Joanen 1974; Lance 1984).

From October to March, adult male and female alligators do not feed and spend most of their time in dens or holes, dug deep under the banks of small ponds or canals. On warm sunny days they may emerge to bask, but will not feed. In late March or early April, depending on ambient temperatures, the animals move from their winter quarters into the deep, open water of canals or lakes. Occasional bellowing by both male and female alligators, usually just before dawn, can be heard at this time. As air and water temperatures increase by mid-April, feeding begins and the intensity and frequency of bellowing increases.

Courtship activities begin in late April and early May, and by late May have reached a peak. Shortly after courtship and copulation, the female leaves the deep water areas and moves into the shallow waters of the open marsh. Here they usually settle in small isolated ponds, where nest construction takes place. The nest building period begins about the first week in June and may extend until the first week of July. A single clutch of eggs is laid during this period. Clutch size in Louisiana averages 39 (range 2-58). All of the eggs in a clutch are laid at the one time, usually at night, and hatching occurs 62-66 days later (Joanen 1969; Joanen and McNease 1971, 1975, 1980).

Although individual alligators lay the entire clutch in one night, it takes about two weeks for the entire population to complete egg-laying. This two-week period may vary from year to year depending on the ambient temperatures during March, April and May; in cooler years nesting may start as late as June 20th, whereas in warmer years, it is as early as June 5th (Joanen and McNease 1979).

The female remains in the vicinity of the nest throughout the incubation period (Kushlan 1973; Kushlan and Kushlan 1980) and assists the young by opening the nest in response to vocalizations by them, when hatching is imminent (Herzog 1975). After hatching the female remains close to the nest site, usually building a den in the vicinity, and does not return to deeper water until the following

spring. Young are believed to overwinter in the same den as the mother, and often remain at the nest site until their third year (Chabreck 1965). Males and non-breeding adult females remain in deep water canals and bayous throughout the summer and move to their winter habitat in late October (Joanen and McNease 1970, 1972). In the northern Louisiana cypress-tupelo lake habitats, movement of alligators is much more restricted, with breeding and nesting appearing to take place in the same area (Taylor 1984).

MALE REPRODUCTIVE CYCLE

Data on testicular weights have been collected from March to October by both Joanen and McNease (1975) and myself (Fig. 1); a single observation was made on a basking (2.8 m) animal shot in February. The peak in testes weight occurs in April and May, followed by a rapid decline in mid-June to a nadir in August.
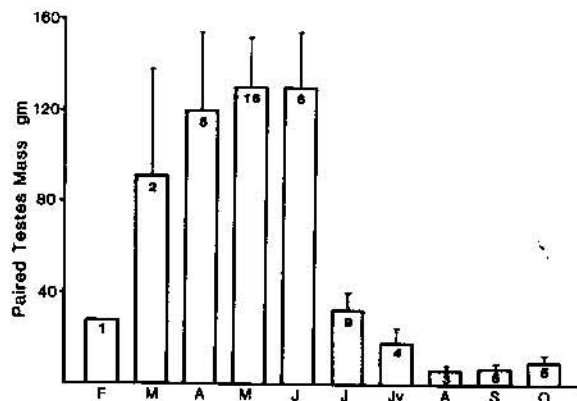

Fig. 1. Seasonal variation in paired testes mass in *Alligator mississippiensis* collected in southern Louisiana. The means with SE's represent the pooled data collected over several years. The samples collected in June have been divided into those collected in the first two weeks and those collected in the second two weeks to emphasize the rapid decrease in mass. Numbers in bars are sample sizes.

