assures us a constant supply of inexpensive trash fish not suitable for human consumption; the price is $5 \not\in$ per kg.

Breeding of Crocodiles in Captivity

We have two large breeding ponds, one about a half acre (0.2 ha) in area, the other almost one acre in area; at present we are building a third breeding pond. The ponds are surrounded by a land area somewhat larger than the water area; this large area permits a good deal of freedom of movement to the crocodiles. Shade is plentiful at both pools. Near the water's edge the land area is covered with concrete to prevent too much soil, sand and debris from falling into the water; away from the water, there is both sand and grass. The ponds are concrete and of irregular shape. The depth is about 1.5 m. The ponds are never drained because this disturbs the crocodiles; instead, fresh water is circulated as necessary. About 300 m³ of water are used per day. The water is not treated and algae has not been found to be a problem. Around the edges of the land area, there are 50 nesting stalls each measuring about 4x4 m, with a 60x60 cm door facing the pool; this door is easily defended by the female. The top of the stall is open to the air and each stall has a drainage ditch in the rear to avoid flooding of the nests during rainy periods.

Adjoining the large breeding ponds are smaller feeding ponds, which are approximately 8 m square and 50 cm deep. The water level of the feeding ponds is maintained 20 cm lower than the water level in the breeding ponds to minimize contamination. Each day at 1630 hrs fish are dumped in the feeding pond; the pond is cleaned daily after feeding. The crocodiles are given as much food as they will eat, and any food left over is subsequently removed. Since the crocodiles all come to the feeding ponds, it is possible to observe any illness or injury to individuals.

Each pond contains over 200 individuals, with ages varying from 12 to 35 years. We have found that siamensis reaches sexual maturity in 10-12 years and that porosus reaches sexual maturity in 12-15 years. The sex ratio in the ponds is one male to three females, but we believe that during the breeding season one male forms a relationship with only two females. The presence of the third female helps assure that each male will be able to have two receptive females. The mating season lasts from December until March and the majority of mating activity occurs at night. During this period, the males occasionally fight among themselves, usually at night; such fighting results in one or two deaths per year.

Eggs are laid from the end of April until July. We place nesting materials of dried grass in a loose pile in the nesting stalls about two weeks prior to egg laying. Females usually choose a stall about one week before

the eggs are laid; they make frequent trips into their stall, and actively defend its area against other females. Fighting occasionally occurs between two females attempting to nest in the same stall. The female takes from one to seven days to prepare the nest; nest building activity is greater during the night. The female mixes grass and sand with her hind leggs, forming a soft depression about 20 cm deep and 25 cm wide. She rarely uses her front legs in nest building, but her mouth is used to help crush grass to mix with the sand. Large tears can be seen streaming from the corners of the female's eyes from three to five days prior to egg laying. The laying of eggs usually takes place between 0600 and 0900 hrs. The 20 to 50 eggs are laid in the depression in about five minutes. The female then uses her tail to sweep a larger pile of grass over the eggs, building a nest with a total height of about 70 cm from ground level. Occasionally the female urinates on the nest; we believe this may help the decomposition process.

After egg laying, we chase the female out of her nesting stall; she is denied subsequent entry. The temperature of the nest is tested at least four times a day, especially just after sunrise and just before sunset. If the temperature exceeds 98° F, grass is removed from the top of the nest, thus lowering the temperature; if the temperature drops below 95° F, grass is added to the nest to raise the temperature. During an unusually dry year, water is sometimes sprinkled over the nest to maintain sufficient moisture.

If a shortage of stalls occurs, several nests are moved into one stall. Porosus lays about 30-50 eggs, which hatch after 78-80 days; 40-50% of the eggs hatch. Siamensis lays about 20-40 eggs, which hatch after 67-68 days; 50-60% of the eggs hatch. In 1970, we were able to hatch a total of 3500 eggs.

Care of Young Crocodiles

When the eggs are hatched, the young crocodiles are placed in concrete nursery tanks measuring $30 \times 50 \times 40$ cm. These tanks have a wooden floor and a small bathing trough; they are screened against rodents and insects, especially mosquitoes. About 8-15 young are placed in each of over 200 nursery tanks. The young do not eat for the first week or ten days; thereafter, they are fed coarsely chopped fish until they are large enough to be moved to a larger tank, at which time they are fed whole fish. Around 20-30% of the hatchlings die in the first year of life; some of these early fatalities are stuffed and sold as souvenirs. The fatality rate among crocodiles over one year of age averages less than 5% per year.

As the young crocodiles grow, they are moved to larger and larger concrete tanks, always being kept with age-mates and in crowded conditions. We have 30 tanks 1.25 cm square, 28 tanks 2 m square, and 80 tanks 3.6 m square. Partitions between tanks can be removed to make larger tanks.

Summary

To summarize, we feel that there are eight necessary factors leading to our success in breeding porosus and siamensis:

- 1) Climate. The climate at Samut Prakan is the same as that of the natural habitat of these two species.
- 2) The breeding population. Our breeding populations are quite large, with over 200 invididuals in each of two breeding ponds.
- 3) Feeding. The crocodiles are fed as much as they will eat; feeding is done in the water, not on land.
- 4) Nesting stalls. The stalls are individual, with a small, easily defended door facing toward the water.
- 5) Nesting material. Nesting materials are similar to those used in the natural habitat, and the female is allowed to make her own nesting arrangements.
- 6) Incubation. The incubation temperature is carefully checked, but is controlled by 'natural' means.
- 7) Sex ratio. The sex ratio of one male to three females allows enough flexibility to ensure that each male will have access to two receptive females.
- 8) Breeding area. The breeding area is large enough to allow the crocodiles a large degree of freedom of movement.

We are very fortunate in Thailand to have the requisites for breeding crocodiles, and we will be happy to make facilities available to IUCN for the breeding of other endangered species of crocodiles. We will care for them, feed them, show them to the public to increase interest but, most important, when we have breeding success, we will ship the offspring to other breeding stations and zoos which are approved by IUCN. Hopefully, in the future, we will even be able to return crocodiles to their former natural habitat, or at least to protected national parks or game reserves. To speed the arrival of this time, I invite any accredited scientists who would like to conduct research in crocodiles to come to the Samut Prakan Crocodile Farm. We are eager to make your research most profitable for the continued existence of the endangered species of crocodiles.

ANNEX

A NOTE ON SOME DISEASES OF CROCODILES IN THAILAND

U. Srisomboon, D.V. M. Bangkok, Thailand

Until 1970, diseases of crocodiles in Thailand had not been studied; although the Bangkok Zoo has several species of crocodile, they have been found to be the animals most resistant to disease in the zoo, so veterinary care is seldom required. Until the private crocodile farm belonging to MrUtai Yang-prapakorn was opened to the public in 1970, few crocodile carcasses were sent for examination to the Veterinary Laboratory at the Department of Live-stock Development. Since the opening of the Farm, I have been the consulting veterinarian for Mr Utai; I have set up a small laboratory at the Farm, and am now studying normal blood counts. The normal blood structure is as follows:

| White blood corpuscle | $609,200 / \text{mm}^3$ |
|-----------------------|---------------------------|
| | 497,700 / mm ³ |
| Haematocrit | 25 - 28 % |
| Haemoglobin | 7.34 gm / 100 ml |

Mature crocodiles do not seem to be susceptible to infections; only benign tumours caused by chronic wounds are observed. These are removed by surgery when necessary. Wounds usually occur during fighting among the crocodiles, especially among males in the breeding season.

In crocodiles up to the age of $1^{1}/2$ years, infections of the alimentary tract are sometimes observed; most of these are due to food poisoning. The species of bacteria found include Enterobacteria, Staphylococcus spp., Streptococcus spp., and Leptospira.

We have experienced trouble among crocodiles which the Farm has bought from outside sources; these animals have often been mistreated and most of them are in poor condition. The first symptom observed is the inflammation of the eyelids, followed by general weakness and diarrhoea; death usually follows in about two days. Post mortem examination shows that the alimentary tract is involved. Bacteriological examination has shown that a pathogenic strain of enterobacteria was involved. Since we take

sanitary precautions with the fish we feed to the crocodiles, there are few such cases among the crocodiles hatched at the farm.

Generally, the crocodiles seem to be quite immune to disease; in 1970, 39 cases of disease or injury only were found in a population of 11,000 individuals. These were distributed as follows:

| Disease | Cases |
|--|-------|
| Leptospirosis | 2 |
| Roundworkn (Ascaris) | 2 |
| Tapeworm | 1 |
| Pneumonia | 3 |
| Stomatitis | 6 |
| Food poisoning | 1 |
| Benign tumour | 18 |
| Pericarditis | 2 |
| Oedema in pericardial cavity | 3 |
| Pleuritis | 1 |
| Andrew Commence of the Commenc | |

Conclusion

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Disease in mature crocodiles is not common, though some young crocodiles at the age of 1-2 years may be affected by enterobacteria. In a few cases, leptospirosis is involved; contamination of fish is probably the cause. Sanitary precautions in feeding minimize the incidence of disease.

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Paper No 11

CROCODILE REARING AND RESTOCKING

A.C. Pooley Natal Parks, Game and Fish Preservation Board

In almost every country in which the Nile crocodile Crocodylus niloticus is found, it is in a serious plight. Illegal poaching by tribal people with their simple but highly effective traps and snares, as well as professional hunters operating with power boats, spotlights and modern firearms have decimated this animal over most of its former range. In addition, each year more swamps and marshlands are drained, rivers dammed, riverine forest denuded and disturbance of breeding areas created. Suitable habitat is disappearing rapidly. Conservation departments have been slow to introduce protective legislation for an animal that does not engender sympathy; because most departments are short-staffed and have enormous areas to police, this protection is largely ineffective.

The writer is fortunate to have been working with the Natal Parks, Game and Fish Preservation Board in Natal, where complete protection has long been given to crocodiles in the game and nature reserves, and, for some time, even outside these areas. Interest in captive propagation arose largely because of a noticeable reduction in the crocodile populations outside the wild life sanctuaries; the Board encouraged this interest and permitted the author to establish an experimental crocodile farm in northern Zululand. The programme of protecting nests from predators, artificially incubating eggs, distributing hatchlings and releasing young reared animals has proved to be a successful conservation exercise.

During the past few years there have been several attempts at commercial crocodile farming but most have failed because the prospective farmers lacked experience. Many thousands of eggs perished and young stock died of disease.

The purpose of this guide is to describe a simple method of rearing crocodiles, based on practical experience of hatching and rearing 1000 crocodiles over several years. In addition, other workers and the available literature have been consulted and most of the commercial farms operating in Africa have been examined. Many conservation bodies may in the future establish crocodile rearing projects and others will be responsible for issuing permits to private enterprise. Some legislative and administrative recommendations are therefore also included.

Conservation Recommendations

General

Legislation should be in operation throughout the country protecting the crocodile. It should be unlawful to kill, capture by any means whatsoever, disturb wilfully or pursue any crocodiles, or harvest, collect or gather any crocodile eggs without a permit.

A permit should be required to import or export any crocodile whether dead or alive, or any portion of a crocodile, whether processed or not, from any country.

No crocodile egg or eggs should be allowed to be imported into, or exported out of any country, without a permit.

No person should possess, sell, buy, donate, receive consequent upon a donation, convey, keep in captivity or display any live crocodile, without being the holder of a permit.

Before any rearing scheme is commenced, a survey of the breeding grounds should be undertaken to determine the number of nests available.

These breeding grounds should be fully protected and tourists on foot, by vehicle or in launches should not be allowed to visit or disturb breeding crocodiles.

The area should be fenced off for better protection if there is undue disturbance by large mammals, domestic stock or humans.

Prior to the commencement of egg-laying it may be necessary to take precautions to prevent fires from nearby human habitation from spreading to the breeding grounds.

Predators, such as troops of baboons and monitor lizards, should be artificially reduced if found to occur at breeding grounds. Predator control should in no way disturb the crocodiles and should be carried out prior to egg-laying or after hatching of every nest has been completed.

In addition to the culling of predators, protective screens may be used over nests. These should be placed in position soon after laying commences. When a nest is found, the soil is dug away and levelled to within a few inches of the top layer of eggs. A 1 m square screen, constructed of heavy gauge wire mesh (either plain or plastic coated) with a mesh size of not less than 3.5 cm, is laid over the nest area and pegged at 30 cm intervals around its perimeter before the nest is again covered over with soil.

At some breeding grounds, where several crocodiles nest in close proximity in sandy soil, it may be difficult to determine the exact position of each nest. To locate the eggs a 75 cm length of welding rod is used to probe the soil for nests.

During a season of exceptionally high floods it may be advisable to collect all the eggs from a particular breeding ground before these are destroyed, for artificial incubation, hatching and distribution of the young to safer areas. Often, the sparse vegetation affords little or no protection to hatchlings in the vicinity of breeding grounds.

The presence of numerous predators, such as monitor lizards, storks, herons or pelicans, is also a threat to the survival of eggs and hatchlings. After incubation, the hatchlings can be distributed to more suitable habitats.

If the policy is to incubate, hatch and rear the young for release at a later stage, then the following factors should be considered.

To avoid egg wastage, decide how many crocodiles are to be reared. Artificial incubation should hatch 80% of the total number of eggs collected. Thus 500 eggs will be required to produce 400 crocodiles.

If eggs are to be harvested annually, nests should be raided in rotation, collecting from a given nest one year, then leaving it undisturbed the next year. If nests are systematically robbed year after year, the parent will abandon the nest site. Where crocodiles nest colonially, every effort must be made not to disrupt the cology. Colonial nesting offers more successful defence against predators, which may devour the eggs before protective screens can be placed. The collection of eggs should be staggered throughout a breeding colony and here it is useful to map the locality of each nest for future reference.

Control of commercial farms

Before granting a permit for private enterprise to establish a farm, the Department should investigate the applicant's land tenure and financial resources, particularly since the farm will have to operate for some three to four years before producing crocodiles suitable for culling. The applicant's ability and experience of rearing crocodiles should be determined. A plan of the proposed farm, including details of water and food supply, as well as the proposed methods of harvesting food, should be examined.

It is suggested that permits should be issued on the following basis:

No permit for egg harvesting should be issued until adequate rearing

facilities have been prepared. The permit should state name of holder and/or his authorized representative, the annual total number of eggs allocated for harvesting and the area where collection is permitted.

Permits should be issued on an annual basis only. The applicant should understand that the department may refuse to renew or issue further permits if the farm is not managed satisfactorily or if permit conditions have not been observed.

The applicant should understand that the farm and all production records should be available for inspection by an official of the conservation department.

The farmer should be required to submit monthly reports detailing the total number of nests raided, eggs harvested, egg-mortality and number hatched. Thereafter, details of numbers held in captivity, mortality and its causes if known, and animals sold or culled, should be submitted in each monthly report.

It is recommended that the permit holder should release 5% of his annual crop of hatchlings in order to restock the natural habitat. In addition, a further 5% of the hatchling crop should be reared to a length of 1 m before being similarly released; thus bringing the total release of young crocodiles to 10% of the annual crop of hatchlings.

The distribution of hatchlings and of young reared animals should be supervised by the conservation department.

Practical Farming

Hatchery requirements

The practice of building the hatchery alongside the rearing ponds is not recommended because of the liability to disease-transport by flies, ants and beetles attracted to the discarded egg shells and, in turn, to the food in the rearing ponds.

The hatchery site should be chosen with a view to the prevailing wind direction and heavy rains and it should have a sunny aspect. The area should have a well drained sub-surface, since an impermeable layer of rock just below or at nest-depth will lead to the flooding of each nest after heavy rain. The hatchery should not be built close to any foot path, road or human habitation, the reason being that the young are sensitive to vibration or surface-disturbance close to the time of their emerging, so this should be minimized.

The hatchery should be adequately fenced against burrowing and avian predators, using netting of 1 cm mesh buried to a depth of 60 cm and extending above ground to a height of 2 m. Larger mesh (or even criss-crossed strands of baling wire) may be used to make the roof.

A section of the enclosure should provide shade at all times of the day and should afford shelter during heavy rain or hailstorms. A windbreak should also be provided where the young may find shelter.

A shallow pool or trough of water about 30 cm deep must be provided under the shaded area of the enclosure. This should be designed to enable the young to rest partly submerged, and must allow easy access an exit from the pool. Once hatching commences this pool should be drained, cleaned and refilled daily.

Harvesting eggs

Eggs should be collected soon after being laid, especially if the journey back to the hatchery involves a considerable distance over rough roads. With eggs in an advanced state of incubation there is the danger that the delicate system of blood vessels or the yolk sac will rupture. Excessive bumping or jolting will bring about premature hatching and these crocodiles have a poor survival rate.

Collection should preferably take place during the cooler hours of the early morning or late afternoon. Opening a nest at midday, or placing eggs on the hot sand near the nest produces a severe temperature shock that may cause premature hatching, even if the eggs would have required another two to three weeks incubation. Prolonged exposure will certainly kill the embryo.

Each egg is marked on its upper surface to show how it lay in the nest, and individual clutches are kept separate from the time of collection to final incubation. When hatching commences it is then easy to determine from which clutch the croaking sounds come, and this eliminates the unnecessary disturbance of hundreds of other eggs. After collection of the eggs the empty nest cavity is filled in and levelled off ready for the next season.

Transport of eggs

Corrugated cardboard containers well padded with grass, straw or even vegetation are ideal, being light and easily carried long distances if necessary.

Once packed, care should be taken to keep the containers shaded from

direct sunlight. In particularly hot weather the contents of each container can be thoroughly sprinkled with water before the lid is closed.

An alternative method is to pack the eggs in wooden boxes filled with soil from the nest. The box then must be filled completely to avoid damage to the eggs during transport. The disadvantage of this method is the weight of a full box.

