# CAPTIVE BREEDING OF ALLIGATORS AND OTHER CROCODILIANS

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ABSTRACT. Although "ranching" of crocodilians has become the preferred method of sustained utilization, in some cases there is a role for closed system farming programs. Some 25,000 crocodilian skins were produced in 1990 by captive breeding; however, many attempts at captive breeding meet with limited success. This paper examines the history of early crocodilian farm programs and outlines the present status of crocodilian breeding programs. Current areas of active research and problems requiring further study to improve and better understand the complex physiological science of captive crocodilian breeding are also discussed.

## Introduction

Although the first alligator farm in the United States was established in 1891 in Jacksonville, Florida (Joanen and McNease 1982), it was not until 1964 that extensive research was initiated in Louisiana by the Department of Wildlife and Fisheries on the ecology, reproductive biology, and captive propagation of *Alligator mississippiensis*. This program included the design of an experimental alligator farm at Rockefeller Wildlife Refuge that led to the development of methods for artificial incubation of alligator eggs, heated controlled chambers for the culture of juvenile alligators, and breeding pens for adult alligators (Joanen and McNease 1971, 1974, 1975, 1976, 1979, 1987).

A wealth of data was obtained over the next thirty years at Rockefeller, supporting the concept of alligator culture as a viable conservation strategy and a sound economic venture. Today there are over 100 established alligator farms/ranches in Louisiana housing well over 250,000 alligators, and the feasibility of raising crocodilians in captivity for commercial and conservation purposes is well documented (Joanen and McNease 1990, 1991, Webb et al. 1987, Hutton and Webb 1992).

Similar early work by researchers examined captive breeding in other crocodilians (Blake 1970, Blake and Loveridge 1975, Downes 1973, Pooley 1971, 1973, Yangprapakorn et al. 1971), and with the data accrued at Rockefeller launched crocodilian farming, ranching, conservation, and management programs worldwide [Webb et al. (eds.) 1987]. There are presently at least 597 commercial farms and another 75 experimental or non-commercial crocodilian facilities in some 47 countries worldwide (Luxmoore 1992). These farms/ranches maintain an average of 1,700 crocodilians each, for a total stock of over 1.1 million.

The purpose of this paper is to examine the captive breeding aspect of crocodilian farming. The early developmental history will be reviewed, followed by current status of captive breeding of the most important commercial species. Lastly, areas of active research and problems requiring further detailed study will be examined.

## Farming, Ranching, and Conservation

Recent studies have demonstrated that crocodilian ranching (rather than closed system farming) is the preferred form of sustained utilization (Hutton and Webb 1992). Ranching is generally more economically advantageous than closed breeding systems, which can be costly and labor-intensive to initiate, and frequently meet with limited success for the first several years. Ranching also wisely uses crocodilian eggs/hatchlings which otherwise would be lost to a very high natural mortality. Ranching programs often require release of some percentage of larger juvenile "head-start" crocodilians back to the habitat from which the eggs/hatchlings were obtained, usually at a size large enough to limit natural mortality. Closed system farming has adult breeders and obtain all stock in hatchlings from captive laid eggs. Many of the Louisiana "farms" combine ranching with closed system farming, though the majority rely strictly on ranching. However, not all crocodilian species exist in large enough numbers to support as extensive a ranching program as is present in Louisiana.

Captive breeding is useful; however, in several situations. In some species, wild populations may not be large enough to support a ranching program, and wild egg collection may be prohibited or severely limited. In some instances, where wild populations are very low, captive breeding might be considered as a method to obtain juveniles for restocking to replenish the wild population. In some locations, habitat for crocodilians has been depleted by human factors and captive breeding may again provide juveniles for reintroduction in similar suitable habitats. Caution must be taken; however, not to regard captive breeding as a panacea for the conservation of wild crocodilian species and their habitat (Hutton and Webb 1992).

In 1990, about 15% of skins produced worldwide were from captive breeding, however approximately 25% of animals currently maintained on farms are derived from captive breeding, and should contribute more to the skin industry over the next few years (Luxmoore 1992). Although most classic skins (_Alligator_, _C. niloticus_, _C. novaeguineae_) are produced by ranching rather than captive breeding, a significant portion of the _Crocodylus porosus_ skins are produced through captive breeding; and some rare species (_C. rhombifer_ and _C. siamensis_) are almost exclusively produced through captive breeding (Luxmoore 1992).

Rockefeller Refuge's first experimental alligator farm

A thorough review of some fifteen years of research on captive propagation of the American alligator done at the Rockefeller Refuge was recently published (Joanen and McNease 1987). It should be stressed that a strong interest in the breeding physiology of wild alligators led to the study of alligators in captivity in order to closely observe alligator courtship, breeding, nesting, life history, etc. which would be more difficult to document in the field. The discovery that alligators would breed in captivity later led to research as to the economic feasibility of commercial raising of alligators. In the early years of our program, stringent legislation and concern over the "threatened" classification of alligators prohibited the collection of wild eggs/hatchlings for ranching except for very limited experimental collections on state-owned lands on which no wild harvest occurred. Thus captive breeding (rather than ranching) was the only source of stock for alligator farming trials initially available. A brief summary of the captive breeding aspect of this research is presented below.

The first studies (1964-1971) involved the housing requirements of wild adult alligators brought into captivity for breeding purposes. However, excessive fighting and territoriality in communal pens was detrimental and led to deaths of several alligators (Joanen and McNease 1971). Data from these studies indicated that wild caught animals maintained in single pairs had less territoriality and nested with some degree of success. The clutch size and hatch rates from 5 pairs of alligators in 1/4 acre pens were comparable to the wild, but 2 females nested only once in the five year study and one did not nest until the third year.

It was felt that a higher level of productivity would be needed for a commercial farm operation, as separate pens for each pair of wild caught alligators was cost-prohibitive. This led to the raising of alligators entirely in captivity to be used as breeders. Alligators were reared from hatching until 4'-5' long (approximately 3 years), then were stocked into breeder pens. These animals were more docile and had less social competition between dominant animals.