Histological examination of testes indicates that even as early as February, providing there have been some warm sunny days, spermatogonial division is already well advanced. By March, late stage spermatids are present in the seminiferous tubules, though mature spermatozoa are not seen until late April and early May. Peak production of spermatozoa occurs from mid-May to early June. Spermatozoa are present in the penial groove from about the first week in May until early June. The percentage of immotile or dead spermatozoa increases from early June to the third week in June when more than 90% of the cells are dead (Joanen and McNease 1980). In mid-June spermatogenesis stops abruptly and the testes regress rapidly. By late July and early August regression is complete. No material from October

has been examined histologically, but from the recorded weights of testes collected in this month it does not appear that the next cycle of spermatogenesis is initiated until the following spring. More samples are needed from animals taken throughout the winter months to determine when the cycle actually begins.
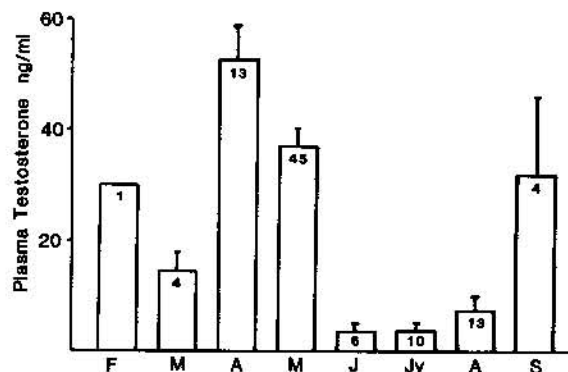

Fig. 2. Seasonal variation in plasma testosterone concentrations in male *Alligator mississippiensis* in southern Louisiana. Only one animal was sampled in February.

Plasma testosterone production in male alligators also peaks in April and May, and as spermatogenesis ceases and the testes regress, so too it drops to extremely low levels in July and August (Fig. 2). A second peak of testosterone occurs in September although histological examination of testicular tissue from September samples does not indicate any resumption of spermatogonial division in the seminiferous epithelium at that time.

FEMALE REPRODUCTIVE CYCLE

The reproductive cycle of the female follows the same general pattern as that of the male, in that ovarian development is initiated in early spring as ambient temperatures increase. By early April ovarian follicles (16-25 mm diameter) have already increased in size from the resting stage (5-8 mm) seen the previous September. By early May the diameter increases to 25-34 mm, and by early June to a preovulatory maximum of 45 mm. The time between ovulation and egg-laying has been estimated as 3 to 3.5 weeks (Joanen and McNease 1980).

During the follicular growth phase (April-May), estradiol concentrations in the plasma increase to a mean of about 600 pg ml^{-1} (Fig. 3) and plasma testosterone to a mean of about 2 ng ml^{-1}. Blood plasma from female alligators with developing ovaries has a characteristic cloudy or "milky" appearance as a result of high circulating levels of the yolk precursor protein, vitellogenin.

In all egg-laying vertebrates, the process of vitellogenesis is remarkably similar (Ho et al. 1982). In response to pituitary gonadotropin secretion the
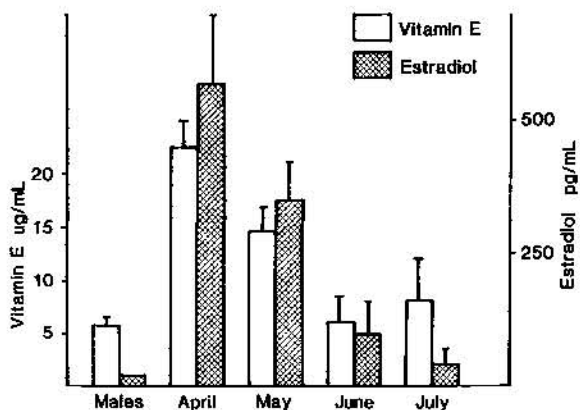
Fig. 3. Monthly variation in plasma estradiol and plasma vitamin E in female *Alligator mississippiensis* from southern Louisiana. Plasma levels in male alligators are included for comparision.
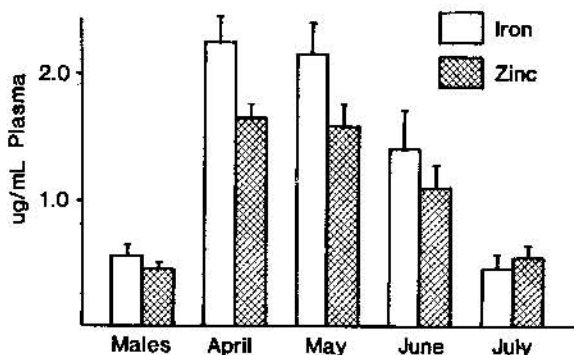