A mattress of straw or dried grass 30 cm deep can be laid on the back of a vehicle or in a boat before loading the eggs. This is important if the journey back to the hatchery is likely to be a bumpy one.

The permissible time-interval between collection and re-burying of eggs depends largely on the prevailing temperature conditions. Suitably-packed eggs can be transported by air, boat or road for several days, but when air temperatures drop below 15° C for a period of some hours, death will occur.

Incubation techniques

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Each egg should be examined carefully before re-burying. Pierced, badly dented or flattened eggs should be discarded, as should infertile and rotten eggs which are detectable by their glazed or discoloured blue/green or grey appearance. The contents of an addled egg will be liquid. The main reason for removing these eggs is to avoid attracting ants, beetles and other harmful insects to the nest.

Within the hatchery, artificial nests are excavated in the sand in parallel rows, allowing a footpath 1.5 m wide between rows and spacing nests 1 m apart. A nest size of 45 cm square is adequate, even for large clutches, and should initially be dug to a depth also of 45 cm. The eggs are then buried in three layers as is usually found in the wild nest. A space between them allows for humidity. The soil should be damp enough to squeeze a handful into a form. The depth at which the top layer should be buried below the surface depends on the soil type. Thus, in loam or clay, they should be 15 to 20 cm deep and in fine sand about 30 to 45 cm.

an average depth of 30 cm. This should be checked at intervals because temperatures tend to rise as incubation progresses. Once the eggs have been buried a series of temperature recordings should be taken at two-hourly intervals. From these it will be possible to establish whether sand should be removed or added over the nest site to achieve the desired nest temperature.

Hatching success is greatly improved if a book recording details of each clutch is kept, which indicates the number of eggs remaining in each clutch and the date on which hatching commenced. This is important because, while

some clutches may hatch prematurely, others may require up to an additional 14 days of incubation. Generally, once hatching commences and the crocodiles are seen to be normal, the remaining eggs are not left to incubate more than ten days. If the hatchlings are premature (i.e. with extended abdomen), the remaining eggs may be left up to 14 days, after which period they are opened and will survive even if still premature. Often the unhatched crocodile becomes entangled with the umbilical cord and movement within the egg is restricted. Unless these eggs are opened the crocodiles will perish.

In regions of poor summer rainfall or during a drought, it is necessary to check the moisture content of the soil weekly. If necessary, the nests can be sprinkled with water until the sand around the eggs is suitably damp. This should be done during the early morning or late afternoon.

As incubation progresses, the egg shells may crack extensively and pieces may peel off. Providing the nest soil is suitably moist this is not harmful. Should the soil become dry, the inner rubbery skin of the egg will harden and adversely affect hatching success. Eggs in this condition can be thoroughly dampened to soften this skin.

Nests should never be opened or inspected during the heat of the day. Even if the young are heard croaking the nest can be left until it becomes cooler.

The incubation period may vary between 11 to 13 weeks, with an average of 84 days. This will depend largely on the weather and nest temperatures. Incubation may extend to 98 days.

If, after 84 days from the time of collection of newly laid eggs, there is no apparent sign of hatching, the nest should be visited twice a day and the surface sand distributed by scraping or patting over the nest. After 90 days, the nest may be opened to expose the eggs for an hour during the early morning. Frequently this change in temperature induces hatching. The playing of tape recordings, if available, of the grunts or croaks of the young is an excellent stimulus to hatching.

No attempt should be made to break the umbilical cord of hatchlings still attached to the empty egg shell. This cord will soon dry out, become brittle and snap off of its own accord. For this reason crocodiles in this state are not immediately put into the water.

Once discarded, the egg shells should be removed from the hatchery before they attract numbers of insects. Addled eggs and dead embryos are removed and buried elsewhere.

Hatchlings are normally kept for a period of 24 hours before removal to the rearing ponds. Before removal they are washed and packed in closed

containers for transport. Any that may be premature (shown by their having an extended yolk sac) are retained in the hatchery until such time as the umbilical scar has healed. These individuals should be separated from the others.

Rearing Pens

Siting

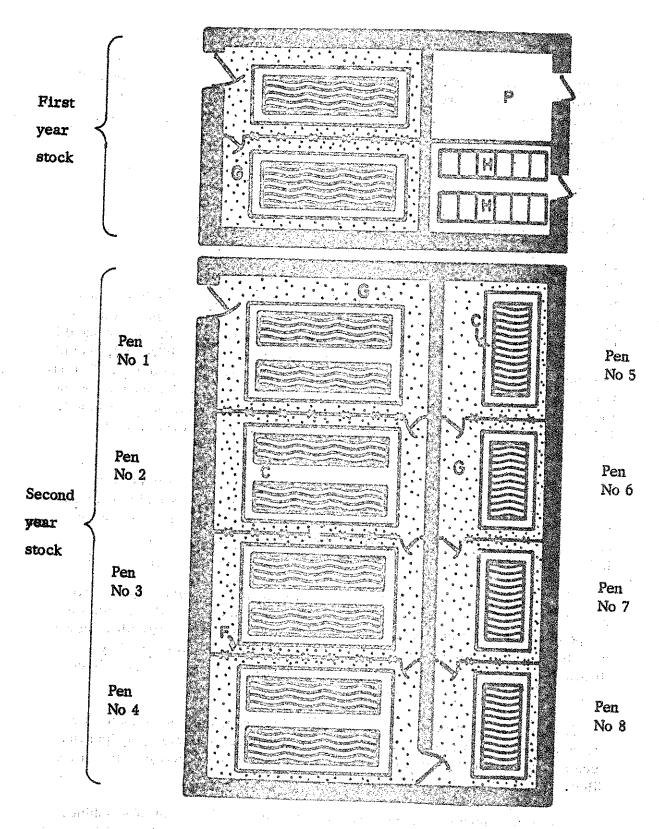
When selecting a site for a rearing station, several factors should be considered: the volume of water available throughout the year; the distance to pipe water to the ponds; and pumping costs. The quality of the water should be established. Samples should be tested for salinity and acidity and, should the supply be from mineral springs, analysed for harmful chemicals. Chlorinated water must be regularly tested to ensure that the chlorine content is not too high and the nature of any factory effluents present should be determined. It is of great importance to establish whether fish, frogs, crabs, molluscs or aquatic insects survive in the water intended for use.

Bacterial analysis is advisable in instances where the water is drawn from a river that drains an area densely populated by humans and livestock. If the water is found to be contaminated, the use of the stagnant pond rearing pen system is not advisable, particularly when <u>Salmonella</u> spp. are present in high concentrations.

A filter system has advantages if water is pumped straight from a river carrying a heavy silt load. Apart from not being able to see the animals in the pools, the use of unfiltered water makes the pools more difficult to clean and pipe lines become clogged with sludge. This can be eliminated by drawing water from a deep pit close to the river, so that the water collected seeps through sand or mud and is thus filtered.

A reservoir or a series of supply tanks is very useful as an additional method of filtering water and, in the event of failure of pumping equipment, such a reserve supply may prove vital to the health and survival of the crocodiles.

The ponds should be sited to receive the maximum amount of sunshine, particularly during the winter months. The type of pens required will depend on winter temperatures. Should these be cold, earth dams will be useful. An ideal combination is to have earth pools for winter and cement pools for summer use. The soil types are the next consideration. If sandy and porous, earth dams are impractical, or require a lining of concrete to retain water. On the other hand the water supply may be inadequate.



Theoretical farming complex, incorporating design faults.

| C | Commence | | 1.1 | |
|-----|--------------|----------------------|----------------|-------|
| • | cemenced | perimeter. | 9503 M CO.14 | abada |
| 373 | | The same of the same | مرسول المساورة | |

F G Wire mesh fencing

(Stippled areas) Gravel or grassed floor

H Nest boxes, in hatchery room

Food store and preparation from

A series of winter air temperature recordings would be useful in the siting of rearing pens, since very often valley temperatures are several degrees lower than they are 50 to 100 m farther up-hill. Preference should then be given to the warmer aspect, taking into account the direction of local winds and heavy rains.

Drainage of the ponds must be carefully considered. If these are built on a slight rise, drainage is far easier than if the ground is level. It is not desirable to allow water fouled in the ponds to stagnate nearby, so the drainage system must be efficient.

It is recommended that the pens be spaced a minimum distance of 8 m apart, and that drainpipes from the ponds should be led underground 10 m away from each pond, and only then into an open furrow.

Design faults

Several design faults which should be avoided when planning a rearing station are shown in Fig. 1. Some commercial farms suffered very severe losses and others were forced to close down because of the disease problems resulting from such faults.

In one farming complex as many as 15 pens (enclosures with pools) were built adjacent to each other, and the whole complex surrounded by a wall 2 m in height. Fresh air circulation was hindered by this outer wall and also, between pens 1 and 5, 2 and 6 etc., was blocked again by inner walls dividing these pens. The air in the pens was stale and a strong odour was prevalent. Furthermore, the hatchery was built adjoining the rearing pens, while food was prepared next to the complex where large numbers of fish were scaled, gutted and chopped up daily. Large numbers of flies were attracted to the hatchery, to the food and into the pens to faeces and uneaten food.

Many of the pens contained two pools each. The pen area was 25×2 m and the pools were 60 cm deep. The pools were separated by a smoothly plastered apron about 1 m wide, with an apron of the same width around the perimeter of each pool. The main basking area was of coarse sand, gravel or grass. These pens housed 200 crocodiles of from two to three years of age, the largest animals being up to twice the size of the smallest.

The pools were drained and scrubbed clean daily, but the basking area in each pen could never be satisfactorily cleaned because crocodile faeces and small scraps of uneaten food remained in the gravel or grass. It will be seen from the sketch that pens 1 and 2, 3 and 4, etc., are divided only by a wire grid. For purposes of hygiene therefore, they were not in fact separated at all.

Entry into the complex was gained through a single entrance gate in the outer wall and then through each pen in succession.

During the first few months of operation, there were no disease problems apparent in this system. With the onset of colder winter temperatures, however, there was a reduced intake of food, lowering the crocodiles' disease resistance. The smaller animals then succumbed to respiratory ailments in the cold cement pools and the infection spread rapidly. The majority of the animals became ill and refused food, the weaker ones died, and paralysis or partial paralysis of limbs followed, with diarrhoea and blood-stained faeces. The resultant epidemic brought about 200 deaths in a single month. Because of the layout of the farm the sick animals could not be isolated to prevent contamination of the healthy specimens. The bacteria Shigella sp. and Salmonella sp. were isolated from dead crocodiles. The bacterial load in the grass and gravel areas built up rapidly and was transmitted to other pens rapidly by flies, and by people walking through the pens, until every pen contained crocodiles in various stages of illness. A further complication arose from the fact that the crocodiles were not graded into size groups so that bullying at feeding times became inevitable. The smaller animals were bitten on the snout and their jaws and teeth were damaged. Wounds in the gums caused infection to set in, making them soft and spongy, leading to necrosis of the mouth. This infection spread through the process of swallowing and also caused death.

Recommended systems and the second state of the second sec

Mark Mark Contractor

Single units (cemented pens) (Fig. 2): An important requirement is that the pools should be at least 60 cm in depth, otherwise the water becomes too hot in summer. The pool floor should be sloped towards the drain outlet pipe, to facilitate cleaning and washing away of uneaten food particles. Ideally the outlet pipe should be 10 cm in diameter, with a stopcock outside the enclosure, so that the pool can be cleaned and emptied both efficiently and quickly. It is essential to place a screen in the drain pipe to prevent crocodiles escaping or from being sucked out of the pool during cleaning. After some time, stagnant ponds may become difficult to clean because of the rich growth of algae on their sides. Hard-bristle scrubbing brushes are needed to dislodge this growth. Small amounts of copper sulphate in the water will help control algae, if used regularly.

The entire pond and apron of the enclosure must be smoothly plastered to facilitate cleaning. It is useful to have a water supply point close to each pool from which a hose pipe can be led to pressure-spray and clean the entire pool and its apron.

An important part of the design is a partly-submerged and gently-sloping

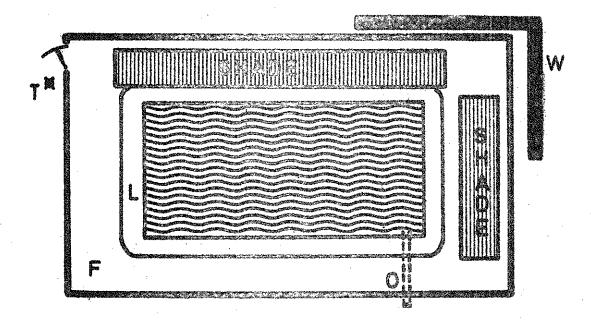


Figure 2. Plan view of single-unit cement rearing pond.

F Smooth cemented floor

L Inclined 45 cm wide cemented ledge

O Underground outlet pipe T Water supply point (tap)

W Wind-screen

Pen size: 9 x 6 m Pool size: 7 x 4 m

ledge, some 45 cm in width, around the perimeter of the pool. This provides a shallow resting zone for the crocodiles and allows easy access into the water. This ledge is also important in that the crocodiles rest there when feeding, and it also prevents them scraping their bellies and damaging their claws on entering or leaving the pool. The amount of space around each pool is calculated to allow ample basking room for each animal, and an area of shade must likewise be provided.

It is advisable to roof over the entire pen with wire netting, or criss-crossed strands of wire, against predators. The wire netting sides of the pens should not be larger than 1 cm mesh, otherwise hatchlings will injure themselves by trying to climb through this. Young crocodiles can climb vertical wire netting with ease and will escape unless the enclosure is either roofed or its side walls sloped inwards at an angle of 20°. A skirting board

(planking, sheet iron, tin or plastic sheeting) placed against the wire netting flush with the floor prevents them from climbing up the fence to a height, and then dropping back onto the concrete below.

These pools are useful for summer because they can be scrubbed clean and because the volume of water used is small. Normally they need only be emptied, cleaned and refilled every third day and there is no wastage through seepage.

The main disadvantage is that cement is a cold surface in winter and crocodiles will be prone to respiratory ailments. If local winter night temperatures of the water or of the air are likely to fall to the 7.2°C, this type of pond would not be suitable. Care must be exercised while cleaning these pools, to avoid a crocodile injuring itself by falling into the empty pool.

Cement pond (trickle system) (Fig. 3): The advantage of this system is that during hot summer weather, when crocodiles are feeding at their maximum rate, small uneaten food particles, faeces and urine, are not trapped in the pool. The constant dilution of the pond's water ensures a low bacteria level.

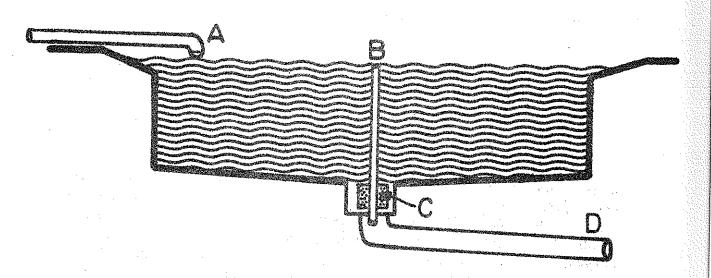


Figure 3. Trickle-system cement rearing pond.

A Water supply hose

B Siphon outlet pipe

C Watertight rubber plug

D Underground drain pipe

Pool size:

9 m diameter

The pool is drained and scrubbed clean weekly, as is the entire floor of the pen which is smoothly plastered. The enclosure embodies the same design requirements as seen in Fig. 2.

The pool should be circular or cone shaped, at least 50 cm deep at the edges and 60 cm in the centre. An earthenware bend of 10 cm in diameter is sunk flush into the centre of the floor and into this fits a rubber plug. In this a 5 cm diameter hole is bored, through which a 66 cm length of polythene pipe is fitted vertically into the plug so that it can be pushed in or pulled out as required. A wire mesh shield is fitted over the top of this outlet pipe to prevent the escape of small crocodiles. Water is fed constantly into this pool, circulates, and is siphoned out at the same rate as the inflow.

It is helpful to attach string wire handles to the rubber drain plug, so that it can easily be pulled out when the pool is to be cleaned.

Single earth dams (Fig. 4): These are ideal for use in climates where low winter temperatures are likely to cause respiratory illness in the young animals. Earth pools are easy and cheap to build and are a 'natural' habitat where vegetation can be planted, small live fish introduced, while insects,

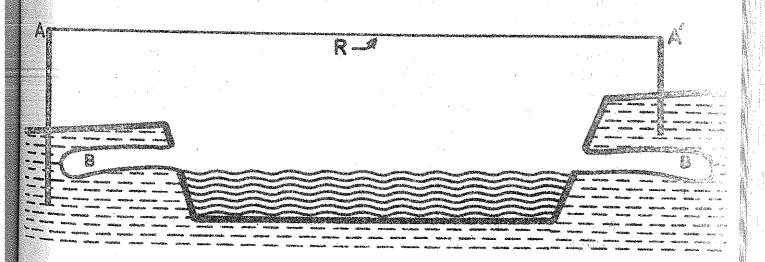


Figure 4. Isolated earth rearing pond or dam.

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A Upper fenceline

R 14 gauge wire roof-grid

B Burrow

frogs and other creatures attracted to the dams will be an important addition to the diet and health of the crocodiles.

During cold weather the crocodiles will burrow into the mudbanks and thus survive nights of heavy frosts. Because of their burrowing capabilities it is important to provide a strip of land, 4 m wide, between the pool's edge and the boundary fence. This is particularly important if the pool is situated at the bottom of a hill such that its lower bank is artificially built up. Where pools are excavated on a level site this precaution is not necessary. The crocodiles burrow into the bank above normal water level and may tunnel beyond the fence line. Normally this will not matter since the burrows will be well below ground level, but if the pool stands on a hill slope the lower fence line should be buried deep enough to intercept the burrows (Fig. 4).