The results of telemetry studies with wild adults (Joanen and McNease 1970, 1972) were used to identify basic habitat needs when constructing pens to house adult alligators. These studies indicated that deep open water areas (such as bayous, canals, large lakes) were needed for courtship and copulation; and small potholes and ponds in heavily vegetated areas were needed for use as nesting sites. These habitat types were later incorporated into pen designs (Joanen and McNease 1987). Reproduction of a large group of alligators cultured since 1972 has now been achieved, and their reproductive histories have been carefully documented.

Important aims of the early studies were to investigate the maximum stocking densities which pen-reared alligators could tolerate in captivity, given the provision of suitable habitat requirements for each sex. Various stocking densities, male:female ratios, and land:water ratio/pen design, and diets were studied.

Pen design refinements developed over the years were incorporated into the construction of four breeding pens in 1975; all were about 0.8 ha (2 acres). The pen design, dimensions, fencing, vegetation, maintenance and husbandry have been described in detail (Joanen and McNease 1987).

The method of feeding has been described previously (Joanen and McNease 1971, McNease and Joanen 1987). Several feeding sites were established in each pen to help disperse the alligators, usually situated near a basking area or a path adjacent to the water's edge. Feeding began in March or April of each year and terminated in September or October; alligators are not fed during late fall and winter, when ambient temperatures are too low. A feeding rate of 6% body weight per week was adhered to during the spring and summer, when most food was consumed.

Two diets were initially tested on the penned breeders; whole fish (Micropogon undulatus) and nutria (Myocastor coypus) carcasses. Also, two pens were heavily stocked, and two pens were stocked at a low density. One high and one low density pen were fed fish, and the other two pens nutria. A vitamin premix was added to the diet of all alligators at a maximum rate of 1% by weight. The specifications of the premix (manufactured by Dawe Laboratories Ltd., Chicago Heights, Illinois 60411, USA) have been published previously (Joanen and McNease 1987).

Early results - captive breeding on Rockefeller Refuge's experimental alligator farm program (1972-1984).

Age at first nesting for captive alligators, housed and reared in controlled environmental chambers for the first three years of life, then placed in outside pens, was five years 10 months. Age of sexual maturity reported for Louisiana alligators held in semi-natural outside pens was nine years and 10 months (McIlhenny 1935, Joanen and McNease 1975).

Nesting rates for captive alligators fed nutria (Pen 6; low density) were consistently higher than for those fed fish (Pen 5; low density). During a four year period, when the alligators were seven to 10 years of age, an average of 62.8% of nutria fed animals nested annually, whereas the equivalent rate for those fed fish was 26.8%. The low nesting rate in Pen 5 (fish) increased abruptly to 56% when the diet was switched to nutria in the spring of 1982 and this change was maintained the following year (57%)(Joanen and McNease 1987).

Independent of diet, nests from first time nesters had an average clutch size of 25 eggs. Joanen (1969) reported an average clutch size of 38.8 eggs for wild nests in southwestern Louisiana, and penned alligators approached this level in their third or fourth year of reproduction (Figure 1).

Alligators fed a nutria diet consistently had higher fertility rates than those fed fish but both groups had lower fertility and hatch rates than recorded for the wild populations. Initially the hatching rate of eggs from captive alligators fed nutria remained slightly above the value determined for wild eggs left in the field to incubate, but was well below the 91% achieved with eggs collected from the wild and incubated in controlled incubator chambers. Eggs from captive alligators fed fish demonstrated very low hatching rates, averaging 27.4% over five years. This problem will be discussed in detail later in this paper in the diet/nutrition section. When the captive breeders were about 10 years of age (1983) reproductive success was quite good, with some pens having some 80-85% nesting rates (Figure 2), 85% fertility (Figure 3), and 60-65% hatch rates (Figure 4).

Higher stocking densities on both diets led to higher plasma corticosterone (stress hormone) levels in captive adult alligators; and correlated with lower nesting success than in alligators maintained at low stocking densities (Elsey, et al. 1990)

<u>Recent results - captive breeding on Rockefeller Refuge's experimental alligator farming pens (1985-1992)</u>

More recently, as the alligators in our captive breeding stock have aged, reproductive success has declined dramatically. Although clutch sizes in captive animals have remained fairly high (30-45) (Figure 1), the nesting rates (Figure 2), egg fertility (Figure 3) and hatch rates (Figure 4) have all dropped dramatically. From 1987 to 1988, hatch rates dropped from 34.3% to 6.8% in Pen 5, from 32.6 to 25.8% in Pen 6, and from 25.8% to 9.8% in Pen 8. Hatch rates ranged from 45.3-48.9% for these pens in 1986 and from 38.3%-65.3% in 1985. In 1989, no eggs hatched from those nests produced in Pens 5 and 7, and only 13.5% hatched in Pen 6. The great majority of eggs incubated that appeared fertile died in weeks 1-3 of incubation. Numerous eggs were also misshapen, poorly calcified/soft-shelled, crushed, or infertile. Since 1983, all pen alligators were fed a nutria diet with supplement vitamins and since 1990, a mixture of half nutria and half commercial dry pelletized rations was fed to breeder alligators.

An extensive set of research projects was then initiated to attempt to solve the problem of poor egg hatchability; as we are encouraged by the fact that good nesting attempts are made in all pens and clutch sizes remain normal. Also, the nesting rates (percent females in a pen that construct a nest) may be skewed to the low side in recent years in pens 5-7, as the "proven nesters" have frequently been caught and relocated to new pens to evaluate different stocking densities, male:female ratios, and pen designs.

Louisiana' statewide farm breeding results, 1992

There are currently 122 licensed farms/ranches in Louisiana with a total inventory of approximately 288,000 alligators. Thirty-three farms have captive breeding stock; although only 19 farms have alligators old/large enough to be considered capable of breeding (Table 1).

In 1992, some 418 nests were constructed, and 4,389 hatchlings were produced (10.5 per nest). This is a downward trend from 1990, wherein 7,607 hatchlings were derived from 482 nests (15.8 per nest). The average nesting rate was 30.9%, with a 42.4% hatch rate. Only 3.2 hatchlings were produced per adult female alligator maintained (breeders plus non-breeders).