Fig. 4. Monthly variation in plasma iron and plasma zinc in female *Alligator mississippiensis* from southern Louisiana. Plasma levels in male alligators are included for comparision.
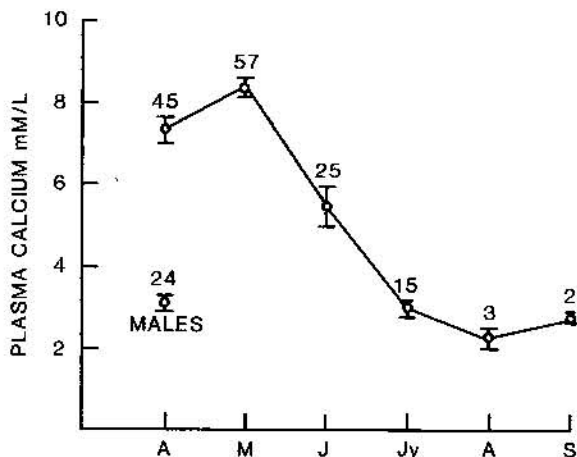

Fig. 5. Seasonal variation in total plasma calcium concentrations in female *Alligator mississippiensis* from southern Louisiana. Plasma concentrations in male alligators are included for comparison. Numbers are sample sizes.

ovarian follicles increase in size and secrete the hormone estradiol-17β. The estrogen secreted by the developing ovarian follicles acts on the liver to stimulate the synthesis of massive amounts of the

yolk precursor protein, vitellogenin. The vitellogenin is secreted into the blood stream and transported to the ovary, where it is taken up by the ova and transformed into yolk.

During the yolking phase of ovarian growth remarkable changes take place in the chemistry of the blood plasma: total protein, total lipid, cholesterol, vitamin E, calcium, magnesium, iron and zinc all increase dramatically (Figs 4 and 5). A small blood sample taken at this time can provide a considerable amount of information on the reproductive status of the animal. By simply measuring total plasma calcium, an estimate of the percentage of a population likely to nest in a given year can be determined accurately (Wilkinson 1984). Following ovulation, plasma estradiol returns to non-detectable levels, and all of the plasma constituents that showed an increase during vitellogenesis return to levels similar to those seen in males and non-breeding females (Lance *et al.* 1983).

Another function of the estradiol secreted by the ovary is to stimulate growth of the reproductive tract in preparation for egg-laying. Both the albumin secreting portion and the shell secreting portion of the oviduct hypertrophy in response to estrogen. In order for shell formation to occur however, parathyroid hormone is required. This hormone mobilizes calcium from the bones, which is subsequently removed from the blood and deposited in the shell. Femurs from female alligators that have laid eggs show a considerable loss of bone when compared to femurs taken from males or non-breeding females (Elsey and Wink 1985).

The post-ovulatory follicles of reptiles form structures similar to the corpora lutea of mammals. In all species studied these structures secrete the hormone progesterone (Lance and Callard 1980). Progesterone is believed to inhibit contraction of the oviduct and thus prevent premature egg deposition. It also acts in concert with estrogen to promote growth of the reproductive tract; it may also inhibit gonadotropin secretion by the pituitary and thus prevent any ovarian development while eggs are in the oviduct. Only five animals with eggs in the oviducts were examined by me; all had well developed corpora lutea, but none had elevated progesterone levels in the plasma. It is possible that the severe stress of catching them on a baited hook may have resulted in spuriously low levels, and more data are clearly needed on this important point.