The enclosure fence should be of 1 cm diameter mesh netting for young crocodiles, buried to a depth of 1 m, to exclude burrowing predators. Because these pens are a natural habitat, birds may become a nuisance, either as a threat to the crocodiles or as food competitors. The pens therefore should be roofed, for which a broad-mesh grid made of 14 gauge wire is suitable.

In areas where the soil is porous or sandy the floor of an earth dam can be sealed with concrete or plastic irrigation sheets. A layer of earth conceals this artificial floor.

Drainage is effected by a central pipe and the water siphoned out as in the previous system. The disadvantages of earth dams are that they require a larger volume of water to allow for seepage, and require more maintenance. Earth dams cannot be efficiently cleaned. Even if they are provided with a system of constantly circulating water they eventually become fouled, particularly during hot weather when feeding rate is at its maximum. Ideally, one should have only half the available number of pools occupied at a time, so that they can be used in rotation. In this system, the animals can be moved to fresh pools every two months (or as necessary), leaving the 'used' pools to be drained and allowed to dry out and bake in the sun. After two months' rest thex will be clean and ready for use again.

When the crocodiles are to be removed from an earth dam they will prove difficult to capture with a hand net since most will take refuge in their burrows. A simple capture method is to make tubes from 1 cm mesh wire netting, and about 45 cm in length which are firmly pushed into the burrow entrance and their bases packed around with mud. The tubes are tilted uppards at a slight angle and held in place by prop-sticks. The pool is then drained completely and when the crocodiles venture out, they can be easily caught.

Rearing Techniques

Handling

Dealing with a large population of crocodiles comprising different age groups and sizes requires a great deal of rearing and handling experience. This ability is vital because crocodiles are more delicate than is generally realized and a thorough knowledge of their behaviour and requirements under captive, artificial conditions is essential if rearing is to be successful.

Many disease symptoms are easily overlooked if the observer is not familiar with the normal behaviour of crocodiles under a variety of conditions. It is essential to know intimately how they normally walk, swim, sleep, feed and bask in relation to the time of day, the air and water temperatures, the amount of sunlight or rain, both by day and by night, as well as at different seasons of the year. One should notice the appearance of normal faeces from healthy animals, to be able to detect evidence of diarrhoea.

The observer will soon notice that from one clutch of eggs hatched, some individuals will be aggressive, others less so, others may be shy and some extremely timid. The growth of some individuals will be rapid, others less so, and a few may be classed as runts, hardly growing at all.

It is not easy for an inexperienced person to determine the cause of illness or death, should this occur, and it is time-consuming to capture and administer drugs to sick animals even if the ailment has been correctly diagnosed. Besides, drugs are not always very effective, are difficult to administer and do not prevent sick animals from contaminating the water in a pool. Handling of the animals can often be injurious to their health and behaviour. Therefore, strict emphasis on the prevention of disease, rather than its cure, is by far the best way of ensuring a healthy crop.

Almost inevitably the water in the pools will harbour concentrations of bacteria such as Salmonella sp., but providing strict hygiene and other conditions are observed, the low bacterial level will not be harmful. The commonest forms of disease or conditions adverse to healthy development are summarized in the section on common ailments.

It is recommended that where and when possible, animals found freshly dead should be dissected and vital organs such as the brain, heart, lung, liver, spleen, kidney and stomach removed for veterinary research. Bloodslides should also be taken and faeces samples collected. The various specimens must be carefully labelled, frozen as quickly as possible and packed on ice in a vacuum flask for immediate despatch to the nearest veterinary research institute or pathologist. Alternatively, sich animals may be sent alive for research purposes.

It is advantageous for the handler to become thoroughly acquainted with the animal's internal anatomy to be able to distinguish between healthy and diseased organs. This knowledge, coupled with the veterinary report, and the symptoms noted before the animal died, will be helpful for future diagnosis and treatment.

Diet

Fish is a most suitable foodstuff for the bulk feeding of a large captive population. A variety of methods can be employed to harvest fish but seine or gill-netting is the most effective. Whole fish chopped up into suitable pieces, and including the livers and hearts forms a balanced diet which may be supplemented by game meat, if available, to make up bulk. However, meat on its own is a poor diet. Small whole fish are particularly suitable. The crocodiles derive calcium from the bones and scales, plus sufficient roughage to facilitate digestion, while the flesh, liver and heart are rich in nutrients and protein. The main difficulty usually lies in harvesting sufficient fish to meet the crocodile's demands.

Any method of supplementing the diet by the addition of live creatures is recommended. For this purpose, a light left burning in each pen about 15 cm above the water is useful for attracting insects. Various types of insect traps may also be used.

In an area where large quantities of meat are available as a result of game-cropping, the livers and hearts of these animals are particularly valuable. Bones can be ground up and thoroughly mixed with the meat to provide calcium if this meat is to be the sole diet of the crocodiles. Cod liver oil mixed thoroughly with the food is beneficial, particularly before the start of cold weather. This is given three times a week, one teaspoonful mixed in for each 1 lb (450 g) weight of food (see also section on common ailments).

Preparation of food

In preparing food for young crocodiles it is important to reduce it to pieces small enough to be swallowed without difficulty.

Large fish should be cut into elongated rather than square pieces since the bones can cause damage during swallowing. Similarly, whole live fish should not be too large lest the dorsal fin cause damage to the reptile's throat and gullet.

Food should not be prepared near the rearing pens, but should preferably

be done in a gauze-enclosed room (to screen out insects) having a large trestle table or cutting block. The floor of the room should be smoothly plastered and well-drained so that all the equipment including the feeding trays and knives can be scrubbed and hosed down.

Deep-freezing is effective for storing food cut into small portions and frozen quickly. Large fish should be scaled and gutted, their heads and fins removed, and washed before being deep-frozen. The food must be completely thawed out before being used for feeding; generally this occurs satisfactorily while the whole fish are being chopped up if the small pieces are laid out on flat metal trays, rather than put into buckets.

Surplus food should never be re-frozen, since repeated thawing permits the bacteria to multiply rapidly so that eventually the crocodiles are being given bacteria-laden food.

Small whole fish are thoroughly washed to remove slime, and packed onto shallow wire trays for freezing. Before feeding, these should be washed again, then allowed to thaw out.

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Feeding

The most desirable feeding method is to estimate the amount of food that each group will consume at each meal. By establishing a regular pattern, feeding at the same time each day, it is easy to calculate how much is required. The crocodiles become accustomed to a routine and food is then consumed while still fresh. In the hot summer months, they will devour a full meal every 24 hours, but the feeding rate will slacken off towards the onset of the colder months when temperatures start to fluctuate from day to day. It is then wise to start reducing the feeding frequency and food quantities until food is only required every second or third day according to the local climate. Generally, young crocodiles will refuse food when the air or water temperature falls below 60° F (15.6° C). Even in mid-summer sudden cold spells may occur and at these times it is not worthwhile feeding the animals or trying to coax them to eat until the weather returns to normal.

During hot weather conditions it is preferable to feed late in the afternoon or evenings, the main reason being to avoid placing the food on a hot cement surface. The food should preferably be spread out around the edge of the pool under the shaded area so that the animals do not have to climb over one another or compete unnecessarily to reach it. Because of the more severe evening temperature drop in winter it may be necessary to feed much earlier in the afternoon. In cemented pens the area where the food is laid out should be cleaned and scrubbed two hours after feeding time and any uneaten food removed from the water with a hand net; while at the earth pools, the food

should be placed each feeding time at a different spot along the bank. A useful aid to hygiene is to keep a few barbel Clarias sp. in each pool to clean up scraps of uneaten food (see also section on common ailments).

Population in relation to pen size

Twenty-five crocodiles is considered to be the maximum manageable number per unit, since it results in less competition for food which reduces bullying and fighting which in turn means fewer injuries. A low stocking rate also results in a more even average growth rate; but most important is the fact that the health of the crocodiles is of a higher standard than in a more crowded pen. Disease problems are greatly reduced and the symptoms are easier to detect in a small group. If the units are spaced 8 m apart, there is also less danger of an infectious disease spreading to other pens, while the cleaning of pens is facilitated and the disturbance caused when capturing crocodiles to be moved to other units is minimized. Thus, to house 500 crocodiles in groups of 25, 20 separate pens will be required, whilst an additional two pens should be provided to allow for intensive care of the sick, injured and weaker animals.

During the first year, when animals are graded quite frequently, they will often be moved from one pen to another. It is helpful to keep a record of the numbers housed in each pen so that it is possible to keep track of numbers and movements.

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Cause

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Broken limbs. Faulty pen design. Crocodile has either climbed up the side of the enclosure and fallen from a height, or fallen into an empty pool. und konsel omersk je kylling.

Treatment or prevention

Bind broken limbs with waterproof adhesive tape. Isolate animal, avoid handling. Place skirting board 30 cm high round fence to prevent climbing. Before draining a pool, herd animals into the water, so that they remain in the pool when this has been drained.

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Simple cuts, nails worn, toes bleeding or raw. Small cuts in belly skin and thoracic region.

Throat red and inflamed. Animals refuse to feed. Repeated scratching of eyes and ears.

Crocodiles found dead in pen or at bottom of pool.

No sign of injury.

Teeth missing, gums and tooth sockets soft, spongy, coloured brown. Scars around snout and jaws. Tongue normally yellow may be spotted with fungal patches.

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Cause

Sharp object in pen. Faulty pond design. Claws get damaged and skin scraped over rough surface, usually at edge of pool.

Certain algae cause irritation. Poor hygiene, greasy water because pools not cleaned. Check water for acidity, salinity and chlorine content, which may be too high.

Drowning. Below 15° F (7.2° C) animals in the water lose muscle control and balance.

Sunstroke.
Obstructions in gut.

Dissect, check for fish bones in gullet or intestine.

Overcrowding, fighting at feeding times.

Gingivitis infection may result, is spread by swallowing and leads to necrotic enteritis.

Treatment or prevention

Clean caseous matter from wound. Apply merthiclate, isolate the individual. Area around edge of pool should be plastered.

Remove animals to another pool. Allow used pool to bake in the sun after being thoroughly scrubbed out. Change water more frequently and treat pools with copper sulphate.

Check overnight water and air temperatures. (These should be recorded routinely.) Move animals to earth dams where they can burrow for warmth. Ensure adequate shade at all times of the day for the entire population in a pen.

Reduce pool population. Grade crocodiles into size groups regularly. Ensure good portions are small enough to be swallowed readily. Observe strict hygiene in feeding and cleaning of pens. Aerosol merthiclate is a good treatment. Keep animal out of water as much as possible.

Deformities and stunted growth; teeth break off easily or grow crookedly. Spasmodic jerking of limbs, head or tail. Animal trembles when handled.

Hatchlings found dead.

1.00

Animals unwilling to feed. Food taken and then discarded in the water.
General loss of appetite over several days. Animals behave sluggishly.

Belly distended, animal moves sluggishly, finds difficulty in walking.

Abdominal swelling in recently hatched crocodiles.

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Cause

Severe calcium/ vitamin deficiency, or very cramped quarters.

Possibly overcrowding. The young tend to pile up on top of each other for warmth, suffocating those at the bottom. Lack of shade and water. Sudden change or marked drop in temperature.

Food mushy, not palatable. Excessive handling or disturbance. Sudden temperature change. Sudden change of diet.

Insufficient roughage in diet. Sudden change in food. Constipation.

Umbilical abscess. Poor hygiene.

Treatment or prevention

Add calcium or bonemeal to diet plus multivitamin supplements. Feed with live whole fish (unscaled), frogs and crabs. Vitamin E is particularly beneficial.

Divide a section of the hatchery into small compartments to hold fewer animals. Provide a framework of sacking and straw under which hatchlings can crawl for warmth in cold weather.

Reduce feeding rate to every 2nd or 3rd day. Ensure fresh food.

Move animals to earth dams if warmth required. Add Cod Liver Oil to food. Feed extra quantities of liver in winter.

Provide whole small fish, insects, frogs, crabs.
Mix coarse grit and small bone chips with meat.

Often too advanced for treatment. Apply antibiotic powder to open wounds. Treat each hatchling with aerosol antibiotic wound spray.

Paralysis of one or both hind limbs. Eyes closed or partly closed. Tongue puckered and dehydrated. Animal arches spine or raises head and tail vertically in convulsion. Complete paralysis may follow. Diarrhoea evident. Faeces contain blood.

Diarrhoea; diarrhoea with loss of appetite.

Eyes water, exude matter and eventually close. Animal lies with jaws agape, sometimes held vertically. Breathing laboured, may sneeze often. Loss of righting reflex, circular swimming, seizures. Animal 'star gazes'. Pupils enlarged. Animal trembles uncontrollably.

Cause

Either Salmonella sp. or Shigella flexneri bacteria. Usually caused by one or a combination of the following conditions:

Overcrowding, resulting in a high bacterial concentration. Contaminated food, poor hygiene in preparing food and in feeding. Stagnant water, changed infrequently.

Sudden change in diet. Food not fresh. Poor hygiene in preparing food and feeding. Contaminated water. Sudden spell of cold weather.

Respiratory ailment.
Animal chilled by
sudden change or
lowering of temperature, cold draughts.
(Post mortem will
reveal mucus in nasal
passage, lungs inflamed or congested.)
Hypoglycemic shock
(in colder weather).
Steatitis (deficiency
of vitamin E).

Treatment or prevention

This condition is highly infectious. Isolate sick animals immediately to avoid serious epidemic. Clean pools and change water daily. Disinfect drains. Sterilize all feeding utensils. Reject contaminated food. Cease feeding for a week or more. Mix antibiotics (Tetracycline) with food, giving several times the normal dose per lbweight of crocodile. (Replaces that lost or dissolved in pool water during feeding.)

Avoid sudden change in diet. Reject mushy or tainted food. Sterilize knives, boards and food trays routinely. Scrub pools and pens thoroughly. Disinfect drains. Change water more often. Add vitamin E to diet.

Move animals to earth pools where they can burrow for warmth. Feed diet enriched with vitamins E and A and Glucose, well mixed with food. It will be necessary to supply glucose and vitamin E throughout the cold winter months. Avoid handling animals in this condition unnecessarily. Any disturbance causes extreme agitation.

White spots on skin, scales sloughing on tail, skin peals between toes. Fungus or slime seen around the vent and behind limbs where skin may be cracked and stained brown.

Cause

Fungus (Aspergillosis).

Poor hygiene, greasy water, fouled earth dams.

Animals using burrows susceptible if an earth dam is used for a long period.

Treatment or prevention

Scrub pools, removing any grease or fat. Empty pool and allow to bake in the sun. Move animals to a fresh pool. Move animals from earth pools immediately & drain pool for at least a month. Wash animals in tepid water, paint infected areas with merthiclate and keep out of water for some days.

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Distribution of Hatchlings

Cardboard containers made for day-old chickens make excellent hatchling transport boxes if provided with a layer of straw or grass 3.5 cm deep. Each compartment should not contain more than six hatchlings. Any container should allow adequate ventilation and should have a lid. Crocodiles are best transported in a darkened container in which they tend to remain quiet and docile, whereas in an open one, they will continually attempt to climb out and will injure each other by scratching and climbing over one another.

Thus packed they can be transported by vehicle, boat or by air. Bumping should be avoided, as should cold draughts and exposure to direct sunlight for prolonged periods. If air temperatures become particularly hot the crocodiles can periodically be sprinkled with water.

Preference should be given to well-vegetated pools, swamps or marshes of permanent water such as the reedbeds or well-vegetated zones of large lakes and rivers. The crocodiles should be distributed over as wide a range as possible, individuals spaced at intervals of a half kilometre. Attention should be paid to the available potential food supply in the form of aquatic insects, fish fry, etc. Where possible, avoid restocking habitats which already support a high population of adult crocodiles.

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MANAGEMENT OF THE CROCODILE INDUSTRY IN PAPUA AND NEW GUINEA

M.C. Downes Senior Ecologist, Wildlife Laboratory, D.A.S., Konedobu

Introduction

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Plan I

Following the peak year of crocodile killing in 1965-66 there was much agitation to introduce legislation and a management programme to maintain the skin trade. Native people were concerned at the decrease in crocodiles in districts where there was little other money available to the people.

A private member's bill was passed by the House of Assembly outlining in general terms the possible measures thought to be necessary.

In 1968 the Wildlife Ecology Section of the Agriculture Department recommended the particular regulations which were ecologically sound and appropriate to the special situation in the Territory. In brief these included:

- a) System of licences for hunters, skin buyers and exporters through which limitations on the buying and selling of skins could be policed.
- b) Collection of detailed statistics on skin production and export.
- c) Prohibition of sale and export of skins over 20 inches in width, corresponding to crocodiles between 8 and 9 feet long. There was no ban on the killing of crocodiles.

In 1969, a research station was established at Lake Murray in Western Papua, in the midst of a very extensive swamp system, as a base for field research into the ecology of crocodiles.

In 1970, the station was enlarged to accommodate 500 small crocodiles, to find methods and costs of growing crocodiles from 18 inches to the optimum commercial size in captivity.

History of the Industry

In the 1950s European traders and itinerant shooters built up the export of raw skins, first on the Fly River and later in the Sepik. The level of hunting remained much the same for a decade, utilizing mainly the larger saltwater crocodiles in the bigger rivers, lakes and tributaries.

During this time shooting gangs of indigenous hunters were trained in skinning and preservation techniques. With the decline in the saltwater skins there was a greater need to forage into the intensively overgrown swamps for freshwater crocodiles, and the indigenous hunters in their canoes, working either for traders or themselves, gradually took over the hunting operations. Skins were sold to traders or to co-operative skin buying societies formed for the purpose.