It remains unclear if breeding results on Louisiana farms will improve over the next few years. Certainly more hatchlings will be produced as the immature brood stock becomes sexually mature; however, there appears to be a decline in reproductive effort over time as mature breeders age.

Captive breeding in other southeastern states.

Florida. In 1991, some 58 licensed alligator farms in Florida produced 21,645 hatchlings (4.29 per adult female), slightly increased from 4.15 hatchlings per adult female in 1990 (D. David, pers. comm.). From 1984-1990, the average hatch rate on all Florida farm eggs was 35% (Cardeilhac 1990). Cardeilhac (1988) suggested that farmers must maintain an annual hatch rate of 7 hatchlings/female to be successful.

Georgia. Although only a few alligator farms exist in Georgia, captive breeding has been undertaken on the majority of these farms. Four operations produced 341 hatchlings in 1989, and 661 hatchlings were produced from 5 of the 6 licensed farms in 1990 (Luxmoore 1992).

Texas. Some 42 alligator farms are operating in Texas, but most are new and have very limited stock/commercial activities at present (Luxmoore 1992, B. Brownlee, pers. comm.). The majority are obtaining stock by ranching; but four farms had captive in 1992; 992 eggs were collected from 28 nests, and 452 hatchlings produced (B. Brownlee, pers. comm.).

Mississippi. Five alligator farms are presently licensed in Mississippi, of which two have recently constructed breeder pens. At this time the brood stock are all immature (J. Lipe, pers. comm.).

Captive Breeding - other crocodilians worldwide

Despite extensive research, captive breeding of crocodilians still is poorly understood; and most importantly significant differences between species can make comparisons of breeding/culture regimes difficult (Hutton and Webb 1992). These species-specific traits have been discussed previously (Webb 1990, Hutton and Webb 1992) and will be briefly reviewed below.

The social behavior of crocodilian species varies greatly, and has important implications for management of breeding herds (Lang 1987, Hutton and Webb 1992). It is paramount to realize that solitary nesters (*A. mississippiensis*, *C. porosus*) frequently breed poorly in captivity; whereas communal cavity/hole nesters (*C. niloticus*) in general are more successful with captive reproduction.

Most crocodilian brood stock perform better if raised entirely in captivity rather than being captured from the wild as adults for brood stock (Joanen and McNease 1971, 1987, Hutton and Webb 1992). In the Nile crocodile; however, this is less of a problem (Hutton and Webb 1992). Captive reared stock have been found to better tolerate variable pen designs/housing conditions than their wild counterparts brought into captivity for breeding purposes, and will breed at an earlier age than wild crocodilians of the same species (Joanen and McNease 1987, Hutton and Webb 1992) brought into captivity. It would be of interest to document the reproductive success and age of first nesting of sub-adults (4'-5') caught from the wild, then maintained in captivity.

Some of the many variables that make comparisons between brood stock productivity difficult are: species differences, age, early history, housing conditions, land/water ratios, diet, sex ratios, husbandry practices, stocking rates/density (Joanen and McNease 1987, Hutton and Webb 1992). All these compounding variables can make comparisons relating to one factor unclear. An excellent review of the husbandry and management of captive breeding herds of some of the most commercially important species was recently published (Hutton and Webb 1992) and is highlighted below.

Nile Crocodile (*Crocodylus nilotus*). Nile crocodiles are communal nesters which can nest as early as 6 years if entirely captive raised. Generally females should be housed with larger, older males. Suitable raised banks should be available for these hole nesters. Most farms employ one of two breeding systems, either a few females in a small enclosure with one male, or up to 300 females with as many as 60 males in a large (several hectare) pen. Nile crocodiles breed very well in captivity, with a high percentage of females producing eggs for as long as 20 years

(Hutton and Webb 1992). Marias and Smith (1992) report 42% and 77% nesting rates on two large breeding units in 1989-90; with clutch sizes of 43 and 52 with 70-85% hatchability. These were large breeding pools containing 130 and 132 females, again a situation that is possible due to the communal nesting habits of Nile crocodiles. However, not all communal nesters breed this well in captivity; a recent study found 35% infertile eggs laid by captive C. johnstoni as compared to a 3-6% infertile rate for wild eggs collected the same year (Webb 1990).

Estuarine Crocodile (Crocodylus porosus). These solitary mound nesters may reach sexual maturity in 8 years. Crocodile farms have maintained C. porosus in large communal pens (multiple males and females); or in small enclosures of 1-5 females with 1 male. As has been seen in alligators, with time and increasing age of adults, nesting rates in communal pens generally decreases to 20-30%, with poor egg quality (some 30% viable, Webb 1990, Hutton and Webb 1992). Even more so than in alligators, females and males both fight amongst themselves, leading to adult mortality (Webb 1990). Variable results are obtained with small breeding groups (1 male:2 females, 1 male:3 females, etc.); and single pairs of 1 male and 1 female apparently nest more successfully (Webb 1990).

Common caiman (Caiman crocodilus). Captive raised female caiman can become sexually mature at age 2.8 years, and are less territorial than alligators and saltwater crocodiles, and therefore can breed well in captivity (Hutton and Webb 1992). A sex ratio of 2 females:1 male has been recommended, and suggested enclosure designs previously described (Hutton and Webb 1992).

New Guinea Crocodile (Crocoylus novaeguineae). The majority of the C. novaeguineae skins produced are obtained from ranching and wild harvest; although limited captive breeding is underway in Singapore and other areas (Hollands 1987, Luxmoore 1992).

With this background on captive breeding of crocodiles, we now will address some new areas of current research presently underway at Rockefeller Refuge. The areas we are attempting to address are how to improve the nesting/reproductive success of captive crocodilians, increase hatchability of crocodilian eggs, and minimize the high rates of early embryonic death we frequently incur.

Social interactions/"stress".