DISCUSSION

The annual reproductive and activity cycles of male and female *A. mississippiensis* in Louisiana are summarized in Figure 6. From a farming management point of view, the male alligator presents few problems. A single spermatogenic cycle closely tied

to environmental temperatures occurs every year. The importance of temperature as a trigger for spermatogenesis in alligators was pointed out by Murphy (1980), who noted that adult alligators living in ponds artificially heated by effluent from a nuclear reactor, produced spermatozoa two weeks earlier than adults living in adjacent, natural ponds.
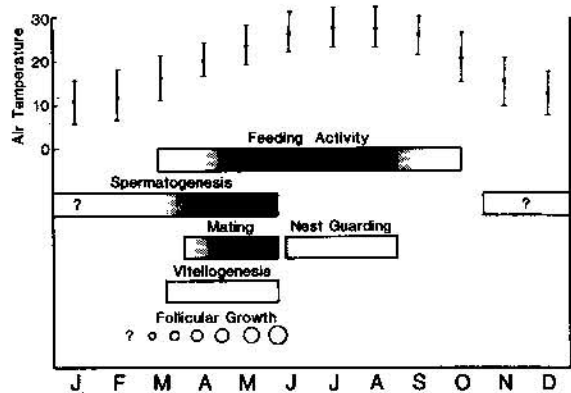

Fig. 6. Annual activity and reproductive cycles of male and female *Alligator mississippiensis* at Rockefeller Wildlife Refuge, Louisiana. The ten year mean monthly temperature with mean monthly high and mean monthly low temperatures are included. Question marks indicate where data are lacking.

It is still not known if diet in captive alligators has any major effects on sperm production, nor is it known if social interaction with other alligators is necessary for successful spermatogenesis. I am not aware of any alligator farmers encountering reproductive problems with male alligators. However, it should be pointed out that we know very little about semen quality and the viability of spermatozoa in crocodilians.
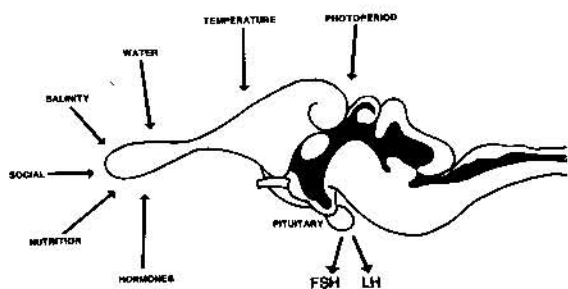

Fig. 7. Cross-sectional representation of an *Alligator mississippiensis* brain with some of the known stimuli that affect reproduction.

We know from ecological studies that a host of environmental factors affect nesting by both alligators (Joanen 1969; Chabreck 1975; Goodwin and Marion 1978; Deitz and Hines 1980; Metzen 1977; Wilkinson 1984) and crocodiles (Modha 1967; Graham 1968; Webb *et al.* 1977, 1983). I have shown schematically in Figure 7 a cross-section of an

alligator brain with some of the known stimuli that affect reproduction. Each of these factors may affect different points in the reproductive cycle, and if reproductive failure is the end result of an inadequacy in any one of them, all may be considered of equal importance. If temperature is too low for example, the pituitary gland may fail to secrete gonadotropin and thus no ovarian follicles will develop, or ovulation may be delayed to such an extent that nesting and hatching occur well beyond the normal period, which results in high embryo and hatchling mortality. The role of photoperiod on reproduction in alligators has not been studied, although it is known that populations at the northern extreme of their range reproduce two weeks later than those at the southern extreme.