By the late 1960s lack of skins had forced most of the Europeans out of the business. A few remained as traders, but at the present time the skin trade is essentially native operated. In the past year (1970) high water levels and low world prices for skins have caused a break-down in the whole trade. Co-operative skin buying societies have little money to buy goods, and are failing; most private traders are already in other businesses and the poorly organized transport of skins causes significant deterioration in the quality and number of skins reaching the coast.

Management of the Industry

The management of the industry hinges on a few special features which should be explained. The most obvious feature is that despite a production worth more than 10 million dollars over the years, there is a startling lack of any concerted action from within the industry to improve or manage its activities. The hunters are mainly primitive villagers who have learned the rudiments of skinning and skin preservation from passing Europeans. They sell in the village to itinerant skin buyers who have been predominantly short-term traders with little interest in the long-term prospects. In turn these sell to exporters who generally are representatives of overseas companies.

Thus the system of licences was vital for co-ordinating the diverse elements of this scattered trade and managing it as an industry. Without statistics the trends in the industry cannot be measured or analysed; without support and co-operation from those engaged in the industry and a two way passage of information, no management programme can succeed.

On the whole, the hunters are competent at securing the crocodile and in the initial preparation of the skin. However, during its passage to the coast the skin can lose much of its value through lack of reasonable attention. Lack of salt, poor handling, no protection from moisture, are a few of the factors causing deterioration. If supplies are short the villagers are soon discouraged from providing adequate numbers or quality of skins.

This is of primary concern for the management of the industry. In fact the current system of marketing between hunter and exporter can only cope with the immense distances, and primitive transport arrangements, when skins are plentiful, prices are high and the profits for middle men are large enough to cover considerable losses.

The second important feature of the New Guinea situation is the impossibility of applying western type game laws to native hunters in the bush, particularly those relating to the killing of bush animals. Traditional game laws of the western world are backed by a reasonable chance of being caught by a game warden; or they appeal to the conscience or understanding of an indoctrinated shooter. Neither of these factors apply in New Guinea at present.

Therefore, special attention was concentrated on control of the market at the level of skin buyer and exporter, and on the economic motive to influence controls of over-killing. It was the economic value of the skins which caused the drastic over-killing of the crocodiles in the larger size range from 1956 - 1966.

As a first step the sale and export of crocodile skins over 20 inches in belly width was prohibited. This corresponds to a crocodile over 8 feet in length. This was the sector of the population most heavily hit by the commercial hunting. It was appropriate that the value of these skins should be removed. Although the size at breeding differs with the species, crocodiles above 8 feet are probably all successful breeders.

Later, consideration will be given to a similar restriction on the sale and export of small skins, although these are probably much more expendable and there is in fact far less incentive for their sale due to very low prices.

A third special feature of the New Guinea situation is the extensive tracts of lowland swamp habitat where crocodiles have only slowly been decimated. There are still many areas difficult of access and, even without management, these will provide a small trickle of income for several years. With management, they could provide a source of income and cultural pride for Papuan and New Guineans for years to come.

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Ban on Large Skins

In the East and West Sepik and Madang Districts, the ban on the sale of skins over 20 inches was opposed and has been removed in those districts. In all other parts of Papua and New Guinea the full regulations apply.

It is obvious throughout the latter areas that there is a reduction in the number of larger crocodiles being killed for commercial purposes. The new regulations have succeeded in this particular objective. Whether this in turn will result in an improved production, it is the aim of the ecological research to determine.

There is no doubt that some large crocodiles are still being killed either for safety, food or illegal sale of skins. But with very few uncontrolled outlets for skins the reduction in the market pressure for breeding-sized crocodiles could bring the hunting pressure back part of the way to that prevailing prior to development of the skin trade.

Crocodile Farms

In order to provide some economic activity in swamp areas with few other commercial products, the people in crocodile areas are being encouraged to experiment with crocodile rearing pens in the villages. It is still possible for the people to catch large numbers of small crocodiles, and if food is cheap and plentiful, their natural interest in handling and rearing these animals could be encouraged.

This is essentially a village level project and is not concerned with breeding nor release into the bush.

Figure 1 (see opposite)

The major areas of alluvial riverine plains, swamps and tidal swamps containing crocodiles in Papua and New Guinea. A few crocodiles inhabit the coast and estuaries of all islands in the Territory.

The Future

There are still sufficient numbers of wild crocodiles to repopulate many districts naturally if the harvest of mature and almost mature animals is kept within ecologically determined limits.

The area of suitable habitat is adequate. Changes in habitat are not yet significant, but mining operations and release of tilapia may yet prove to be seriously detrimental to crocodiles.

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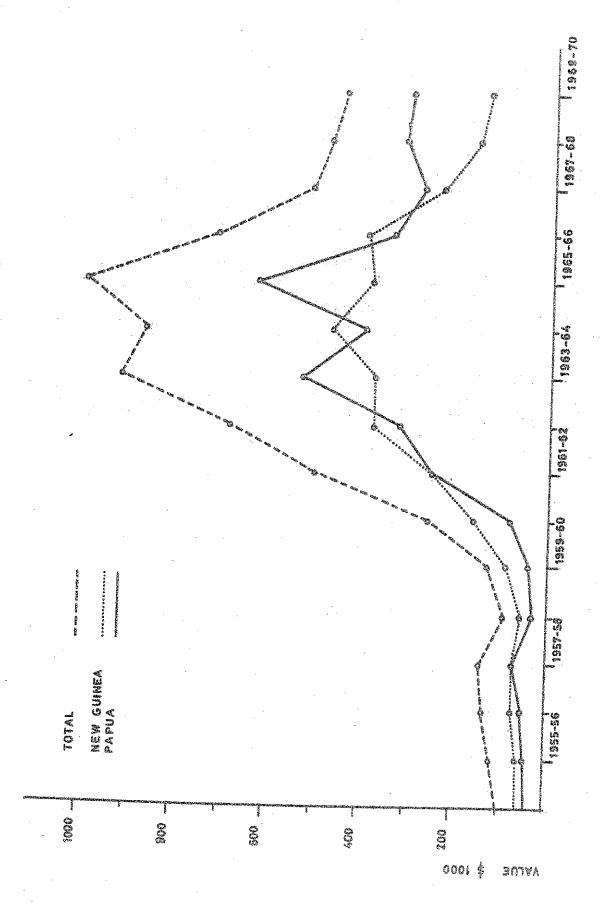
Supplies for the hunter, facilities for preservation and marketing are poorly (ganized and haphazard. No skin quality control nor improvement facilities exist. Unless the industry becomes organized in these matters, it is likely to fizzle out long before the ecological research has provided the basic data on which the conservation of crocodiles and the management of the industry will depend. For this purpose the Department of Agriculture is bringing together representatives of the various aspects of the industry in an effort to achieve the necessary re-organization.

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Annual export value of raw crocodile skins for the years 1954-55 to 1968-70 Figure 7.

MANAGEMENT OF THE AMERICAN ALLIGATOR

Robert H. Chabreck Louisiana Cooperative Wildlife Research Unit, Louisiana State University, Baton Rouge

Introduction

The American alligator Alligator mississippiensis is native to the south-eastern part of the United States. It occurs throughout the states of Louisiana and Florida, and inhabits parts of Texas, Arkansas, Mississippi, Alabama, Georgia, South Carolina and North Carolina.

It was a very important part of the fauna of the southeastern states in the past, and efforts are now being directed toward restoring it to that position. This reptile is looked upon as a renewable resource and has a definite place in the economy of the states involved. It was an important commercial animal in the past, and the tremendous sums spent by the states on management and research, reflect their interest in returning the alligator to this status.

Early settlers and explorers in this region reported the occurrence of large numbers of alligators and the literature contains numerous reports on the abundance of the reptile. Commercial harvesting of alligator skins began in the mid-19th century (Smith, 1893; Audubon, 1931), but sizeable kills of alligators did not begin until late in the 19th century (McIlhenny, 1935). By the end of the 19th century the number of alligators had been greatly reduced; Stevenson (1904) estimated that the alligator population was reduced by 80% between 1880 and 1904. In spite of the heavy kill during this period, alligators were still plentiful in the more remote areas. However, the harvest continued at a rapid rate, and by the middle of the 20th century the American alligator was practically non-existent over most of its original range (Chabreck, 1967a). Concentrations of the animals were found only in areas where rigid protection was provided.

Even though the alligator population continued to decline each year after 1950, no great concern was shown for its welfare until the 1960s. All states within its range enacted protective legislation during this period. Even with closed hunting seasons, illegal hunting continued, and the interstate shipment of skins created new problems. Skins taken illegally could be shipped to states outside the alligator's range, where possession was legal because of the absence of specific protective regulations.

In 1970 the United States Congress put into effect the Endangered Species Act which provided federal penalties for the shipment of alligators or their skins across state lines if taken contrary to federal or state law. This act, coupled with closed hunting seasons by the states, was sufficient to curtail the alligator skin trade, in so far as practical, and subsequently the illegal kill of the animal.

Protection

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Prior to passage of the Endangered Species Act, alligator populations were protected by state hunting regulations and in state and federal refuges and parks. Committee of

Closed seasons

In spite of closed hunting seasons in the individual states, an illegal kill of alligators took place; however, closure by the states was effective in reducing it. The states are well staffed with law enforcement personnel, and areas with properly planned programmes were effective in apprehending law violators. Nevertheless, the high price for alligator skins, and an attitude of indifference by local courts, contributed to the continuance of illegal hunting.

The prosecution of alligator law violators has been handled through local courts, and many courts do not consider these violations to be serious offences; consequently light penalties are given to convicted violators. However, in areas where strong state laws have been rigidly enforced and have received strong backing by local courts, illegal hunting has been significantly reduced. parties, the responsing period the profit of the angle that the Philips are also be

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and their tipe with the contract of the contract of the territory of the state of The American alligator has a high reproductive potential, and past evidence shows that this reptile responds rapidly to protection. In areas with an effective tive protection programme, they were soon a common part of the local fauna.

Several states in which the alligator population has shown sufficient recovery are likely to establish regulations permitting a controlled harvest. With past experience as a guide, the harvest regulations should be designed to protect the breeding population.

Giles and Childs (1949) felt that it was not advisable to harvest adult

females (over 6 feet (1.80 m) long) from mid-June to mid-September, since nesting was in progress at this time. They also felt that by restricting the harvest to bayous, rivers and canals the take of adult females would be minimized, since they commonly established territories in less accessible areas away from such waterways.

Using radio telemetry, Joanen and McNease (1970) found that, during the breeding season, adult females travel more than normally and spend a portion of their time in deeper waterways and lakes. They recommended that the season be opened only after mid-September. The young are hatched after that time, and the females remain in the less accessible areas.

While size limits can effectively restrict the killing of adult females, they also serve to protect adult males. The alligator is polygamous, and an alligator population normally has a surplus of adult males. Consequently, regulations designed to selectively harvest adult males would be advantageous.

In the future, serious enforcement problems could again arise if a state legalized the taking of alligators without requiring that the animals or skins taken be properly tagged. All alligator skins placed in interstate shipment should be properly tagged, so that the source can be correctly ascertained. Unless this is done, law enforcement efforts will be greatly handicapped. Also, if a harvest is operated on a sustained yield basis, tagging will be necessary in order to limit the take and to restrict the take to specific areas.

Refuges

Wildlife refuges have proven to be very beneficial in the management of the American alligator. Sizeable numbers could be found only on federal, state and private refuges during the early 1960s. Protection and suitable habitat were the main factors responsible for the concentrations found in these areas. Although habitat preservation is important, protection from poachers was the primary factor affecting populations.

After the states enacted laws against their killing during the early 1960s, the alligators on wildlife refuges provided a nucleus from which other populations could rebuild. Unlike most reptiles, alligators move about a great deal and journeys of 20 miles (30 km) or more during a season are not uncommon (Chabreck, 1965). Also, refuges have proved to be a valuable source of alligators for restocking purposes.

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Restocking



Whenever an animal population is depleted in an area, one of the first thoughts of most people is that animals from elsewhere should be introduced into the area. Very often this simple solution proves to be effective and the animal flourishes after release. Unfortunately, however, this is not always the case and, as a result, many restocking efforts have met with failure. The factor or factors, which operated to eliminate the original population, operate in the same manner to remove the introduced one.

The restocking of native game animals, such as the White-tailed deer Odocoileus virginianus and wild turkey Meleagris gallopavo, was very successful in re-establishing these species where previous populations had been eliminated through hunting. Where suitable habitat is available and adequate protection is provided, native animal populations should become re-established through restocking.

From 1958 to 1970, about 1700 live alligators were taken from federal and state wildlife refuges for restocking purposes. Most alligators released were from 2 to 5 feet (60 to 150 cm) long, and all were tagged prior to release. In all areas where releases were made, it was agreed that the hunting season for alligators would remain closed for a period of not less than five years.

In 1965, eight areas were surveyed where alligator releases had been made by the landowners in the previous year. Each landowner was contacted as to the status of the animals; only one reported that they had remained in the area where they had been released. Two other landowners reported that the animals were in the area but had moved from the release site. The other five landowners reported that the alligators were seen for a short while and then disappeared. The disappearance was attributed to drought by one landowner, but the other four felt that high water from a hurricane was the cause.

Data on the recapture of tagged alligators revealed that transferring alligators to new locations caused the normal movement rate to increase by three or four times (Chabreck, 1965). Of the 29 alligators recaptured after being transported to a new location, all had moved one mile or more from the release site after the first year. After the third year, eight had moved more than 13 km from the release site and one had moved 30 km. Practically all showed a strong homing instinct, travelling in the general direction of the area from which they were originally captured.

Pen-reared alligators responded similarly to wild alligators, when transferred to new locations and released. Alligators, reared by Louisiana State University for experimental purposes, were released on marshland owned by the Louisiana Wild Life and Fisheries Commission. Of 254 pen-

reared animals released, most dispersed to remote areas and were not seen again; however, two were recaptured 22 months after release (Ted Joanen, unpublished data). Both were females and were 1.64 m long when released. When recaptured, one was 1.84 m long and the other 1.85 m long. Only one was weighed prior to release, and it weighed 19.050 kg; when recaptured, it weighed 21.320 kg. One alligator was recaptured in the same area as released and the other was recaptured 2 miles (3.2 km) northeast of the original release site.

While restocking may be a valuable tool in re-establishing alligators in an area, dispersal of the reptiles from the release site should be anticipated.

Habitat Management

The American alligator is found mostly in areas with fresh to slightly brackish water (Chabreck, 1965). Although they may wander into areas with salinities as high as 20 %, this is temporary, and alligator concentrations usually occur in areas with salinities less than 10%. A habitat management programme should, therefore, provide methods of maintaining low water salinities.

Areas with stabilized water levels offer distinct advantages as alligator habitat. Coastal marsh impoundments were studied in Louisiana, and those permanently flooded with fresh water contained much higher alligator populations than those permanently flooded with brackish water or fresh water which was drained during the spring and summer to enhance plant growth (Chabreck, 1960). In the permanently flooded fresh water impoundments, both deep and shallow water and an abundant supply of food were available.

Joanen and McNease (1970) found that adult females sought out open water areas during the courtship and breeding period. They believed that such areas were an important part of the animals' habitat. Studies in Florida by Hines et al. (1968) revealed that water level fluctuation may be a limiting factor because of nest destruction. They cited examples in the Everglades where altered drainage patterns had resulted in the summer flooding of vast areas; nests constructed earlier in low-lying areas were inundated and the eggs were destroyed.

Flooding from hurricanes often results in nest looses over fairly large areas. Such tropical storms are common summer occurrences in the Gulf of Mexico, and sea water pushed by strong winds may be driven inland for 15 to 20 miles (24 - 32 km).

Alligator Census

For the proper management and wise utilization of any wildlife population, a knowledge of the population is essential. The size and composition of the population, plus the annual production and annual mortality should serve as a basis upon which harvest regulations are formulated. Detailed information should be obtained when deciding the number of animals to be removed from specific areas.

Several methods such as night counts, recapture of tagged animals, call counts, nest counts and total population computations, have been used for the inventory of alligator populations (Chabreck, 1966).

Night counting is widely used because it is easy and provides information on the ratio of the various size classes in the population. Call counts and nest counts provide information on the breeding population. A method of total population computation using a combination of night counts, nest counts and data from kill surveys has been used to determine the total number of alligators in a particular area.



Alligator Farms

An alligator farm is a fenced area containing alligators, and in which the young hatched are a product of the reproduction of the adult animals confined within the area. There is an increasing interest in alligator farming as a business venture (Chabreck, 1967b).

At present there are a number of alligator farms in the southeastern States. However, I have no knowledge of any which are operating at a profit. Several farmers are now producing a sizeable number of young, but the investment and operating costs are high and several years of production will be necessary before a profit will be realized.

Louisiana and Florida have established research stations where studies on alligator farming are being conducted. Problems given special attention at present are stocking rates of breeding pens, pen sizes, pen construction, feeding, egg incubation, rearing of young, and diseases.

Many states now have special regulations governing alligator farms, and wish to encourage legitimate operations. If alligators could be produced under artificial conditions in sufficient numbers, this would perhaps remove some of the pressure on wild populations.

Information and Education

Although hide hunters were primarily responsible for the decline of the American alligator, a large number were killed as vermin or for sport. Fictitious scenes in movies branded the animal as a vicious swamp creature and a menace to society. Such irresponsible actions by this industry did the animal a great injustice and instilled a sense of fear in the minds of the people.

During the past five years, the status of the alligator has been given wide publicity by various news media and, as a result, the public's attitude toward the species has been greatly influenced. The public now looks upon the alligator with concern, and not with horror as they did is the past. This change of attitude clearly demonstrates the effect of a strong publicity programme.