As mentioned, agonistic/aggressive behavior and disputes over territory, nesting space, and dominance hierarchies can hinder successful reproduction, especially in alligators and C. porosus. We have seen that acute restraint stress will raise plasma stress hormone (corticosterone) levels in adult alligators, and concomitantly depress the plasma sex steroids, estradiol and testosterone (Lance and Elsey 1986, Elsey et al. 1991). Other stressors that have been shown to adversely affect the normal physiology of juvenile alligators are crowding (Elsey et al. 1990) and exposure to salt water (Lauren 1985). Overcrowding could lead to stress-related disease, and heavy leech infection was shown to be correlated with a sixfold increase in eosinophilia in wild alligators (Glassman et al. 1979). Crowding stress also may affect the immune system of the alligator. Juvenile alligators acutely stressed (restraint) had significant increases in leukocyte counts, with an increase in the percent heterophils and a decrease in the percent lymphocytes by 24 hours (Elsey unpublished). Similarly, stressors could adversely affect the immune system functioning and lead to disease and reproductive failure in captive adult crocodilians.

Overcrowding/stress.

Early research conducted at Rockefeller showed that alligators maintained at high stocking density had elevated plasma corticosterone levels, and those with lower stocking density had lower stress hormone levels, and correlated with better reproductive rates (Elsey et al. 1990). This may have been due to a stress induced suppression of sex steroids by the elevated plasma corticosterone levels, as our acute stress experiments suggested.

Thus, we constructed a large breeding pen in 1989, 16-acre in size, stocked with 16 females and 5 males. This pen was much larger than our other pens of 2 acre size, and was an attempt to minimize any territorial disputes/fighting over nesting space or "crowding stress". Unfortunately, an unusually hard winter freeze in December 1989 killed 1 male and 6 females in this pen. Four females nested in 1990, 6 in 1991, and 5 in 1992. Fertility was 60.8% in 1991 and 42.1% hatched that year. Data are not available for the fate of eggs produced in 1990 and 1992 as they were shipped elsewhere for laboratory evaluation. The nesting rates are not dramatically improved from our other pens, despite the extra space provided per female.

Recently, in C. porosus, Webb (1990, Hutton and Webb 1992) has noted larger clutch sizes and higher egg viability in "unitized" pens. These consist of a small pen with 20-30 $m^2$ water and housing a single pair of crocodiles (1 male, 1 female). Encouraged by the work done on C. porosus, we constructed six "single pair" pens in June/July 1990 and stocked these with alligators transferred from our other breeding pens. Nesting rates have improved in that four of the six females nested in 1991 however, fertility was only 35.1% and hatchability 8.7% in 1991. All six nested in 1992; but eggs in 1992 were sacrificed for biochemical analysis (lipids, fatty acids) thus were not incubated. Three nests in 1992 had normal appearing eggs, 2 had 16-21 soft-shelled, non calcified /oviductal material type eggs, and one nest contained only scanty oviductal material. Research is currently underway to try to understand why the fertility of our captive breeder's eggs has declined recently, and why the hatchability of these eggs once produced, is so low.

Age

Advancing age could explain some of the reproductive failure seen in our breeder herds. Similarly, Cardeilhac (1990) reported that 50% of 18 breeders necropsied at 26 years of age had oviducts blocked by egg or follicle retention from not being reabsorbed in prior years. It is unknown how long crocodilians continue to nest in wild populations.

Hormonal Therapy

A study done in 1970 at Rockefeller Refuge on the effectiveness of injecting human chorionic gonadotrophin (HCG) on female alligators met with limited success. Six adult female alligators were caught from the wild, 3 were given 800 IU/lb. of HCG and 3 were give 50 IU/lb., and they were then placed in captivity. Only one female given the higher dose nested (Joanen and McNease, unpublished progress report). Attempts at artificial insemination were unsuccessful in 1970 and 1971 (Joanen and McNease unpublished repts, 1971 and 1972). Likewise, Cardeilhac et al. (1981, 1982) demonstrated that female alligators are unusually resistant to attempts to induce ovulation by hormone injections (HCG, progesterone, luteinizing hormone releasing hormone) and insemination.

Oxytocin was used to induce oviposition in captive Caiman crocodilus yacare at the New York Zoological Park (Brazaitis 1984). Several doses of one IU/100 g body weight was administered intramuscularly, and over several days 20 eggs were expelled. Three eggs were crushed/damaged and thus not incubated, and 7 were infertile. Three embryos died before 30 days of incubation, 5 died late in incubation, and 2 viable male hatchlings were obtained (Brazaitis 1984). Oxytocin has also been shown to induce oviposition in a dystocic saltwater crocodile at a single lower dose of approximately 1 IU/kg IM. (Carmel 1991). Twelve of 27 eggs obtained hatched successfully.

Male alligators have been shown to respond to mammalian FSH and GnRH with increased testosterone secretion (Lance and Vliet 1987, Lance et al. 1985). Also yohimbine, an alpha-2-adrenergic blocker given to captive male Nile crocodiles increased the frequency of the headslap display (a behavior seen in reproductive activity) but did not increase copulation frequency. However, the females in the male treated groups had higher egg fertility (34.1 and 39.0% treated as compared to 30.5% in the control group), thus there may have been more successful (though no increase in frequency) copulations (Morpurgo et al. 1992). However, in general most researchers feel crocodilian reproductive failure is due to a female physiology problem rather than male sterility/abnormality, although little is known about the quality of semen or spermatozoa viability in crocodilians (Lance 1987). The reproductive endocrinology of crocodilians has been reviewed in detail (Lance 1987, 1989), and extensive blood serology work has delineated the normal annual reproductive hormone cycles in alligators (Lance 1987, 1989). Some data is also available on the reproductive hormones of wild *C. niloticus* (Kofron 1990).

Diet/Nutrition/Supplements.