From our experience, diet has been shown to be extremely important. A diet of marine fish alone results in a gradual decline in clutch size, percent fertility and percent hatchability, and will almost certainly result in complete cessation of egg production in some individuals (see Joanen Chapter 32). In severe cases, fatal pathological conditions may result (Wallach and Hoessle 1968; Frye and Schelling 1973; Larson *et al.* 1983). It is now known from a large number of studies that when an animal is fed a diet of frozen marine fish, the oils in the fish form lipid peroxides which cause tissue damage. Vitamin E protects the tissues against this damage to some extent, but if dietary vitamin E is inadequate and the fish lipid peroxides are excessive, the end result is vitamin E deficiency (Scott 1978; Van Vleet 1980).

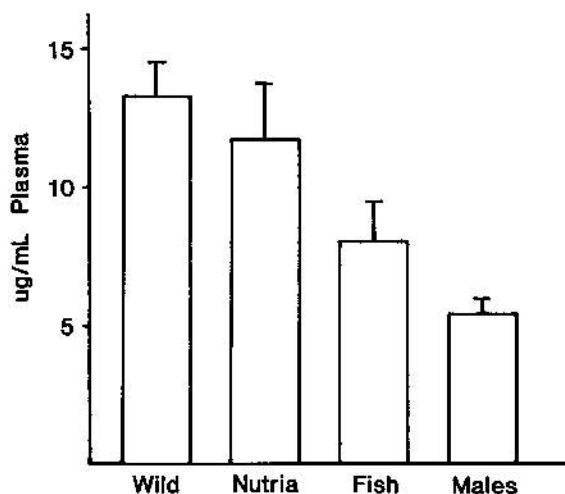Fig. 8. Mean plasma levels of vitamin E in wild, captive nutria-fed and captive fish-fed female *Alligator mississippiensis* during the breeding season. Concentrations in male alligators are included for comparison.

Embryos are more sensitive to vitamin E deficiency than are adults, therefore, if the vitamin E getting into the eggs is only slightly less than normal, embryo mortality will be high. Thus an adult female

alligator fed fish shows only slightly lower vitamin E levels in the blood than wild or meat fed controls (Fig. 8), and has no overt symptoms of vitamin E deficiency. Yet the eggs produced by these females will have lower than normal vitamin E in the yolk. The embryos in these vitamin E deficient eggs are unlikely to complete development. If live or fresh fish are available, vitamin E deficiency is unlikely to occur.

Since crocodilians are carnivores, nearly all the essential trace elements and amino acids are present in the diet and deficiences in these are rare. However, alligators fed monotypic diets such as chicken carcasses have poor reproductive success. It is possible that an imbalance in the amino acids available after digestion may have caused inhibition of protein synthesis in such cases (R. A. Coulson, pers. comm.). Similarly, diets of poor quality protein lack the correct ratio of amino acids and result in a very low efficiency of conversion into protein (Coulson and Hernandez 1983).

A diet with a very high phosphorus to calcium ratio can result in calcium deficiency and bone deformity (in order to excrete the excess phosphorus, calcium must also be excreted). Such cases have been encountered in reptiles fed a diet of fish meat or red meat alone (without the bones or skin) in which the calcium to phosphorus ratio is 1:25 and 1:44 respectively (Cowan 1968; Wallach 1969). If reproducing females were stressed in this way, radical disturbances in calcium metabolism would obviously interfere with normal eggshell formation. This problem does not occur if a calcium supplement is supplied or, if whole carcasses are used to feed the animals.

Stress in domestic animals has long been known to affect reproduction (Stephens 1980), but it is only within the past few years that non-mammalian vertebrates have been shown to be equally as sensitive to it. Acute stress (such as restraint) will cause an immediate rise in plasma corticosterone and an equally rapid decline in plasma testosterone in male alligators (Lance et al., unpublished data). Although the data are sparse, it appears that chronic stress, such as overcrowding, can cause significant elevations in plasma corticosterone and can reduce egg production in alligators fed both fish and red meat (Joanen et al., unpublished data).