Public support is essential in any wildlife management programme. A vigorous and well planned programme of information and education can be very important in gaining public support. However, care must be taken not to over-sell an idea to the public. Although illegal hunting cannot be tolerated in a well administered programme, the legal harvest of alligators on a sustained yield basis should be a part of most management plans. Therefore, the idea of total protection should be expressed with reservation.

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Paper No 14

NATIONAL PARKS, REFUGES, ETC., AS TOOLS IN CROCODILE CONSERVATION

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I would particularly wish to draw attention to the title of this paper. National parks and other categories of refuge are not, and can never be, any more than 'tools' in crocodile conservation. This paper's meant to stimulate discussion and hence attempt to throw up some of the problems affecting crocodiles in national parks. It concludes that the creation of national parks as an act in isolation will do little to help crocodile conservation.

National parks legislation must tie in with other legislation and both must be enforceable. We all know of excellent legislation on the books which is no more than 'paper' legislation. I envisage national parks for crocodiles as a follow-up to national or state legislation designed to provide a viable future for crocodiles outside of any proposed national parks. The contribution of the parks is to set aside areas of land where the animals, in this case crocodiles, have first right and where humans or human development pressures are controlled or prohibited. National parks must, of course, be patrolled by wardens and the fines for poaching within national parks should be much more severe than outside.

All this brings us to the first problem -- conservation legislation. I would like to quote a few sentences I wrote on crocodiles published in the WWF Year Book for 1969:

"Few Governments have suitable conservation legislation for crocodiles. Where legislation does exist often no attempt is made to enforce it. Furthermore, the remote areas inhabited by crocodiles are usually difficult to police. There is little realisation of the profitability of crocodile skin poaching. It is essential, both for the morale of wardens and as a deterrent to poachers, that fines be realistic. Quite clearly a fine must be greater than the operator can recoup in a week-end's work. I have recommended, for first offences, that the fine should not be less than ten times the value of skins poached. Naturally the poacher must lose the skins and all gear in addition to the fine. Subsequent fines should be much larger. Many poachers will evade capture completely or for long periods of time. Unless fines are severe these will merely be added to operating costs."

This brings us to the role of the fama warden. Wardens have a difficult task under the best of conditions. Crocodile habitat often makes their work extremely tedious and only a highly paid body of men with a sense of dedication, backed up by Government and the Courts, can be expected to perform their duties satisfactorily. It is impossible to enter into any discussion of the role of the fauna warden without a discussion of penalties for poaching.

In my experience many magistrates let crocodile poachers off with only token fines. Hence a situation in which maximum penalties exist but no minimum fines, is unsatisfactory both for conservation and for the fauna wardens. Very few poachers are usually apprehended and those few who are caught and then successfully convicted must consider it very amusing if only a nominal fine is imposed.

For instance, in Western Australia the maximum penalty for illegal possession of freshwater crocodile skins - \$200 per skin -- is rightly very severe. However, this would not be sufficient to deter poachers of saltwater crocodiles. A stiff fine is essential as a deterrent to poaching. Poachers are able to calculate the chance of being apprehended and are at work for large financial gain. Nominal fines of even a few hundred dollars are merely added to operating costs.

In this connection it may be useful to quote the sort of skin values which individuals or two man partnerships brought out of Western Australia in 1969. These figures are based on discussions with crocodile skin buyers who know the individuals concerned and who were offered the skins. The two poachers, operating in Western Australia at the time of my survey, were probably working on their third haul for the season (which lasts for less than six months). The first haul was brought out shortly after the end of the wet season and was valued at between \$15.000 and \$20.000. I am told that this figure, on present prices for freshwater skins, represents about the maximum number which they can move out of the State by road at one time. If it is assumed that only two hauls are taken each year and the most generous allowances are made for vehicle depreciation/operation then they probably clear between \$20,000 and \$30,000 each season. I quoted these figures to the Government of Western Australia because I noted almost complete ignorance of the profitability of operations among those people charged with law enforcement. In my view a magistrate in possession of this information would be unlikely to consider the offence as petty. My recommendation to the Government of Western Australia was that there should be statutory fines for first offenders of not less than ten times the value of the skins confiscated. Naturally skins and all gear must be confiscated.

Such fines may appear severe but then the profits to be made from crocodile shooting are enormous. Potential poachers weigh the potential gain against the chance of being caught and the likely fine if they are caught and convicted. So long as a single weekend's operation will cover the fine, even although they may lose some skins, the odds are heavily stacked in their favour and poaching will continue.

A crocodile shooter, who strongly advocated a fauna reserve for crododiles in the Kimberleys, appealed to me to tell the Government to impose fines ten times greater than normal for any poaching within the reserve. Shooters know the need for strong deterrents. A major problem for conservationists in most places is to have sufficiently large fines imposed for the fines to have real deterrent effect.

Until such time as Government and the Courts face up to their responsibilities and back up the fauna wardens these men will be apathetic towards their work. What is the use of tracking down a poacher, at considerable physical risk to yourself, and going through all the rigmarole of bringing him to Court, if you know he can recoup the fine in a couple of nights?

The role of tha fauna warden both inside and outside national parks is one that requires careful thoughts. In areas where he is backed up by a sound network of honorary wardens he can become a most effective intelligence officer. However, this entails good liaison between him and the honorary wardens and between the Government Department concerned and the professional wardens.

Turning to national parks themselves, I would like to quote from the same WWF article:

"National Parks, designed specifically for crocodiles, are needed for many species. They are essential where it is impossible to police adequately large areas of the habitat, or where a species has become critically endangered. Within these restricted areas it should be possible to keep poaching to a low level which the populations can withstand. National Parks are there to conserve the crocodiles. Human entry - crocodiles being popular with tourists must be controlled and it may be essential to greatly curtail or even exclude this altogether during the egg-incubating season when the females are guarding the eggs. Dr Cott has shown enormous wastage of incubating clutches of eggs in the Nile crocodile population inhabiting Murchison Falls National Park in Uganda, as a result of tourist launches being allowed to approach the rookeries and so frighten the nesting females into the water. Baboons and monitor lizards (Varanus) are then able to dig up and eat the eggs. This would be impossible while the female was at the nest."

So far I have hardly touched on the biological considerations of national parks for crocodiles. I make no apology for making them appear of secondary importance. Of course, they are not, but the political issues are so

complicated, and their solution such essential prerequisites, that I feel that one must give them detailed attention in the first place.

In setting up any national park or refuge the best available expert advice must be sought and the advice must come from someone free from political pressures. This generally means that he must come from outside the State or country concerned, although, of course, he must be thoroughly familiar with the biogeography of the territory. National parks for crocodiles should be sited in ideal areas of habitat from the crocodiles' point of view but preferably also in regions not too remote from the outside world so that the parks can be adequately patrolled by wardens. Size is of major importance, care being necessary to see that the park is large enough to be completely viable. For instance, the national park about to be gazetted in the Kimberley Division of Western Australia for the estuarine crocodile extends along the Ord River and its adjacent swampland for over twenty miles. All the area is prime habitat for C. porosus, yet is easily patrolled by wardens, one end being just over ten miles from Wyndham, an important township where a fulltime fauna warden is stationed. The total area of the proposed park is about 120 square miles. I would reiterate that there are many of us well qualified to select sites for crocodile national parks. The real problems are political and centre round effective protection for an animal living in difficult and often remote terrain which has a high commercial value and is, therefore, subject to intensive poaching effort.



CROCODILIANS AND PUBLIC RELATIONS

James H. Powell, Jr. Plainview, Texas

In his book, The Empty Ark, Philip Kingsland Crowe (1967) remarks that "friends of the crocodiles... have a hard time selling their ideas". Though still a problem, this apathy has shown signs of cracking. Crocodilians have almost, as it were, awakened to find themselves popular. As just one example, in the finale to the current edition of the 'Ice Follies' alligators are depicted in a sympathetic light, while in the lobby, souvenir stands sell, along with colour programmes and skating dolls, some rather realistic rubber replicas of these reptiles. Properly exploited, this current surge of public interest could be a potent weapon. Now, if ever, is the time for crocodilian conservationists to 'sell their ideas'.

The significance of crocodilians might be divided into the practical and the intangible. The latter is, I think, the greater, but let us begin with the practical, for - albeit for worse -- we live in a materialistic world. The question I am most often asked about my work is "What good are crocodilians?". So far, I have always succeeded in holding my temper, avoiding an assault charge, and attempting some sort of answer. And there are answers. True, one might argue that the super-leather which can be tanned from crocodilians' belly-skins, and which has so nearly brought about their downfall, is used to make luxury status-symbols which the world really needs like Custer needed more Indians. Subtler, but more truly important, is the crocodilians' role in ecology. These reptiles feed heavily on predaceous fish which feed in turn on game and food fishes; both sport and commercial fishing decline where crocodilians have been over-hunted. In areas of the tropics and sub-tropics subject to a dry season, their diggings become important water holes for wildlife and even for domestic stock. And in parts of South America where Caiman crocodilus yacare consumes large quantities of snails, many of them cattle disease vectors, livestock epidemics have often followed the caimaneros (Buchinger, 1965). Since ecology is now receiving wide attention, I think much should be made of the ecological importance of crocodilians and the negative impact on the environment their destruction can have.

Much, but not too much, lest we, too, join technocracy and forget that the ultimate value of a crocodile lies not in its belly-hide, nor its value as a tourist attraction, nor even in its ecological significance, but simply in the fact that it is a crocodile: big and ancient and monstrously magnificent.

It is of magnificance and not economic: that chapter 41 of Job sings. We need crocodilians, not because they are useful, but also in respects in which they are not, and it is sometimes necessary to remind ourselves that the useless can also be precious.

For this, I can think of no better memory aid than to emphasize the close relationship between the Crocodilia and the dinosaurs. For above all else, crocodilians are Archosaurs, the last of the 'Ruling Reptiles'. The perennial popularity of the 'Lost World' school of science-fiction illustrates the very deep, even emotional, fascination which the great reptiles of the Mesozoic hold for the public. I sometimes think that if only the human race could see a live dinosaur, it would die happy! How absurd, then, to exterminate the nearest thing to a live dinosaur we shall ever have this side of a time machine! As Edwin H. Colbert (1945) points out, the largest of the living crocodilians are "reptiles of no mean dimensions when compared with some of the large dinosaurs". Certain extinct forms were even bigger. The 45-foot Phobosuchus of the late Cretaceous was as large as Tyrannosaurus rex, while the gavial-like Rhamphosuchus of the Pliocene of India may have reached 60 feet. In other words, the largest carnivorous reptile yet discovered was not a dinosaur, nor even from the Mesozoic, but a gigantic crocodilian from the late Tertiary. The age of great reptiles need not be over unless we make it so, and I think a skilful presentation of the past and present magnificence of the crocodilian line would do much to show the importance of saving these final remnants of the most spectacular land fauna of all time - the great reptile empire of the Jurassic and Cretaceous.

However, for this magnificence to be other than theoretical, it will be necessary for individual crocodilians to be allowed to reach full size — which in reptiles is a very different thing from sexual maturity. Letting a crocodile breed before killing it may preserve the species, but this is not enough for those who want to see the last Archosaurs in all their Mesozoic splendour. A potential for dinosaurian size becomes academic if the animal is 'cropped' at ten feet. As the lumber industry quite correctly points out to the Sierra Club, there are more redwood trees today than ever before; as the Sierra Club quite correctly points out to the lumber industry, most of these are saplings. If crocodilians are to be cropped on a sustained yield basis, then there must also be areas where they are not cropped — some corner of Louisiana where 18-foot alligators can again cruise the bayous, some fragment of Tanzania where 20-foot crocodiles can still give the shores of Victoria Nyanza the aspect of a lost world.

So much for ends; now to means.

In December 1967, Life magazine devoted an entire double issue, entitled "The Wild World", to the values of wilderness and the need for its preservation. I don't know what the chances would be of our getting a major national

magazine to devote an issue to crocodilians; but if we could the potential impact would be immense.

Meanwhile, I think the members of this Group should prepare a book on crocodilians, tentatively entitled Living Crocodilians of the World. I know of no non-technical book devoted exclusively to crocodilians, although they are discussed in many general works on reptiles; and I feel a publication of this sort would fill a real need, and help to focus interest on these animals. The details of the format can be worked out in discussion, but in general I visualize something similar to the late Armand Denis's Cats of the World. There should be a chapter summarizing the history of the Crocodilia from the late Triassic to the present, with emphasis on their Archosaurian affinities. Each of the living forms should be individually discussed, with range maps and as wide a selection of photographs as possible. Conservation will, of course, be stressed, though with care to avoid sermonizing, as the public can quickly sense — and resent — disguised propaganda.

Each member of the Group would contribute chapters on his specialities. In some areas, it may be desirable to seek the collaboration of colleagues outside the Group. As an example, although the American alligator falls within my geographical territory for the purposes of this meeting, there are many students of this species far more competent to write about it than I am. Since no one person would need to write more than a few chapters, it should be possible to get the book into press quickly, before the public interest in crocodilians wanes. Royalties from sales could well go to a special fund for crocodilian conservation projects.

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Editorial note

The proposal made in this Paper was discussed with great interest, but was eventually left in abeyance for the reasons recorded in the Summary of the Meeting (Section 24 of Part 2 of the Minutes) on page 25 above.

Paper No 16

BIOLOGICAL ISOLATION OF SYMPATRIC SPECIES OF SOUTH AMERICAN CROCODILIA

Federico Medem Instituto "Roberto Franco", Villavicencio (Meta)

In Colombia there exist four different species of caimans and two of crocodiles, some of which are geographically isolated by the Eastern Andes which divide the country into two extensive areas: the first comprising the Caribbean and Pacific coastlands and the river systems NE and NW of the Andes; and the second, the Orinoco Plains and the Tropical Rain Forests of the Amazon.

The first is inhabited by the Spectacled caiman Caiman sclerops fuscus and C.s.chiapasius and the American crocodile Crocodylus acutus, while the second forms the habitat of the following crocodilians:

Orinoco crocodile Crocodylus intermedius, confined to the Orinoco Basin.

Black criman Melanosuchus niger, confined to the Amazon Basin.

Spectacled caiman Caiman sclerops or crocodilus, subspecies and several different local populations.

Smooth-fronted caiman Paleosuchus trigonatus.

Dwarf caiman Paleosuchus palpebrosus.

In contrast to the crocodiles and to the Spectacled and Black caimans, both species of Paleosuchus are not gregarious but are found singly or in pairs.

In addition to geographical isolation between the species, there exists also an ecological one; in fact certain species show a preference for a specific habitat or ecological niche, even if they may not be completely bound to it.

A remarkable case of apparent geographical isolation is that the Orinoco crocodile does not enter the Amazon Basin by way of the upper Orinoco, the channel of Casiquiare and the Rio Guainia (upper Rio Negro), but the limit of its distribution is found on the Orinoco, upstream from the village San Fernando de Atabapo situated in Venezuela close to the mouth of Rio Guaviare. This fact is not due to commercial hide-hunting in the 20th century for it was observed by Humboldt in 1799 (Medem, 1958b).

Strong currents and even rapids do not inhibit the migration of crocodiles, as is clearly shown by the rapids of Maipures and Atures, situated below San Fernando, as well as by the narrows on the Rio Guayabero. The Casiquiare, a channel which connects the upper Orinoco with the upper Rio Negro, was probably formed in geologically recent times; this, however, would not account for the absence of the Orinoco crocodile in the Amazon, since it is not found in the upper course of the Orinoco proper either. Actually no further studies about the migration of this species can be made, since it has been almost exterminated by excessive commercial hide-hunting, a deplorable fact which applies also to many other crocodilians.

Thus, all interpretations, since they cannot be based on field data, must remain mere speculations. However, the absence of the Black caiman M. niger in the Orinoco Basin can possibly be explained by ecological factors. This species, which grows to about 5 m in length, prefers quieter waters, such as large bends in big rivers, oxbow-lakes, lagoons and inundated forests. It does not avoid strong currents and was found in large quantities in the Amazon proper (Bates, 1864), but it seems to dislike rivers which contain rocks in abundance and the banks of which are partially formed by rocky walls and stone slabs, as occurs along the Guainía and Casiquiare Rivers.

Besides such ecological factors as quiet or running waters, rocky river beds, or falls and rapids which favour isolation, there must also be taken into account the factor of competition. According to information by professional hide-hunters (Medem, 1962), who worked in the Rio Atrato which flows into the Caribbean Sea in the late twenties and early thirties, there existed at that time well-defined ecological niches for the American crocodile and the Spectacled caiman. While the crocodiles were found almost exclusively in the Atrato River, its larger tributaries and big lakes, the caimans were virtually confined to lagoons, creeks and marshes. This seems to have been due to the fact that the crocodiles fed on caimans; thus the latter were forced to retreat to niches that were inaccessible for larger crocodiles, which gave them protection. In 1954-55, I found almost no crocodiles left but caimans in great abundance in all rivers without a strong current; thus, they had re-invaded the now unoccupied niches.

A definite and almost complete separation of ecological niches exists for the Spectacled caiman Caiman sclerops, the Smooth-fronted caiman Paleosuchus trigonatus and the Dwarf caiman P.palpebrosus, even if all three are to be found together in inundated forests during the rainy season.

Like that of the Black caiman, the ecological niche for the Spectacled caiman consists principally of quiet waters, and, therefore, it is not found near rapids and water-falls but prefers the bends of large rivers, lakes and swamps. By contrast, the Smooth-fronted and Dwarf caimans are both found

in another well-defined niche which consists -- in general terms -- of swift running waters in tropical rain forests. They are present in samll creeks with stony beds, in smaller rivers near rapids and water-falls, and in the vicinity of whirlpools. In large rivers they occupy the same swift-water niche, but also invade quieter waters where they commonly hide below branches overhanging the water or beneath large accumulations of fallen trees along the riverbank. This is particularly true of the Smooth-fronted caiman (Medem, 1958b): the masses of fallen trees cause the formation of whirl-pools and sometimes small rapids and, at the same time, are well protected and rich in fishes.