Diet plays an important role in the general health, and therefore contributes to the reproductive capability of crocodilians. Our early results in captive breeding groups clearly showed alligators fed a red meat (nutria) diet had higher nesting, fertility, and hatch rates than those fed fish (Joanen and McNease 1987). Some researchers have advocated a varied diet rather than a mono-diet consisting of a single food source. However, in *C.*

porosus, single pairs fed only chicken produced very well, whereas multiple groups on a mono-diet of chicken did poorly; and single pairs fed fish did well (Webb 1990). In those cases, the pen design effect appears to override the dietary influence on reproductive performance.

We have also been concerned that our breeding herd, and other crocodilians maintained in captivity may not be breeding well due to overfeeding, lack of exercise, and resultant obesity. This could lead to poor muscular condition and contribute to reptilian dystocias (Grain and Evans 1984).

Previously, we fed our captive breeders 6% body weight per week during the feeding season of spring/summer (Joanen and McNease 1987) and have decreased this in recent years. Any benefits from this may be offset by the advancing age of our breeders.

Formulated crocodilian feeds have recently been reviewed; (Staton and Vernon 1991) this paper again emphasized the need for further study of the nutritional/feeding requirements of breeding crocodilians, although a wealth of data has been published on feeding regimes for juvenile crocodilians.

We have advocated adding a vitamin premix at a rate of 1% by weight to the diet of all alligators (Joanen and McNease 1987). To determine if deficiencies of vitamins/trace elements essential for reproduction were present in the captive alligators fed fish or nutria, an extensive blood chemistry analysis was done at Rockefeller in 1980-1982 (Lance et al. 1983). Fish fed alligators had higher plasma selenium and lower vitamin E levels than the nutria fed or wild females; (despite the addition of a vitamin E containing premix to each type diet) which could have caused the reproductive failure. As mentioned, when the fish fed alligators were changed to a nutria diet in 1983, their nesting success increased (Joanen and McNease 1987). However, the fish itself may not necessarily have been the problem, as fresh fish has been shown to be a good source of long chain (C20 and C22) fatty acids needed for embryo survival. However, frozen fish may not have been protected against oxidation of the long chain PUFAs, as described further below. Thiaminase activity has been measured in many species of common food fish (Cooper and Jackson 1981), and thiamin is a necessary part of our vitamin premix.

Hunt (1980) reported that two pairs of C. moreleti at the Atlanta Zoo failed to produce viable eggs until a diet of marine fish was stopped; also crocodilians at the St. Louis Zoo fed mackerel developed severe vitamin E deficiency, with six dying from steatitis (Wallach and Hessle 1968). Some of these conditions may be lessened by feeding fresh fish, rather than frozen, and definitely not rancid fish which may have undergone oxidation (Noble et al 1993, M. Staton pers. comm).

Singh and Sagar (1991) showed an improvement in clutch size (from 26-27 to 31.7) and hatchability (from 44-49% to 62.9%) in captive C. palustris given supplemental vitamin E orally, 400 mg daily for 10 consecutive days 3 months prior to nesting. Their study involved 2 males maintained with 4 females.

Due to the very poor hatchability of the eggs produced by our captive alligator breeders in recent years, we have sent most eggs available to laboratories for biochemical analysis to test for deficiencies/abnormalities that may be present in the yolk/developing embryo. Noble et al (1993, in press) found extensive differences in the lipid and fatty acid composition of the yolks from eggs of captive vs. wild alligators. The yolks for the captive eggs contained considerably lower levels of C20 and C22 polyunsaturated fatty acids (PUFA) and higher levels of C18 PUFAs than the wild. The C20 and C22 PUFAs play an important role in the embryonic development, particularly of the nervous system (Noble et al 1993, Neuringer et al. 1988). These yolk fatty acid compositional differences may be associated with the low hatchability and increased early embryonic deaths we have seen in the eggs produced by our captive breeders (Noble et al. 1993). Similarly, Staton (unpubl. data) found significant differences in the fatty acid composition of eggs and hatchlings from wild vs. captive alligator breeding populations. The essential fatty acid monitoring in juvenile alligators was recently evaluated in detail (Staton et al. 1990).

Preliminary results from Noble's study also indicate captive bred alligators may have a marked reduction in selenium levels compared to the wild alligator eggs; and emphasize the need to supplement diets with Vitamin E plus selenium to protect against oxidation of the long chain polyunsaturated fatty acids. Fresh fish is high in long chain PUFAs and adequately protected from oxidation. Captive alligators fed nutria or commercial mixes (low in long chain PUFAs) or frozen dead fish/fish products (in which inadequate protection against oxidation is present) may have poor breeding performance due to these dietary influences on yolk constituents/embryo hatchability (Noble et al. 1993, M. Staton pers. comm.). Studies are underway at Rockefeller to supplement several groups of our pen breeders with Vitamin E, selenium, and long chain PUFAs in a "sausage" mixed with nutria, and compare these to control groups not given supplementation.

Dr. Paul Cardeilhac (1991) examined the effects of total fat intake, vitamins, antibiotics, highly unsaturated fat intake, and protein intake on alligator breeding performance at several large alligator farms in Florida. Again, multiple pens, stocking densities, age of breeders, and diets made evaluating the effects of these varied nutrients on embryo survival difficult, however antibiotic and vitamin therapy strongly correlated with production of fertile eggs. Antibiotics administered were virginiamycin and oxytetracycline; and multiple vitamins and elements (including selenium and vitamin E) were added (Cardeilhac et al. 1991). We have initiated studies in 1991 at Rockefeller adding a powdered supplement containing these mixtures, however thus far little improvement has been noted. Cardeilhac (1990) also recommends that the diet of captive breeder alligators should be at least 15% polyunsaturated fat.

Eggshell quality.

Early studies on alligator eggshells by Shirley (1982) indicate diets also affect eggshell thickness. Alligators fed fish produced a thicker shell than either those fed nutria or those in the wild; this in turn could be implicated in the high percentage of early embryonic deaths that occurred in eggs from alligators fed fish.