How chronic stress and elevated corticosterone secretion affects female reproduction is still not understood. It is possible that high levels of corticosterone inhibit oviposition, such that eggs are retained in the oviducts until embryonic development advances past the stage where the embryos attach to the shell membrane. If so, high embryo mortality would result, as many would be positioned below the yolk (see Webb et al. Chapter 43). Stress caused by environmental extremes in the wild can

also result in increased embryonic mortality. Reese (1907) noted that in an exceptionally dry year in Florida, alligator nesting was delayed well beyond the normal period, and that the eggs that were laid, contained embryos in an advanced state of development.

A large percentage of wild adult female alligators and crocodiles do not breed in any given year. Even in southern Louisiana, where conditions are considered optimal, only about 60% of adult female alligators nest annually (Joanen and McNease 1975; Lance, unpublished data). In South Carolina only 27.5% of adult females nest annually (Wilkinson 1984). Under farming conditions, where excess food is supplied, the percentage of females which nest annually increases to about 90%, suggesting that nutrition may be involved.

The production of a clutch of 40 eggs, each weighing about 60 g, causes a severe nutritional drain on a female alligator. Not only are protein and lipid stores depleted, but bone calcium stores are also severely taxed. In captivity most females are apparently able to replenish these stores and as a consequence can breed every year. However, we need data on individual animals to see how many consecutive years they are able to produce eggs.

A question repeatedly asked by crocodile and alligator farmers is: "how can we get our animals to produce more than one clutch per year?" *Crocodylus palustris*, the Indian mugger, do produce two clutches naturally (Whitaker and Whitaker 1984), but no other species are known definitely to do so, and whether or not they could be induced to nest more than once in a season is unknown.

If crocodilians are similar to birds and other reptiles they go through a refractory period after ovulation. During this period, which may last for weeks or months depending on the species, the animal is totally unresponsive to hormonal stimulation. A period of reduced temperature and/or reduced photoperiod is required before a second cycle can be initiated (Licht 1972). Crocodilians probably have a similar refractory period because all attempts to induce ovulation with either gonadotropins, gonadotropins plus steroids or gonadotropin releasing hormone have so far proved unsuccessful (P. Cardeilhac, pers. comm.). If this is the case then an artifical "winter" shortly after oviposition would have to be created in order to bring the animals into breeding condition again. The problems of controlling conditions of photoperiod and temperature for a large group of adult crocodilians are obvious.

A second problem likely to be encountered if multiple clutching could be attained is premature senescence. Very large, and presumably old, alligators and crocodiles (Cott 1961) stop producing

and laying eggs. This is not a consequence of age alone, but is probably the result of depletion of all of the ovarian oocytes. It was once believed that non-mammalian vertebrates were capable of producing an infinite number of eggs, since the germinal stroma continued to exhibit cell division throughout the life of a female (ovarian germinal cell division in mammals ceases during embryogenesis or shortly after birth so that the lifetime complement of potential ova are present in the ovary before sexual maturity is attained). However, recent studies have shown that despite the ability of the germ cells of non-mammalian vertebrates to continue to divide, the number of possible oocytes is not infinite. Each animal is capable of producing only a finite number of oocytes in its lifetime (Tokartz 1978).

By attempting to increase the number of clutches in a year, the increased stress on the female would be likely to result in reduced clutch size, inferior quality eggs and ultimately, premature senescence. It would probably be more economical for farmers to strive for healthy females, producing large clutches of eggs, with increased fertility and increased hatchability, than to invest the time and effort to inducing multiple clutches.

REFERENCES

CHABRECK, R. H., 1965. The movement of alligators in Louisiana. *Proc. Ann. Conf. Southeastern Assoc. Game Fish. Comm.* 17: 47-50.

CHABRECK, R. H., 1975. Moisture variation in the nests of the American alligator (*Alligator mississippiensis*). *Herpetologica* 31: 385-9.

COTT, H. B., 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodilus niloticus*) in Uganda and Northern Rhodesia. *Trans. Zool. Soc. Lond.* 29: 211-356.