A fair illustration of the different habitats of the Spectacled and Dwarf caiman is provided by observations made in 1952 in the upper Apaporis River (Medem, 1953a). The Laguna 'Inaná', connected with the river and consisting of three individual lagoons inter-connected by a channel and by a small creek, was studied during 15 days from 1600 to 2200 hrs. The creek was about 500 m long and had a swift current in which the water was lower in temperature than that of the lagoons. The Spectacled caiman occurred in abundance in all three lagoons but the Dwarf caiman, only in the creek itself and in a lagoon near the mouth of the channel, where four to six specimens appeared between 1730 and 1800 hrs each afternoon.

This possibly indicates that water temperature also plays a certain role in the choice of the niche for P. palpebrosus. It was also observed later that the Dwarf caiman shows an extraordinary resistance to low temperature at high altitudes (Medem, 1967). A specimen 74 cm in length was kept in Bogotá (2650 m alt.) without artificial heating at the Institute of Natural Sciences; he escaped and was found in perfect condition after nine days in a small pool, apparently feeding on abundant frog Hyla labialis; the temperature at night was as low as 6° C. On the other hand, a Spectacled caiman, 1.70 m long, died after three days in the Institute where the average temperature fluctuated between 15° and 20° C. The Dwarf caiman later lived in my apartment for more than a year in a shallow water-tank under artificial heating (22° to 27° C), but frequently left the water and remained for several days in a dark corner where the temperature varied between 13° and 19° C; he later lived in the tropics again for another year and, finally, died by accident after entering a salt water tank.

Competition as another possible factor in the choice between the two niches on the Apaporis River should also be mentioned: the Spectacled caiman grows considerably larger than the Dwarf caiman (up to 2.25 m as compared with 1.55 m), is gregarious and feeds frequently on smaller crocodilians. Adult specimens do not enter small creeks, possibly they feel insufficiently protected in rather shallow waters; it has been observed with caimans in their natural habitat and in captivity that, as the individual grows bigger, it prefers deeper water. Thus, the Dwarf caiman seems to be well protected in creeks against predation by Caiman sclerops.

Differences between the ecological niches of the two species of Paleosuchus are still poorly understood, but in general terms the following can be said (Medem, 1967):

- 1) In several river systems or parts of the same river the Smooth-fronted and Dwarf caiman are sympatric.
- 2) In the case of such co-existence one of the two species is always considerably more abundant.
- 3) In other rivers and their smaller tributaries, however, only one of the two species was observed.
- The dorsal side of the Smooth-fronted caiman is covered by a thick growth of dark-green algae which may indicate that it lives in less turbulent and, therefore, also warmer waters than the Dwarf caiman. This is possibly supported by observations in 1969 on the Apaporis River, where several specimens were found living in large stagnant pools in the forest close to a creek.
- 5) In the Dwarf caiman a thick growth of algae was never observed on individuals collected in their natural habitat; however, it was found on specimens kept in captivity in rather stagnant waters after about four months, even if not as abundantly as on the Smooth-fronted caiman.
- or stone slabs in shallow water, situated near rapids and water-falls, always with its head erected and looking upstream. One might wonder if the shiny black colouration of the dorsal side in adult Dwarf caimans may be caused by the effect of prolonged exposure to ultra-violet rays and, at the same time, serves as a protective layer against them.
- 7) Specimens of both species kept in captivity in the Institute "Roberto Franco" in Villavicencio since 1967 and 1968, under rather natural conditions, did not change their specific basking habits.
- 8) A possible competition between the two species certainly exists. As already noted, the Smooth-fronted caiman grows larger than P. palpebrosus and is, moreover, more aggressive, as observed from specimens in captivity. This may explain perhaps the higher degree of abundance of one of the two species in the case of co-existence, and possibly also the apparent total absence of one or other in extensive areas. It must be remembered, however, that the lack of records does not

always mean a species does not occur in the region, but simply that it has not been observed.

Finally, I want to refer to the impact of commercial hide-hunting on two populations of the Spectacled caiman. In 1952, a caiman was collected from the upper Apaporis River, which was later described as a new subspecies Caiman sclerops apaporiensis, distinguished mainly by its narrow and elongated snout from other long-snouted caimans (Medem, 1955). In February 1969, about 74 adult and semi-adult specimens of both sexes were collected on the upper Apaporis in order to carry out studies on certain horseflies (Tabanidae) which frequently feed on their blood. It was found that many individuals did not clearly belong to the subspecies apaporiensis but rather to a local population from the upper Vaupés River, situated east of the Apaporis. Since hide-hunting had already begun in the Vaupés in 1967, and caimans were scarce in 1968, it may be presumed that the population occurring in this river underwent a 'forced migration' and were displaced from their original habitat. Moreover, many of them escaped by way of the Caño Tacunema and other smaller affluents into the Apaporis, since the headwaters of the Tacunema are situated close to Lake "El Dorado" on the upper Vaupés. The habitat on the Apaporis was, however, already occupied by the native population. The presence of numerous immigrants may have had a certain impact on the local C.s. apaporiensis, the former trying to move into already occupied territories and the latter defending these.

As can be deduced from skull measurements of the adult specimens of the 74 caimans mentioned above, it seems that apaporiensis was present in smaller quantities than those individuals belonging to the population from the Vaupes. Hide-hunting begun in the Apaporis in 1969 and increased considerably in 1970-71; according to recent information the caimans are now so shy that they cannot be harpooned any more but have to be shot.

This means that the natural habitat of the Spectacled caiman of the Apaporis has been effectively disturbed and that their habits have greatly changed within a period of only two years, so that further studies on territorial behaviour and competition between the two populations, within their undisturbed habitats, will be difficult to carry out in the future.

The main conclusions can be summarized thus:

South Parketter

- 1) In addition to geographic isolation, all crocodilians are definitely affected by ecological isolation.
- 2) The principal factors for ecological isolation seem to be the presence of swift running, more quiet and even stagnant waters, together with the different temperatures which prevail in each of these niches.

- 3) Competition between different genera, species and even subspecies and local populations has to be taken into account.
- 4) The American crocodile Crocodylus acutus occupies different habitats which range from fresh water streams and brackish water zones to true salt water; thus, it once had an ample geographical distribution along the shores of the Atlantic and Pacific Oceans by means of active migration, and was, moreover, also present on several island groups of the Caribbean Sea in Colombia and the Atlantic Ocean in Venezuela, possibly due to passive migration.
- 5) The Orinoco crocodile <u>Crocodylus intermedius</u> is in contrast to <u>acutus</u> a true fresh water form and confined to the Orinoco Basin. Occasionally, specimens have been reported from Trinidad, W.I., having apparently arrived from the Delta of Amacuro, as the mouth of the Orinoco is called, by passive migration.
- 6) The Black caiman Melanosuchus niger is confined to the Amazon Basin.
- The different subspecies and local populations of the Spectacled caiman Caiman sclerops prefer more quiet waters and, therefore, their ecological niche consists of lakes, ponds, marshes and the bends of large rivers. Active migration, involving movement on foot large distances overland through forests or across plains at night, takes place. Cases of passive migration are also known: in 1961, specimens were collected from Gorgona Island, situated in the Pacific Ocean at a distance of about 15 miles from the mouth of Rio Guapi; according to information, they arrive at the south-western part of that island on floating aquatic vegetation, trees and even on rafts used by the coastal settlers (Medem, 1962).
- In contrast to the above mentioned crocodilians the ecological niches of the Smooth-footed caiman Paleosuchus trigonatus and the Dwarf caiman P. palpebrosus consists of swift running waters in the tropical rain forests. However, on the Orinoco Plains both species are to be found along rivers and creeks of which the shores are covered by gallery forest. They are also present in most of the streams along the eastern slopes of the Eastern Cordillera. This area is known as the piedmont and does not belong properly to the Plains, having been originally covered by rain forests.
- 9) There is a slight but still not fully understood difference in the ecological niches of the two Paleosuchus species.
- 10) The growth of algae on the back of the Smooth-fronted caiman possibly indicates the preference for more quiet and, therefore, warmer waters.

- 11) Such a layer of algae has, however, never been observed in the Spectacled caiman which definitely prefers slow running or stagnant waters. A particular morphological composition of the hide in the Smooth-fronted caiman may possibly favour the thick growth of algae.
- 12) Both species of <u>Paleosuchus</u> move rather quickly on the ground and are, therefore, apt to walk large distances through forests or surmount elevated ridges in order to avoid water-falls.
- 13) The excessive commercial hide-hunting which becomes more pronounced every year has had a strong impact on all crocodilian populations, several of which have now become virtually extinct.

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Paper No 17

THE REPRODUCTION OF THE DWARF CAIMAN PALEOSUCHUS PALPEBROSUS

Federico Medem Instituto "Roberto Franco", Villavicencio (Meta)

No exact data on the reproduction of the Dwarf caiman Paleosuchus palpebrosus existed until recent times. Those given by Medem (1958, 1967) were not based on personal observations but rather on information by Indians or rubber collectors, people possessing great experience with caimans mainly for the reason that they eat them. Donoso-Barros (1966) published the first illustration of a single egg of P. palpebrosus without giving more data. The same author informed me later (in litt. 28 April 1968) that "the egg was found in the cloaca of a female killed by a shot".

The first exact, even if incomplete data were obtained in 1967. On 1 November a nest was detected in the gallery forest, close to a brook, the Caño Pachaquiarito, situated in the region of Peralonzo, a settlement about 50 km SE of Villavicencio in direction to Puerto López, Departamento Meta, Colombia. This nest was investigated on 4 November 1967 and was found to contain 13 eggs. One was later opened and contained an embryo 132 mm in length which was already moving but still not ready to emerge. The remaining eggs hatched between 18 and 29 December 1967, at the Instituto Roberto Franco in Villavicencio (Meta). Since an unpublished paper has been submitted to the Universidad Mayor de San Marcos at Lima, Perú, I will not enter into more details here.

By good fortune a second nest was found on 8 August 1970 by the administrator of a farm who informed me later that it was evidently built the night before. It was investigated on 18 August. It was situated about 6 km W of the settlement of Peralonzo, within a rather dense patch of gallery forest, and constructed on an elevated site, 87 cm above water level, about 3.35 m from the shore of a small brook, known as the Mata Azul. The nesting place was shaded by a tree and scattered underbrush and exposed to sunlight only from 1200 - 1300 hrs daily.

In the case of the 1967 nest, the female was not present. The vicinity of the nest was completely clear of leaves and debris; fresh scratches on the ground indicated the possibility that the female had recently returned either in order to amass more nesting material or to lay the eggs. The nest was constructed of a mixture of rotting and green leaves, grass and twigs, and

earth, with green leaves and grass also used as a lining; the indications were that the nest had been built or re-built recently.

The following measurements and temperatures were taken:

| Measur | ements | Temperatures | |
|--------|---------|---------------------------|-------|
| Height | 490 mm | Environmental | 27° C |
| Width | 1463 mm | In nest (at 50 mm depth) | 28° C |
| Depth | 465 mm | In nest (at 220 mm depth) | 31° C |

All caiman nests, so far studied, have contained an 'egg-chamber', situated in the centre; it consists mainly of earth or clay, mixed with rotten leaves and debris; in older nests the earth becomes hardened almost like 'adobe' (unburnt brick dried in the sun, used to construct the walls of huts) and forms a cover which presumably protects the eggs against desiccation, at the same time keeping the temperature more or less constant.

In the 1970 example, the egg-chamber was situated in the centre, about 560 mm from the outer border of the nest and was 100 mm deep and 158 mm wide. The earth and leaves were still not hard, rather wet and sticky. The top layer of eggs were found at 365 mm below the surface of the nest and the lowest eggs 465 mm down. The top layer (really the ones last laid) had been deposited in a circle, while those of the second and third layer were in irregular, some of them in even almost vertical, positions. All eggs were covered by a sticky mucous substance.

There were 13 brittle-shelled oblong eggs, still white in colour. This indicated that they had been recently laid, since older ones are always covered by a thick black layer formed by debris and the excrement of the abundant ground-termites.

Measurements and weight of the eggs are presented in Table 1.

The eggs, together with some nesting material, were later carried to the Institute in Villavicencio and placed in a Terrarium at a depth of 100 mm. The temperature inside the artificial nest fluctuated between 25° and 31° C, the environmental temperature from 23° to 28° C; heat was maintained at night by an electric light bulb; once a week the nest was moistened; the relative humidity of the air was 90% - 96%. The eggs were numbered and marked 1 - 13, beginning with those of the top layer.

Eggs Nos 1 - 11 hatched normally between 5 November at 1735 hrs and 7 November at 0815 hrs; the individual in egg No 12 was weak, with still a

| Egg | Measurements (mm) | Weights (g) |
|-----|--------------------|-------------|
| 6 | 71.5 x 40.0 | 60. 77 |
| 4 | 70.5 x 41.0 | 69.77 |
| 9 | 69.0 x 41.0 | 69.20 |
| 13 | 68.5 x 41.5 | 67.25 |
| 1 | 68.0 x 40.5 | 68.77 |
| 8 | | 65.00 |
| 7 | 68.0 x 40.5 | 64.20 |
| 10 | 66.0 x 41.0 | 65.50 |
| 12 | 66.0 x 41.0 | 64.82 |
| 11 | 66.0 x 40.5 | 62.50 |
| | 65.0 x 41.0 | 65.00 |
| 2 | 64.5 x 39.5 | 57.80 |
| 3 | 63.0×41.0 | 60.25 |
| 5 | 62.0 x 41.5 | 61.80 |

Table 1. Eggs of Paleosuchus palpebrosus, 18 August 1970.

Note: Size of eggs: max. 71.5 x 40 and 68.5 x 41.5 mm, min. 62 x 41.5 and 64.5 x 39.5 mm; weights: max. 69.77, min. 61.8 g. Weights do not appear to correspond exactly to the size of eggs.

a pronounced vitelline sack but no egg-caruncle; egg No 13 was rotten and possibly not fertile. These two last eggs came from the bottom of the egg-chamber and were, supposedly, laid first.

The hatchlings emit a loud quacking sound inside the shell; as soon as the egg is lifted they break it by means of movements and the small, triangular egg-caruncle and literally jump out to hide immediately among the debris of the artificial nest. In cases where the egg is not touched or lifted, they remain often for hours inside the shell with the tip of snout sticking out and call from time to time. Several eggs were lifted and the same reaction occurred each time; the others were left untouched and most of the hatchlings had emerged from the shells by next day, but in a few cases still remained inside the shells.

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| | | Table 1, | Eggs. of Pale | Eggs of Paleosuchus palpebrosus, | (2 | August 1970. | | |

Size of eggs: max. 71.5 x 40 and 68.5 x 41.5 mm; min. 62 x 41.5 and 64.5 x 39.5 mm. Weights: max. 69.77g; min. 61.8 g. Weights do not appear to correspond exactly to the size of eggs. Note:

The young are covered by a sticky layer of transparent mucous slime which has more or less dried after a day. They remain hidden among the rotting leaves of the nest, but appear from time to time, seeking the artificial light, presumably in order to dry themselves. An individual which was put into shallow water immediately after hatching in 1967 remained weak and died after two days. Evidently recently born P. palpebrosus must stay on the ground until the mucous layer dries completely before entering the water. This they do after approximately two days.

The colours of hatchlings are the same as those of juveniles and adults, with the exception of the cranial table which is yellowish-brown or even yellow in some individuals and later changes to rusty iron colour typical of palpebrosus, in some cases after six or seven months (Medem, 1953). The mandible, somewhat pinkish in adults, is light brown in hatchlings; the dorsum, uniformly black in adults, is covered by black and brown bands in hatchlings and juveniles. It was established for the first time that the incubation period for P. palpebrosus is 90 - 92 days. The hatchlings began to feed on small pieces of chopped up lung on 25 November 1970, i.e. after about 18 - 20 days. They are still doing well (22 February 1971), mostly staying hidden among dry leaves on the ground during daytime and entering the water between 1800 and 1900 hrs.

Corresponding to the numbering of the individual eggs, measurements and weight of hatchlings are set out in Table 2.

Discussion and Conclusions

- 1) Both nests of Paleosuchus palpebrosus were detected at places containing little undergrowth, were close to a tree and exposed to sunlight for several hours a day. This contrasts with the nests of the Spectacled caiman Caiman sclerops (crocodilus), which are situated in the shadow and often among dense underbrush.
- 2) The females were not present close to the nest and were not even found during the following night in the nearby stream, which is also in contrast to the Spectacled and the Black caimans Melanosuchus niger, both of which protect and defend their nests.
- 3) It must be presumed that the female has to return in order to dig out the eggs, since it seems quite impossible that the hatchlings would be able to break the hard cover of the egg-chamber; rainfall, which could soften the earth, is infrequent in November-December. The calling from inside the shell before hatching and the reaction of jumping out as soon as the egg is touched or lifted possibly indicate that the mother aids actively in hatching.