We have frequently noted an obvious tactile difference in alligator eggs produced in captivity vs. those from wild alligators. Captive eggs are frequently rough, with extraneous calcareous deposits or are soft-shelled and misshapen. The wild eggs are usually of a smoother even texture. To determine if the low hatchability of alligator eggs from captive breeders might be due to differences in the morphology of the eggshells, we compared the morphology of eggshells of wild alligators to those of captive alligators using electron microscopy. Our results indicated the number of open pores of eggshells was lowest in eggs of captive alligators with early embryonic death. The number of pores was intermediate in eggs with early embryonic death from wild alligators, and the number of pores was highest in eggs with full-term embryos from wild or captive alligators. It was suggested that decreased porosity of eggshells may be associated with early embryonic death, is more prevalent in captive animals, and may, therefore be related to poor hatch rate among pen-reared alligators (Wink et al. 1990). Other crocodilian species however, normally have very rough, sculptured surfaces and the role of eggshell porosity in determining embryonic hatchability is still unclear (G. Webb, pers. comm.). Clearly; however, we have seen a marked worsening of eggshell quality with advancing age of our captive breeders.

Multiple Clutches.

The question has been posed as to whether crocodilians could produce more than one clutch of eggs per year (Lance 1987). Whitaker and Whitaker (1984) reported that captive C. palustris commonly produces 2 clutches annually. Most mature females lay two clutches of 25-40 eggs per clutch, about 40 days apart; but this phenomenum has not been documented in wild populations. Blake and Loveridge (1987) report on a possible case of double nesting in C. niloticus at St. Lucia in 1984, but believe their observations may have been indicative of "staged" or staggered nesting, where in all eggs in a single clutch are not laid at the same time (Blake and Loveridge 1987).

In alligators, Lance (1989) has suggested that 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. Eggshell formation in alligators also regimes the mobilization of calcium from structural bone (Wink and Elsey, 1986, Wink et al. 1987) to produce 30-40 egg shells, each containing 3.0-5.0 g of calcium (K. Packard, personal communication). The expenditure of energy during nest building and nest guarding also further drain the female alligator, and thus nesting twice in a year seems unlikely (Lance 1989). Lance (1989) also suggested that crocodilians likely have a refractory period after ovulation which would prohibit double nesting; and attempts to induce double nesting might cause premature senescence due to depletion of ovarian oocytes. Also, wild alligators have a relatively short nesting period, with a narrow time frame of warm weather for ovulation, courtship, breeding, nest construction, and incubation. A refractory/recovery period would place the time of incubation/hatching of a second nesting event well into the cool fall/winters experienced in the range of the alligator. Thus, attempts to induce second clutches in captive breeders would likely be unsuccessful.

DNA Fingerprinting.

One final area of new research we are undertaking is that of keeping genetic records, or a "stud book" of captive breeders in our experimental pens. Questions we hope to answer concern multiple parentage (?does more than one male service a female, or are all hatchlings in a clutch sired by the same bull?), and identify the males and females in communal pens which are contributing to the nesting efforts. Whether "pair bonds" exist is another question DNA studies can answer; and answers to these questions may further help our understanding of wild and captive crocodilian breeding biology.

## Conclusion

Although all crocodilian species have bred in captivity (Hutton and Webb 1992), success has been limited and most biologists and wildlife managers agree that ranching programs (which wisely use the segment of crocodilian populations otherwise lost to natural mortality) are the preferred utilization method and source of stock for crocodilian farms. The tremendous expense of captive breeding pens (land, construction, feeds, maintenance, labor) is cost-prohibitive for many species, particularly where only 5-10 hatchlings may be produced per adult female maintained annually. Present soft markets dictate captive breeding not economically feasible for most species, although the more valued C. porosus skins may still be profitable enough to warrant captive breeding attempts.

However, the physiological problems of captive breeding in crocodilians are very interesting, and deserve further study. Much more research is needed in many areas to improve captive breeder performance on crocodilian farms. The many factors that could adversely influence nesting in captivity such as age, stocking density, pen designs, stress, disease, obesity, inadequate nutrition, inadequate vitamins, minerals, trace elements, adverse social interactions and economic factors could be further researched to refine recommendations to commercial farmers/conservationists in attempts to improve captive breeding results.

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LOUISIANA'S ALLIGATOR FARM CAPTIVE BREEDING RESULTS, 1992

| FARM | # MATURE FEMALES | # NESTS | % NESTING | # EGGS | HATCHLINGS PRODUCED | % HATCH | HATCHLINGS PER FEMALE |
|---|---|---|---|---|---|---|---|
| A | 227 | 39 | 17.2% | 1560 | 1385 | 88.8% | 6.1 |
| B | 213 | 85 | 39.9% | 1003 | 355 | 35.4% | 1.7 |
| C | 165 | 50 | 30.3% | 2437 | 150 | 6.2% | 0.9 |
| D | 157 | 45 | 28.7% | 1000 | 501 | 50.1% | 3.2 |
| E | 108 | 60 | 55.6% | 1939 | 660 | 34.0% | 6.1 |
| F | 83 | 30 | 36.1% | 492 | 280 | 56.9% | 3.4 |
| G | 72 | 4 | 5.6% | 90 | 66 | 73.3% | 0.9 |
| H | 66 | 23 | 34.8% | 203 | 84 | 41.4% | 1.3 |
| I | 45 | 8 | 17.8% | 0 | 0 | 0 | 0.0 |
| J | 40 | 4 | 10.0% | 130 | 85 | 65.4% | 2.1 |
| K | 34 | 0 | 0.0% | 0 | 0 | 0 | 0.0 |
| L | 28 | 12 | 42.9% | 234 | 54 | 23.1% | 1.9 |
| M | 27 | 13 | 48.1% | 319 | 150 | 47.0% | 5.6 |
| N | 25 | 15 | 60.0% | 25 | 11 | 44.0% | 0.4 |
| O | 25 | 12 | 48.0% | 432 | 312 | 72.2% | 12.5 |
| P | 15 | 7 | 46.7% | 180 | 82 | 45.6% | 5.5 |
| Q | 11 | 8 | 72.7% | 275 | 180 | 65.4% | 16.4 |
| R | 9 | 2 | 22.2% | all infert. | 0 | 0 | 0.0 |
| S | 1 | 1 | 100.0% | 34 | 34 | 100.0% | 34.0 |
| 19 | 1351 | 418 | Avg. 30.9% | 10,353 | 4389 | Avg. 42.4% | Avg. 3.2 |

FIGURE 1. Clutch size of captive alligators, Rockefeller Refuge.