COULSON, R. A. AND HERNANDEZ, T., 1983. Alligator metabolism: studies on chemical reactions *in vivo*. *Comp. Biochem. Physiol.* 74: 1-182.

COWAN, D. F., 1968. Diseases of captive reptiles. *J. Am. Vet. Med. Assoc.* 153: 848-59.

DEITZ, D. C. AND HINES, T. C., 1980. Alligator nesting in north-central Florida. *Copeia* 1980: 249-58.

ELSEY, R. M. AND WINK, C. S., 1985. Femoral bone as a possible source of calcium for eggshell deposition in *Alligator mississippiensis*. Abstract from the American Anatomical Assoc. Meeting, Toronto, May, 1985.

FRY, F. L. AND SCHELLING, S. H., 1973. Steatitis in a caiman. *Vet. Med. Small Anim. Clin.* 68: 143-6.

GOODWIN, T. M. AND MARION, W. R., 1978. Aspects of the nesting ecology of American alligators (*Alligator mississippiensis*) in north-central Florida. *Herpetologica* 34: 43-7.

GRAHAM, A., 1968. The Lake Rudolf crocodile (*Crocodylus niloticus* Laurenti) population. Unpublished M.Sc. Thesis, University College, Nairobi, Kenya.

HERZOG, H. A., 1975. An observation of nest opening by an American alligator, *Alligator mississippiensis. Herpetologica* 31: 446-7.

HO, S. M., KLEIS, S., McPHERSON, R., HEISERMANN, G. J. AND CALLARD, I. P., 1982. Regulation of vitellogenesis in reptiles. *Herpetologica* 38: 40-50.

JOANEN, T., 1969. Nesting ecology of alligators in Louisiana. *Proc. Ann. Conf. Southeastern Assoc. Game Fish. Comm.* 23: 141-51.

JOANEN, T. AND McNEASE, L., 1970. A telemetric study of nesting female alligators on Rockefeller Refuge, Louisiana. *Proc. Ann. Conf. Southeastern Assoc. Game Fish. Comm.* 24: 175-93.

JOANEN, T. AND McNEASE, L., 1971. Propagation of the American alligator in captivity. *Proc. Ann. Conf. Southeastern Assoc. Game Fish. Comm.* 25: 106-16.

JOANEN, T. AND McNEASE, L., 1972. A telemetric study of adult male alligators on Rockefeller Refuge, Louisiana. *Proc. Ann. Conf. Southeastern Assoc. Game Fish. Comm.* 26: 252-75.

JOANEN, T. AND McNEASE, L., 1975. Notes on the reproductive biology and captive propagation of the American alligator. *Proc. Ann. Conf. Southeastern Assoc. Game Fish. Comm.* 29: 407-15.

JOANEN, T. AND McNEASE, L., 1979. Time of egg deposition for the American alligator. *Proc. Ann. Conf. Southeastern Assoc. Fish Wildl. Agencies* 33: 15-9.

JOANEN, T. AND McNEASE, L., 1980. Reproductive biology of the American alligator in Southwest Louisiana. Pp. 153-9 *in* "Reproductive Biology and Disease of Captive Reptiles" ed by J. B. Murphy and J. T. Collins. Society for the Study of Amphibians and Reptiles: Lawrence, Kansas.

KUSHLAN, J. A., 1973. Observations on maternal behaviour in the American alligator, *Alligator mississippiensis. Herpetologica* 29: 256-7.

KUSHLAN, J. A. AND KUSHLAN, M. S., 1980. Function of nest attendance in the American alligator. *Herpetologica* 36: 27-32.

LANCE, V., 1984. Endocrinology of reproduction in male reptiles. *Symp. zool. Soc. Lond.* 52: 357-83.