- 4) The hatchlings do not all emerge on the same day; thus the female possibly has to return to the nest several times, stimulated by calls. A similar case is described by Alvarez del Toro (1969) in his excellent paper on Caiman crocodilus ("crocodylus" in the text). On that occasion the male excavated the eggs whilst the female waited in the water, calling for the hatchlings.
- 5) In contrast to the hatchlings of the Spectacled caiman, those of P. palpebrosus remain hidden among the nest debris for about two days. In the natural habitat recently born or larger juveniles were never observed together with their mother but always on their own in groups of two to four individuals in shallow waters of small streams. Hatchlings of Caiman sclerops, on the contrary, have been observed close to or even on the back of their mother who leads and defends them; on two occasions from four to six juveniles, of about 60 cm in length and therefore at least a year old, have been observed during the day in company with the female.
- Since Paleosuchus is not gregarious, in contrast to Caiman and Melanosuchus, it seems possible that the female does not protect her brood but leaves them on their own. This, however, would certainly expose them more to predators, among them adults of the same species; and in fact the claws and scutes of juveniles have been found several times among the stomach contents of both Paleosuchus species.
- 7) Juveniles as well as adults of P. palpebrosus possess a highly protective colouration. The contrast between the yellowish-brown or reddish colour of the head, even more pronounced in the water, and the alternating dark and light bands on the back (shiny black in adults) produces a disruptive effect. Thus, the shape of head and body seems to be 'dissolved' among the different coloured dead leaves, stones and gravel in running water, even at a depth of about 50 cm (Medem, 1958, 1967). The Dwarf caiman generally remains motionless on the bottom and so becomes almost invisible.
- 8) According to Alvarez del Toro (op. cit.) a Spectacled caiman in captivity laid eggs 15 days after the nest had been constructed. In the present case the incubation period was counted from 18 August, the day on which the nest was first studied. It is not certain, however, if eggs were laid shortly before this date or on or before 8 August, the date on which the nest had been detected by my informant, who on my instructions had not touched it. However, to judge from the white colour of the shells and the green leaves found inside the nest on 18 August, it seems more probable that the eggs were then less than ten days old.
- 9) In spite of the fact that exact data on the reproduction of palpebrosus are now available for the first time, there still remain many unsolved

problems. This is also true for all the other caimans. For instance, nothing at all is yet known about the reproduction of the Smooth-fronted caiman Paleosuchus trigonatus; eight specimens kept under nearly natural conditions in the Institute since 1968 have for some unknown reason failed to breed.

10) It has become more and more difficult to study the breeding habits of caimans in their natural habitat. Not only have they become scarce due to excessive hide hunting, but they have also retired progressively to less accessible areas. Moreover, their habits have changed: once rather tame and easy to approach, they are now extremely shy and evasive.

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Paper No 18

PARENTAL CARE IN THE CROCODILIA, WITH SPECIAL REFERENCE TO CROCODYLUS NILOTICUS

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Maternal Care during the Incubation Period

Care at the nest

It was well known to writers of the ancient world that the Nile crocodile mounts guard over the nest. Aristotle (trs. Cresswell, 1862) writing in the fourth century B.C., says: "The river crocodile produces as many as 60 eggs, which are white. She sits upon them for 60 days". According to Pliny (trs. Holland, 1601), "The female layeth eggs as big as geese do, and sitteth ever upon them out of the water". Both writers correctly assumed that parental duties devolved upon the mother; and Solinus (trs. Golding, 1587), who writes "In cherishing up their young, the male and female keep their turns", was mistaken in believing that the male of this species takes any share in these duties.

During the whole three-month incubation period, the female remains in attendance, at or near the nest, though her behaviour differs in accordance with the selected site. When the nest is beneath a tree, surrounded by bush or otherwise shaded, the parent generally lies directly on the nest. with the throat or thorax above the egg-chamber. Nests in more open situations are watched from nearby sites affording shade to the guardian crocodile. In Zululand, Pooley (1969a) found nests that were guarded from as many as three additional sites, where shade ranged from light cover to dense tunnels of vegetation from which only the animal's snout protruded. In places where the rookery is fully exposed to insolation, for example on open sand-bars or beaches, brooding females visit the water periodically during the heat of the day, in accordance with requirements of thermal control, discussed elsewhere (Cott, 1961). Such behaviour has been seen at many breeding grounds on the Victoria Nile. On Central Island, Lake Rudolf, Modha (1967) found that even during the hottest hours when other crocodiles were in the water, females were seen on the rookeries: "At intervals they would go down to the water to cool off but were soon out again and lying near the nest".

In some species the female constructs a special shelter from which she can keep watch over the nest. Writing of the Marsh crocodile C.palustris in Ceylon, Waytialingham (1880) states that the females will sometimes go for a quarter to half a mile to find a suitable sandy site for the nest. "They make, first, a large hole for themselves to live in during the day in order to watch their eggs, and then make a small hole near and sometimes at the very mouth of the previous one, and lay eggs in layers..." He further states that the females will not allow anybody to go near the nests, that they make a fearful roaring and attempt to attack anyone who approaches; and that they keep a strict watch and seldom or never quit the nesting place during the day.

Referring to the Estuarine crocodile C. porosus Loveridge (1946) reports that the mother digs two wallows wider than, but not so long as, her body, close to the nest. These wallows soon fill with water, and in one or the other the crocodile remains during the period of incubation. The female of the American alligator A. mississippiensis similarly constructs a nest-side wallow or den from which the nest can be guarded during the incubation period (Clarke, 1888; Reese, 1907).

Predatory enemies of the eggs.

Egg-eating predators take a heavy toll of unguarded clutches, both by day and night. On the Victoria Nile below Murchison Falls important diurnal predators include the Olive baboon Papio anubis, Marabou stork Leptoptilos crumeniferus and Nile monitor Varanus niloticus; with Black kites Milvus migrans and Palmnut vultures Gypohierax angolensis as camp-followers. At night the work is taken over by the Honey badger Mellivora capensis, White-tailed mongoose Ichneumia albicauda and Spotted hyaena Crocuta crocuta; and less commonly by serval Felis serval (Cott, 1969). Mammalian enemies in other parts of Africa include the Egyptian mongoose Herpestes ichneumon in Egypt (Anderson, 1898); and Water mongoose Atilax paludinosus in South Africa (Stevenson-Hamilton, 1954). In Lake Rudolf (Modha, 1967) Grey heron Ardea cinerea, Goliath heron A. goliath and Sacred ibis Threskiornis aethiopicus are known to prey on the eggs.

Other crocodilian species have different, though often related, nest enemies. Thus, in Colombia, eggs of the Orinoco crocodile C. intermedius are eaten by the Great tegu Tupinambis teguixin and by the South American Black vulture Coragyps atratus (Medem, 1958b). In North Australia, eggs of C. porosus are rooted out and eaten by Wild pigs (Barrett, 1939), just as those of C. niloticus are destroyed in West Africa by warthog Phacochoerus aethiopicus and Bush-pig Potamochoerus porcus (Lavauden, 1934). Again, in Ceylon, the kaberagoya Varanus salvator fills the niche, occupied by V. niloticus in Africa, as an enemy of C. porosus (Deraniyagala, 1939).

Active defence of the clutch

The need for nest-protection is apparent enough. The question remains: do the attendant crocodiles actively defend the clutches when they are threatened by predators? Here it is necessary to distinguish between the behaviour of the reptiles in a natural undisturbed state, on the one hand and, on the other, in areas where they have been harried and hunted and have in consequence learned to fear man. Observations made under the latter conditions — of crocodiles readily deserting the rookery and failing to drive away marauders — may give a false picture of primeval nesting behaviour.

I have on several occasions seen nesting crocodiles make sorties against predators. In 1961, while observing a rookery near the Namsika confluent below Murchison Falls at close range from a grass hide, I witnessed a determined attack: a crocodile that had been lying about 15 yards from, and facing the hide suddenly rose up and ran straight in my direction. When it reached the front of the hide — and as I was preparing to leave — there was a rustle of dead leaves and I caught a glimpse of a Nile monitor in rapid retreat. Crocodiles that have been frightened from their nests by launches passing the grounds have on a number of occasions been seen to return to the rookery to chase away a foraging monitor or baboon. The presence of monitors in crocodiles' stomachs, as recorded elsewhere (Cott, 1961), indicates that these egg thieves are sometimes taken unawares.

Opportunities for observing crocodiles in the pristine state are diminishing, and Modha's (1967) prolonged studies at Central Island, Lake Rudolf, on what is one of the largest remaining undisturbed populations of the Nile crocodile, are therefore of special interest. He found that guardian females never tolerated the presence on the rookeries of predatory birds such as Grey and Goliath heron, Little and Great White egret, Sacred ibis and Fan-tailed raven. Crocodiles were seen chasing these birds away from the nests. On the other hand, innocuous species which regularly frequent the grounds, such as Egyptian goose, Spurwing plover and Water dikkop, were ignored.

The literature contains several accounts of attacks upon man by nesting crocodiles — notably by C. porosus, which is generally believed to be the most dangerous crocodilian. Boake (1870) records that a man who was taking eggs from a nest of this species in Ceylon was repeatedly charged by the guardian crocodile and on being attacked by a second individual at the nest was lucky to escape alive. Shelford (1916) refers to an exciting struggle between a party of hunters and a large female crocodile defending its nest on the Baram River in Borneo. A spirited assault upon himself by C. porosus nesting in a pond near Townsville, Queensland, is described by Robinson (1948): "When I was taking the debris away from the nest she charged at me with open mouth and drove me into the boat. One second later and I would have been in her jaws. She came right out of the water and on to the nest, in clear view of the crowd looking on, and only for my having a long stick to jab

into her mouth I believe she would have come into the boat". From the Llanos Orientales, Colombia, Medem (1958a) reports that a Dwarf caiman Paleosuchus palpebrosus attacked a hunter when he approached the nest containing eggs. Del Toro (1969) gives details of nest defence by both male and female Spectacled caiman Caiman crocodilus breeding in captivity. Both parents remained near the nest, not allowing the keeper or anyone else to approach: and it is interesting to note that in this case it was the male who took the main defensive role.

Comatose state in brooding females

Little is known of the night life of females during the incubation period. The crocodile is nocturnally aquatic: yet females are certainly found occupying the grounds at night. However, no all-night observations on particular individuals have been made, and we do not know to what extend an all-night vigil is maintained. In lake- or river-side rookeries it may happen that brooding females take advantage of the nearby water to feed for short periods. Never-theless, available evidence suggests that females fast throughout the incubation period. Hippel, a professional hunter who had wide experience 25 years ago in the Lower Semliki and in Lake Kioga, and who made a study of the diet of his victims (1946), told me (pers. comm. 1952) he had never found food in stomachs of females taken at the nest. Pitman's (1930) experience was similar on the islands and shores of northern Lake Victoria. Stomachs of brooding females examined by me were likewise empty.

Where cover is dense on a crocodile's breeding ground, and especially where the site is at a distance from the water, the reptiles are very loath to move from their nests. In such places, as incubation proceeds, females are frequently found in a comatose state, unwilling to shift even under the greatest provocation. Pitman (1941) reported from Lake Victoria that shots have been fired close to such crocodiles without evoking the slightest response. In 1957, I examined a rookery in a sand-river below Murchison Falls where some nests were nearly a quarter of a mile from the water. Females in their trance-like state lay motionless, like felled logs: one refused to move even when large stones were thrown on her back; others hissed their remonstrance and shifted a few feet into thicker cover. Similar behaviour has been witnessed by Pooley (1969a) in Zululand. He writes: "One female at St Lucia withstood a barrage of sticks thrown at her, adopting an attitude of defiance during the attempt to chase her off the nest. She lay with head held almost vertical, jaws slightly agape, uttering a deep throaty growl each time a missile landed nearby or actually hit her. Our attempts to dislodge her failed".

It seems almost certain that such crocodiles remain on the rookery until hatching time, without once visiting the water. The physiological condition

of these animals, especially in regard to dehydration, is doubtless comparable to that of torpid crocodiles which, under different circumstances, are known to survive long periods of drought, aestivating in caves and holes dug in dry pans or river-beds. Many observers have recorded such behaviour, as, for example, from Lake Rukwa (Swynnerton and Nicholson, in Cott, 1961); Abyssinia (Emin Pasha, 1890); Somaliland (Eliot, 1905); West Nile Province of Uganda (Kittenberger, 1929); and Mali (Lhote, 1948): the latter states that crocodiles inhabiting a temporary lake near Ménaka spend at least six months of the year aestivating in the mud after the lake has dried up.

Parental Care at Hatching Time

Calling of the young

When ready to hatch the young respond to airborne sounds and to terrestrial vibration by calling. Under artificial conditions — if, for instance, eggs are stored in boxes indoors — the human voice, a tape recording of a hatchling's grunt, the slamming of a door, or the shaking of an egg in the hand, will elicit the vocal response; and when one hatchling calls others may join in the chorus. In the field, a pat of the palm above the nest will stimulate calling, and this reaction provides a ready means of ascertaining the time when hatching is due. Under natural conditions the step of the mother or the sweep of her tail near the nest will doubtless have a similar effect. Hunt (1969) reports a like response in hatchlings of the Spectacled caiman: when he lightly brushed the roof of the nest so as to simulate a mother crawling on the ground, croaking was heard.

Maternal reaction to vocalization

The sounds uttered by the unhatched young stimulate the guardian parent to visit the nest and open it, thus enabling the hatchlings to escape from the shells. Experiments to test the female's response to a tape recording of the cries of unhatched crocodiles were carried out on different rookeries below Murchison Falls in 1968 and 1969. At one site the recorder was concealed in an observation hide. The female that had been floating off shore when the recorded was switched on, soon submerged and promptly surfaced at the bank and climbed up towards the hide without hesitation. On another occasion when the recorder was hidden in grass on a sand-bar close to several nests, three crocodiles swam towards the sound. One of them hauled out and came to rest just short of the playing recorder. Modha (1967) had previously

obtained generally similar results on Lake Rudolf. There is, then, no doubt that the croaking of the unhatched brood does alert, and attract, the nesting mother to her brood.

Exhumation of the eggs

It is well known that the female unearths the eggs at hatching time, but details of the process have rarely been observed. Examination of nests that have been opened by the parent shows that alternative methods may be used, according to the situation of the nest. Normally, and where the brood-chamber is covered with hard, firm earth, the crocodile lies with her snout near the nest, and digs down to the eggs with the fore-limbs. At such nest sites one can often clearly see a platform, wedge-shaped in front where the throat had rested, with a trench on each side made by the fore-limbs, with two heaps of excavated spoil that had been thrown back beside the body, and clawmarks left in the wall of the egg-chamber.

On the other hand, where nests are in loose dry sand, liable to cave-in during excavation, the female scoops out a hollow from above the eggs with her body. Mr L.J. Sim, a crocodile hunter in Tanzania, informed me (pers. comm.; 13 March 1958) that just before sunset on 30 January 1956, he saw a crocodile wriggling and squirming on a bare patch of river-bank. On reaching the spot he heard the young croaking from beneath the shallow rimmed crater thus formed. An African assistant told Sim that he had witnessed the same method of liberation, and he was most insistent that the crocodile's feet were not used. This method is certainly consistent with the appearance of shallow basin-like excavations — some over four yards (3.70 m) in diameter — such as I found in 1952, in two colonial rookeries at the south end of Lake Albert (Cott, 1961). Loveridge (1953) saw similar crater-like excavations on dune-sand near Mtimbuka, Nyasaland; and a photograph by Adamson (1955) illustrates a rookery of nest-craters on Lake Rudolf sands.

At hatching time the young are absolutely dependent upon maternal assistance. The eggs are covered by many inches of earth: in some soils, such as loamy clay which packs hard, a man would have to use a panga (machete) to chip the covering away and there is no question of the hatchlings escaping unaided. Unless the parent is at hand to expose the eggs, the young perish in the shell. In the course of surveys carried out below Murchison Falls in 1968 and 1969, when some 350 nests were under observation, I have no record of hatching except from nests that had first been excavated. Modha (1967) made similar observations on Lake Rudolf: he reports that from not one of 150 nests had any hatchlings managed to escape without maternal help. In cases where the female fails to revisit her croaking young, the subterranean chorus may continue for four or five days. When the release is overdue, the surviving hatchlings burst the shell and emerge almost

explosively immediately the eggs are unearthed, though a moment before the shells were not even chipped.

Release of the hatchlings

The remarkable determination of the female to reach and liberate her young has been observed on a number of occasions. This was first demonstrated experimentally by Voeltzkow (in Gadow, 1901), who had a nest surrounded with a fence. When the mother had returned several times and partly destroyed the fence, this was replaced by a stronger one. The mother then dug a deep ditch beneath the fence in her efforts to reach the nest. In Zululand, Pooley (1969a) isolated a nest with a structure of stout poles 15 cm in diameter, supporting an 8-gauge wire fence, the latter firmly bound with sacking, and the nest roofed over with the same material. At hatching time the parent was found to have smashed her way through the barrier and to have opened the nest. Pooley (1969b) also reports that screens of heavy wire mesh, laid over nests to protect clutches from predators, were easily displaced by the parent at hatching time, some of the screens being found 3 m from the nest in a twisted heap of wire and pegs. Jones (in Cansdale, 1955) records that in the Bonthe District of Sierra Leone a nest was first discovered in a rest house only when the adult came one night to dig it oug.

Whether, in the field, the female assists her offspring in the actual hatching process is not known. But recent observations on crocodilians in captivity suggest that it may be so. Hadley (1969) has described hatchings witnessed by him in Livingstone Game Park in 1966. Having dug her eggs from the ground, the mother C. niloticus "carried three or four of them at a time to the water. They were held very lightly in her mouth and she moved her head from side to side slowly in the water as though washing the eggs. She then applied pressure to the eggs and cracked them. One young crocodile emerged from the egg and swam out of her mouth, and a second dropped to the bottom of the pool and shortly afterwards the young crocodile surfaced. This I witnessed twice".

Even more surprising is the parental care of the Spectacled caiman, witnessed at Tuxtla Gutierrez Zoo and described by del Toro (1969). "After 70 days of incubation...the male started to break the nest, scratching at it with his hind legs and tossing mouthfuls aside... Now something very unexpected happened: the male rolled over several of the eggs, crushing them with his hind legs and tail until the young were free. He also took hold of several eggs with his teeth, one at a time, and crushed the shell carefully till the young could escape". The female stayed in the water while this was happening, called to the young, and took them around the pool "just as a hen takes her chicks around the yard".