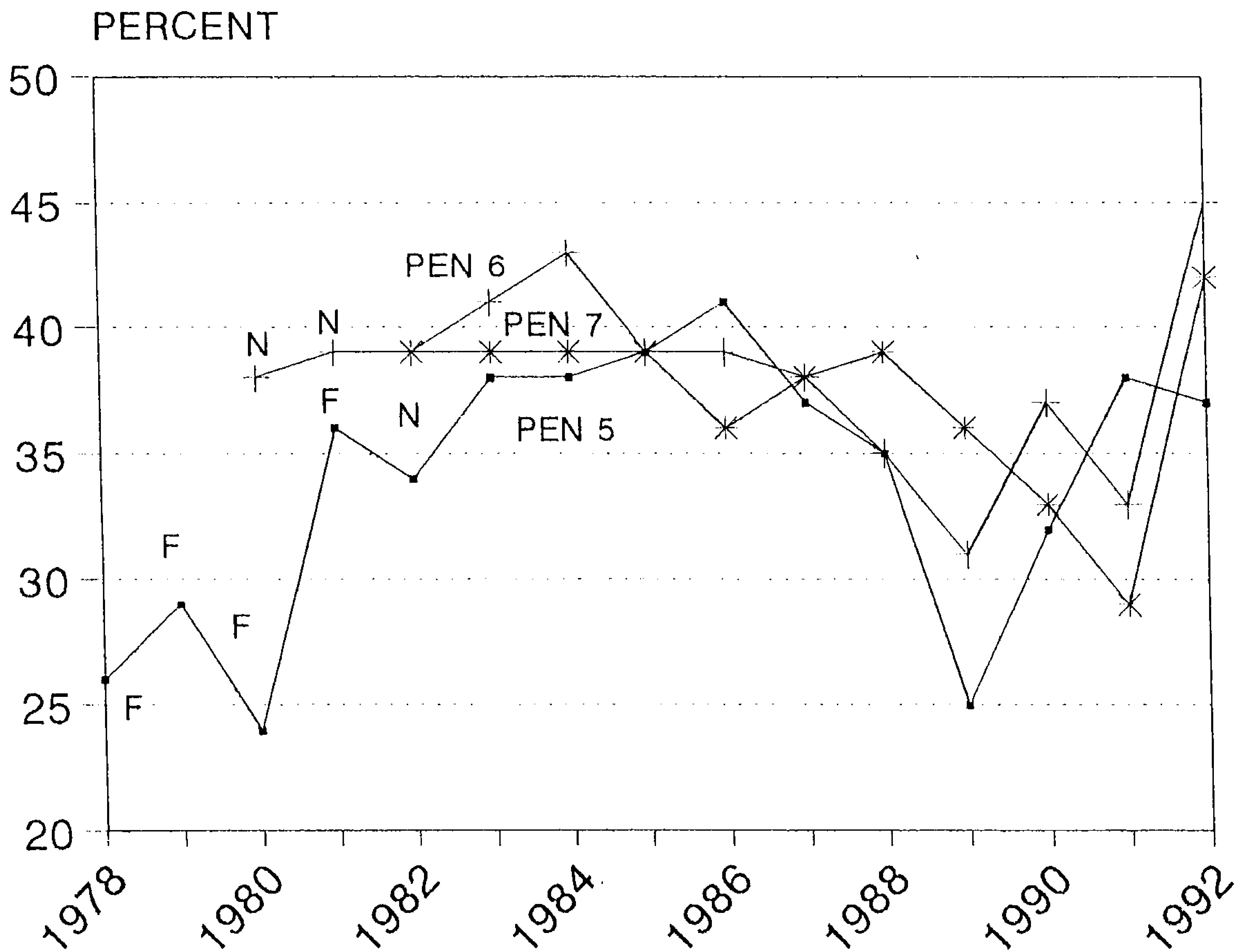

FIGURE 2. Nesting rates of captive alligators, Rockefeller Refuge.