LANCE, V. AND CALLARD, I. P., 1980. Hormonal control of ovarian steroidogenesis in nonmammalian vertebrates. Pp. 361-407 *in* "The Vertebrate Ovary" ed by R. E. Jones. Plenum Publishing Co.: New York.

LANCE, V., JOANEN, T. AND McNEASE, L., 1983. Selenium, vitamin E, and trace elements in the plasma of wild and farm-reared alligators during the reproductive cycle. *Can. J. Zool.* 61: 1744-51.

LARSON, R. E., BUERGELT, C., CARDEILHAC, P. T. AND JACOBSON, E. R., 1983. Steatitis and fat necrosis in captive alligators. *J. Am. Vet. Med. Assoc.* 183: 1202-4.

LICHT, P., 1972. Environmental physiology of reptilian breeding cycles: role of temperature. *Gen. Comp. Endocrinol. Suppl.* 3: 477-88.

McNEASE, L. AND JOANEN, T., 1974. A study of immature alligators on Rockefeller Refuge, Louisiana. *Proc. Ann. Conf. Southeastern Assoc. Game Fish. Comm.* 28: 482-500.

METZEN, W. D., 1977. Nesting ecology of alligators on the Okefenokee National Wildlife Refuge. *Proc. Ann. Conf. Southeastern Assoc. Fish and Wildl. Agencies.* 31: 29-32.

MODHA, M. L., 1967. The ecology of the Nile Crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. *East Afr. Wildl. J.* 5: 74-95.

MURPHY, T. M., 1980. The population status of the American alligator at the Savannah River National Environment Research Park. Unpublished manuscript from the Savannah River Ecology Lab., South Carolina.

REESE, A. M., 1907. The breeding habits of the Florida alligator. *Smithsonian Misc. Coll. Quart. Issue* 3: 381-7.

Scott, M. L., 1978. Vitamin E. Pp. 133-210 *in* "The Fat Soluble Vitamins" ed by H. F. DeLuca. Plenum Publishing Co.: New York.

Stephens, D. B., 1980. Stress and its measurement in domestic animals: a review of behavioural and physiological studies under field and laboratory conditions. *Adv. Vet. Sci. Comp. Med.* 24: 179-210.

Taylor, D., 1984. Management implications of an adult female alligator telemetry study. *Proc. Ann. Conf. Southeastern Assoc. Fish Wildl. Agencies* 38: 221-7.

Tokartz, R. R., 1978. Oogonial proliferation, oogenesis and folliculogenesis in nonmammalian vertebrates. Pp. 145-79 *in* "The Vertebrate Ovary" ed by R. E. Jones. Plenum Publishing Co.: New York.

Van Vleet, J. F., 1980. Current knowledge of selenium-vitamin E deficiency in domestic animals. *J. Am. Vet. Med. Assoc.* 176: 321-5.

Wallach, J. D., 1969. Medical care of reptiles. *J. Am. Vet. Med. Assoc.* 155: 1017-34.

Wallach, J. D. and Hoessle, A. A., 1968. Steatitis in captive crocodilians. *J. Am. Vet. Med. Assoc.* 153: 845-7.

Webb, G. J. W., Messel, H. and Magnusson, W., 1977. The nesting ecology of *Crocodylus porosus* in Arnhem Land, northern Australia. *Copeia* 1977: 238-49.

Webb, G. J. W., Sack, G. C., Buckworth, R. and Manolis, S. C., 1983. An examination of *Crocodylus porosus* nests in two northern Australian freshwater swamps, with an analysis of embryo mortality. *Aust. Wildl. Res.* 10: 571-605.

Whitaker, R. and Whitaker, Z., 1984. Reproductive biology of the mugger *(Crocodylus palustris)*. *J. Bombay Nat. Hist. Soc.* 81: 297-316.

Wilkinson, P. M., 1984. Nesting ecology of the American alligator in coastal South Carolina. Report to the South Carolina Wildlife and Marine Resources Department, Charleston, South Carolina. 113pp.