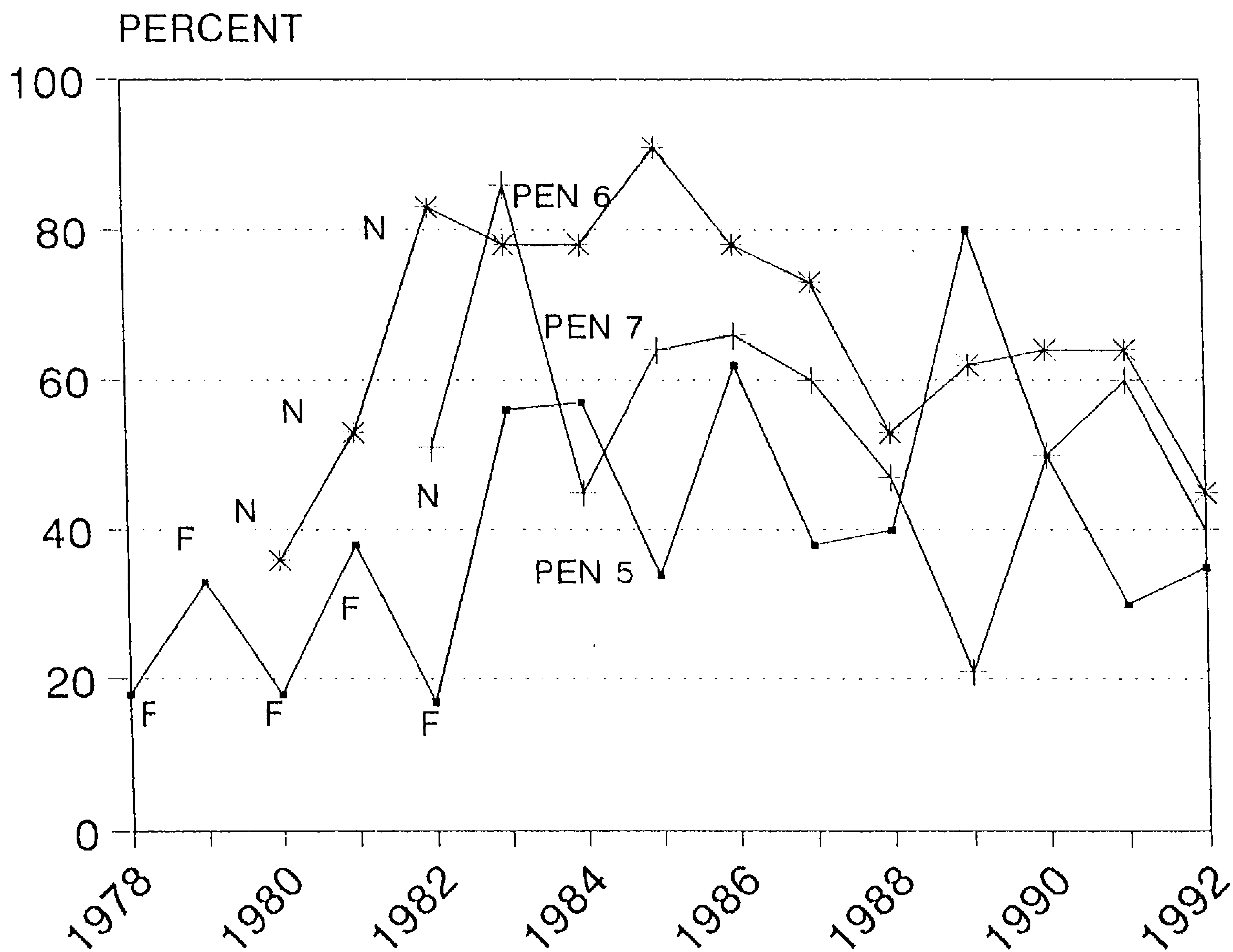

FIGURE 3. Fertility rates of captive alligators, Rockefeller Refuge.

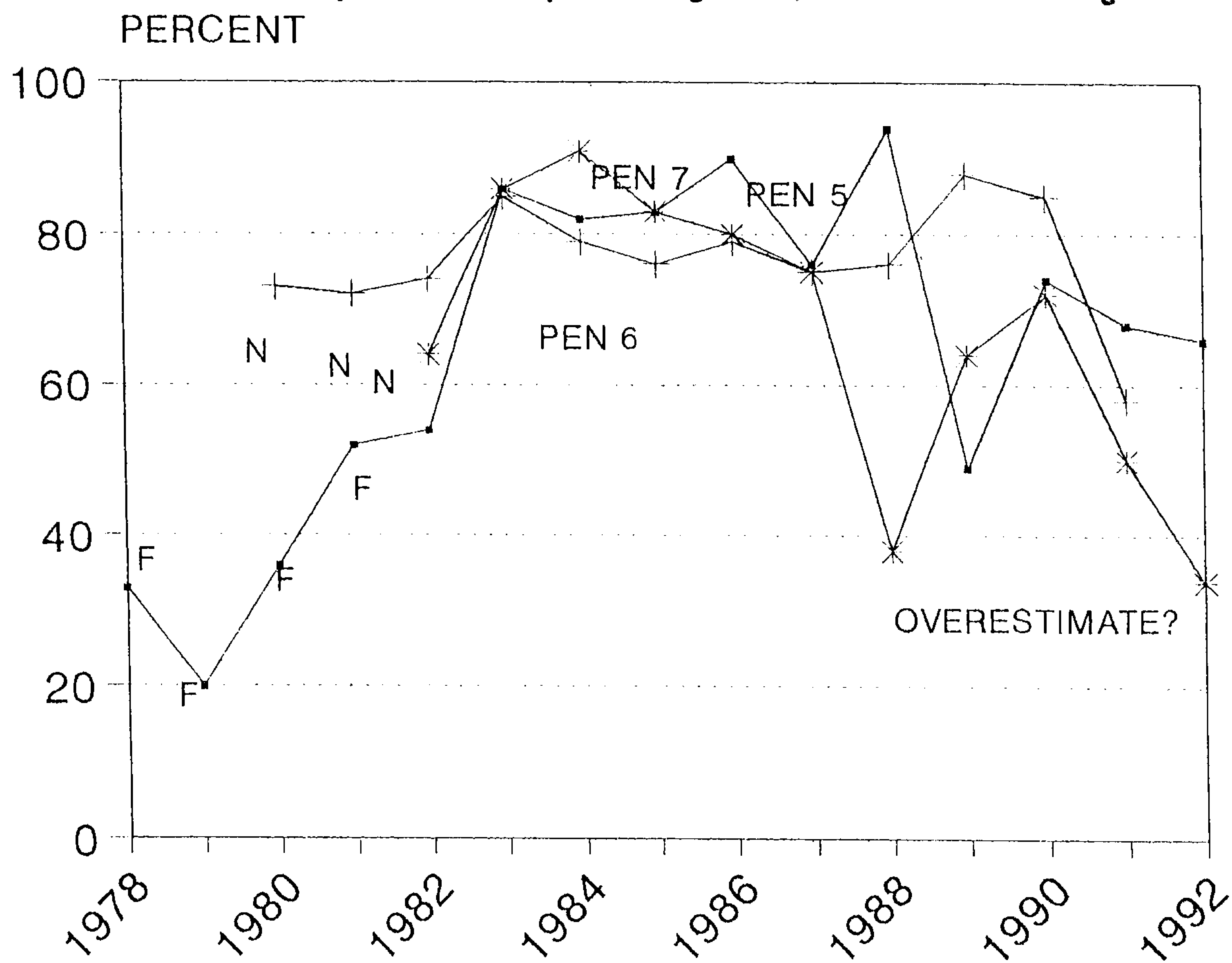

FIGURE 4. Hatching rates of captive alligators, Rockefeller Refuge.