In the light of these observations, the comment by Vansleb, who wrote of the Nile crocodile in 1678, is of interest. He states that at hatching time the female "then goes and opens the hole and breaks the shell with its Musle for the young to creep out".

Post Natal Maternal Care

Early reactions of hatchlings

Observations on clutches of eggs excavated at hatching time show that, as soon as they have broken out of the shell, hatchlings tend to make for a nearby object affording shade and shelter. For example, when in 1968 at Murchison Falls I placed a crude dummy of a crocodile a few yards from eggs that were about to hatch, most of the young, on emergence, made their way to the dummy, some immediately, eagerly and at a run, dragging the umbilical cord and still-attached shell behind them, and took cover beneath the lower jaw and along the flanks of their 'mother'. When in 1969 my African assistant lay down motionless close to an excavated clutch, he likewise became a centre of attraction, and soon had many baby crocodiles sheltering under his chin, arms and sides.

Transit from nest to nursery

This behaviour raises the questions: how do the emergent young react to the presence of the female in a wild state; and what part does the female play at this phase of the breeding cycle? Transit from nest to nursery has never been witnessed. Whether the young are conducted, or carried from the one to the other, is not yet certainly known.

Factors favourable for the nursery site are shallow, confined or still water, with for cover plentiful marginal or floating vegetation such as Pistia stratioides, Cyperus articulatus or Leersia hexandra. The site may be in the lee of a fallen tree, in a creek leading from the main body of water, or inland in a shallow mere. Such nurseries can often only be reached by travel of several hundred yards across country, and in a direction away from the waterside rookery.

As to how the journey is accomplished, accounts vary. An early observation is given by Goldsmith (1805) who states that on being set free the brood "quickly avail themselves of their liberty; a part run unguided to the water; another part ascend the back of the female, and are carried thither

in greater safety". Young have been seen on a number of occasions following the parent. Thus, in Madagascar, Voeltzkov (1899) was reliably informed by his taxidermist that he had seen a large crocodile with a tribe of about twenty young ones travelling over a stretch of sand to the water: the parent was in an excited state -- "Das alte Tier sei auffallig wild gewesen". In Basotseland, Livingstone (1865) was told by his companions that the female leads her brood to the water. Mr F. Wilson (pers. comm., 1952) once saw a crocodile with a brood of newly-hatched young sunning on a bank in Lake Victoria: on being disturbed the parent went into the water, followed by her hatchlings.

With other species, the parent-offspring relationship appears to be similar. In his account of a primeval nesting ground of A. mississippiensis on St John River in northern Florida, Bartram (1792) frequently saw the female "leading about the shore her train of young ones". One alligator which passed close to the side of his boat had young following after her: "they kept close together in a column, without straggling off to the one side or the other". Mitchell (in Kellog, 1929) states that the mother on watch calls the hatchlings to her den, which then becomes their home.

There are other records which suggest that the female may sometimes carry her brood to their new quarters. Chadwick (1931), who witnessed a hatching, states that as each young one crawled from the shell "it swarmed upon the mother and clung to her". In Nigeria, Lamborn (1913) was informed by natives that the young crocodiles, immediately after hatching, attach themselves to the dorsal fringe of the tail of the mother and are thus conveyed by her to the water. Mr J.L. Sim (pers. comm., 13 March 1958) was given similar information in Tanzania: "when the young emerge, they mount the back of the mother, and as soon as it is dark, she transports them through shallow water to a patch of reeds". In Lake Rudolf, Modha (1967) was told by natives that the young are carried to the water on the snout, neck and back of the female. A launch coxwain with long experience of the Victoria Nile at Paraa assured me that in 1967, he personally saw a crocodile on land transporting hatchlings on its back. Similar behaviour has been recorded of the American crocodile C. acutus (Ulloa, in Brehm, 1885). Once established in the nursery site, the young - over a period of several weeks -- constantly clamber on to their parent's head and back as she lies half-submerged: this I have witnessed and photographed at close range on many occasions in Uganda.

Predatory enemies of the young

Unguarded hatchlings, like the eggs, are very vulnerable and are preyed upon by many enemies. In the Victoria Nile these are known to include Nile monitor, Great White egret Casmerodius albus, marabou, Saddle-bill stork

Ephippiorhynchus senegalensis, Fish eagle Cuncuma vocifer, Black kite, Ground hornbill Bucorvus leadbeateri and African civet Viverra civetta (Cott, 1968). Records of other species that prey upon hatchlings are: in Egypt (formerly) Egyptian mongoose Herpestes ichneumon and Soft-shelled turtle Trionyx triunguis (Anderson, 1898); on Lake Rudolf, pelican, Sacred ibis, Pied crow Corvus albus and the catfish Clarias lazera (Modha, 1967 and pers. comm.); and in Zululand, Goliath and Grey heron, Little egret Egretta garzetta, Spotted eagle owl Bubo africanus and Rusty-spotted genet Genetta tigrina (Pooley, 1969a).

The situation is closely similar for hatchlings of other crocodilian species. For example, of the American alligator Le Buff (1957) records otters, skunks, raccoons, large wading birds, turtles, snakes and other alligators as enemies. Audubon (1827) referred to White ibis Guara alba (= Eudocimus albus) and Sand-hill crane Grus canadensis as eaters of the young. The American bullfrog Rana catesbiana has the same habit (Wettstein, 1954).

Maternal defence of the young

The female in charge of her brood becomes an aggressive and dangerous animal -- alert and ready to attack any adversary, both by day and night. During two seasons' work on the Victoria Nile I witnessed defensive behaviour on many occasions. The female at one nursery was seen to make a tremendous leap out of the water and over a fallen tree trunk, to drive away a Vervet monkey that had come down to drink. When we approached another nursery that was sited in a creek forty yards (37 m) from the river, the female on more than one occasion came directly for the boat, porpoising and threshing the water with its tail. At a riverside nursery the female unobtrusively submerged, coming up beneath the patrol-launch and striking it a tremendous blow with its head. A fourth female guarding her brood in a ditch was unusually bold: during days of observation this animal made repeated attacks whenever I approached her closely -- hissing, growling, and making lunges, jaws agape, with incredible agility. Seen at point-blank range, such demonstrations are most impressive.

Descourtilz (1809) has an account of C. acutus making a determined attack on two men when surprised at her nest. Dharmakumarsinji (1947) who watched a female Marsh crocodile for a whole day "maintaining a scrupulous guard" over her newly-hatched young, writes: "I saw this crocodile rush out of the water, at least a dozen times, to drive away Black-necked storks Xenorhynchus, herons Ardea and large white egrets Egretta when they ventured to alight near the young which were lying helpless at the water's edge". The crocodile was afterwards shot and confirmed to be a female. Neill (1946) relates that the calling of a juvenile C. novae-guineae that had

been caught by hand at night, provoked the adult into charging savagely in the direction of the sound. Hartwig (1873) described an attack made under somewhat similar circumstances upon Richard Schomburgk by Melanosuchus niger on the Essequibo: "The mother, a creature of prodigeous size, suddenly emerged with an appalling roar, making desperate efforts to reach her wriggling and screeching offspring... Having been wounded with an arrow, she retired for a few moments, and then again returned with redoubled fury, lashing the waters into foam by the repeated strokes of her tail". McIlhenny (1934) relates how a female American alligator had to be restrained from attacking him when he was handling her young at a nest on Avery Island, Louisiana.

Recent observations have shown that the young remain gregariously with the mother for several weeks, learning to feed and fend for themselves while under close maternal supervision. Thus, on 8 April 1969, a female with her brood was found occupying a waterhole in a narrow ditch opposite Paraa. The hatching date of the clutch was not known. Subsequently this nursery was under observation, at first daily, and later at intervals of a few days. The mother crocodile continued to guard her hatchlings until 28 June — the last date she was seen in the nursery. Her duties had extended over at least 81 days — a period about equal to the incubation period. In other words, it appears that for about six months in the year the breeding female is continuously engaged in pre-natal and post-natal care.

Knowledge of the vital part which parental care plays in the successful rearing of offspring has important implications in the field of management and conservation. Disturbance of females on the nesting grounds causes high mortality both through hatching failure and predation. Protection from interference during the successive phases of the reproductive cycle is therefore essential for recruitment and long-term survival of the population (Cott, 1968, 1969).

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THE SENSES OF CROCODILIANS

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Introduction

Crocodilians, like most active predators, are alert animals, well endowed with sensory equipment, and for their zoological station in life seemingly intelligent in the sense of being able to profit from experience. There is, however, little evidence that their brain structure is more advanced than that of reptiles in general (Goldby & Gamble, 1957).

On the behavioural side, it seems likely that the nesting habits and faculty for maternal care of eggs and newly hatched young are more complex in crocodilians than in other reptiles (Cott, 1961, and in these Proceedings). Reliable field accounts indicate that crocodiles show considerable cunning in stalking and capturing their prey; for example, Cott writes that "adult crocodiles often lurk off-shore near game trails and watering places. On sighting an animal that has come down to drink, the reptile quietly submerges, and cruises under water to the precise spot from which it can make its fatal upward rush". When ambushing prey a crocodile may use its tail to give a disabling blow, or to throw the victim into the water. I have heard it suggested that crocodiles may co-operate in driving fish into the shallows where they are easier to catch, but am uncertain how much truth there is in the idea.

It is well known that crocodiles become increasingly wary in places where where they are extensively hunted. This applies even to nocturnal hunting; the reptiles become 'light-shy' and can no longer be easily approached in the water when a light is shone at their eyes. The ability of the animals to learn very quickly to avoid enemies has been demonstrated by Bustard (1968), who studied a wild population of young, previously undisturbed Crocodylus porosus in an isolated lake in eastern Papua. On the first night when the lake was visited it was possible to approach 11 individuals on the surface and to capture five by hand. On the second night a further ten animals were approached but it was only possible to catch one; on a further patrol an hour later eight specimens were seen but only one permitted close approach and none at all were caught. The captured crocodiles were kept until the end of the investigations.

Despite the fact that many species of crocodilians can be kept fairly easily in captivity and are suitable for certain types of experimental study (Coulson & Hernandez, 1964), no laboratory investigations of their learning ability (as, for example, to learn their way through a maze) or powers of memory appear to have been undertaken. There has been a similar lack of study of their sensory physiology, except perhaps where hearing is concerned, and for the most part our knowledge of their senses is based on the inferences which can be drawn from anatomical structure. This is basically similar in all the 23 or so existing species of this very conservative group.

The Nose and Sense of Smell

The nasal passages of crocodilians show various specializations which will be briefly described, although they seem to be primarily associated with the peculiar type of amphibious predatory mode of life which these animals pursue, rather than directly with the sense of smell. The nostril openings, like the eyes, face upwards and are situated on an elevation at the front of the snout (see Fig. 1A). Each nostril has the shape of a crescentic slit, concave posteriorly, and is opened and closed by a pair of muscles which seem unique to crocodilians. Opening of the nostril is effected by the contraction of a muscle with longitudinal fibres attached to the posterior wall of the bony external nasal opening. The nostril is closed mainly by a circular muscle whose fibres surround the longitudinal muscle like a sleeve. When this contracts it squeezes the longitudinal muscle like a piston against the back of the nostril, closing the aperture. These muscles are of unstriped character and are innervated by the sympathetic nervous system (Bellairs & Shute, 1953). Cavernous tissue, consisting of blood vessels which can be dilated and press against the walls of the nasal vestibule, provides an ancillary method of narial closure. This type of mechanism is found also in certain aquatic chelonians and in desert lizards, both of which lack the more specialized crocodilian narial muscles. In terrestrial forms it helps to keep sand out of the nose.

Each external nostril of the crocodile leads downwards into a short tube or vestibule which opens in turn into the main nasal chamber or cavum proprium nasi. This chamber is more complicated than the corresponding part of the nose in other reptiles. Medially, of course, it is bounded by the nasal septum, which separates it from its fellow of the opposite side. On the lateral wall there are no less than three projections or conchae which bulge out into the basal cavity; they are composed of cartilage covered by mucous membrane. From front to back these projections are called the preconcha, concha and postconcha (see Fig. 1B). In other existing reptiles only a single conchal projection is usually present. Membrane-lined recesses or

paranasal sinuses open into the nasal cavity on either side, while the naso-lachrymal duct enters the nose beneath the posterior part of the preconcha (Parsons, 1970).

The long nasopharyngal tube begins beneath and behind the preconcha and passes posteriorly to open near the back of the skull; in its course it is invested by various bones, i.e. the palatines, vomers and pterygoids; the internal narial openings traverse the pterygoids in the bony palate. The significance of this arrangement is, of course, well known. The internal narial opening is guarded by two flaps of soft tissue, one extending downward from the palate and the other projecting upwards behind the tongue (see Fig. 1B). This latter flap can be thrust upwards by muscular action and, together with the palatal flap forms a kind of valve which prevents water from entering the trachea when the jaws are open. Consequently the crocodile is able to drown its prey without taking water into its own respiratory passage.

Only a part of the nasal cavity is lined by sensory epithelium containing olfactory cells with hair-like processes or cilia; the olfactory nerves arise from these cells, become collected into bundles and pass back to the olfactory bulbs of the fore-brain. This olfactory epithelium is restricted in crocodiles to the posterior and dorsal part of the cavum proprium, and to the dorsal parts of some of the paranasal sinuses. The rest of the nose is lined with epithelium of non-sensory, 'respiratory' type.

It is clear that the olfactory organs of crocodilians are by reptilian standards well developed, although the organ of Jacobson (a specialized and more or less separate olfactory organ which is of great importance in lizards and snakes) is absent, disappearing during embryonic life. The importance of smell in the life of crocodilians is suggested by the presence of two pairs of large musk glands, one beneath the throat on either side, the other just within the cloaca. These are said to be particularly active in the breeding season and Gadow (1901) suggests that the sexes are able to find each other by following scent trails in the water. As a rule, however, the nostrils appear to be closed when the snout is submerged and it is possible that the animals cannot smell under water.

It also seems likely that crocodilians rely on their sense of smell to locate prey, and in particular, carrion. They readily assemble, especially at night, to feed on a carcass, even when this is some distance from the water (Cott, 1961). It should not be difficult to devise experiments on captive animals which throw some light on their olfactory powers.

Eyes and Vision

The eyes of crocodilians are relatively large and possess the usual reptilian

complement of accessory structures: upper and lower eyelids (the former being supported by a distinct supraorbital bone), a well developed nictitating membrane with its own musculature, and lachrymal and Harderian glands discharging into the conjunctival space. In many species the eye colour is greenish-yellow, but in Osteolaemus it is a dark, liquid brown. Crocodilians have some degree of binocular vision, the fields of the two eyes overlapping by some 25°.

Although crocodiles are often active in the daytime and bask at certain times of the day, many features of their eyes suggest adaptation to nocturnal habits (Walls, 1942; Underwood, 1970). For example, the scleral ossicles present in most reptiles (other than snakes) and in birds are absent, though they were present in certain extinct crocodilians. These little plates of bone apparently play an important part in the typical sauropsid method of accommodation. They help to maintain the inward convexity of the corneo-scleral junction and hence facilitate the exertion of pressure on the lens by the ciliary body; this results in increasing the lens curvature in a manner appropriate for close vision. It is generally believed that crocodilians have only poor powers of accommodation so that images of objects close to them are necessarily crude. Moreover, their eyes appear to be correctly focussed for distance vision in air, and it is very unlikely that they can accommodate sufficiently well to see with any precision under water, with its different refractive index (Walls, 1942; Tansley, 1965).

The retina is duplex, containing both rods and cones (see Fig. 2). The rods, which are concerned with vision in dim light, are more numerous; as in many other vertebrates the purple visual pigment rhodopsin is found in the rods when the retina has adapted to dark. There is a small region of special sensitivity (area centralis) where the power of optical resolution is probably greater than elsewhere.

Another interesting feature of the retina is the presence of a well developed tapetum layer which is situated outside the neuro-sensory layers of the retina but internal to the choroid, and contains reflecting crystals of guanine. Tapeta of various types are found in many other nocturnal animals and have the function of reflecting light back on to the visual cells (rods and cones) and so increasing their sensitivity. The presence of the tapetum is responsible for the phenomenon of 'eye-shine', as when the eyes of a cat are illuminated at night by the headlights of a car. A crocodile's eyes reflect light in a similar way and the reddish eye-shine elicited often betrays the presence of the animal to the torch of the nocturnal hunter.

The crocodilian pupil has the form of a vertical slit in bright light. In his fascinating book, The Vertebrate Eye, Walls has pointed out that the vertical pupil is not diagnostic of nocturnal habits as such, but is characteristic of nocturnal animals which also like to bask in bright sunshine; here again, the domestic cat affords a parallel. A slit-like pupillary opening can

be closed more effectively than a circular one, and hence gives a better protection for a retina which is basically suited for vision in dim light.

One might imagine from the conditions described that the crocodilian eye only worked efficiently at night, but it is by no means certain that this is so. Many field accounts suggest that the animals can perceive both enemies and prey at a considerable distance. Moreover, they appear to be capable of precise judgement when stalking and seizing prey in the daytime and have been known to spring out of the water to capture leaping fish or flying insects. Their skilful use of such tactics is surprising in view of their reputedly feeble powers of visual accommodation and seems to merit further investigation.

It is thought that crocodilians, unlike many chelonians and lizards, are unable to perceive colours (Walls, 1942). There are no obvious colour differences between the sexes nor are there other indications that colours are important in crocodilian life. Nevertheless, in view of the relatively close relationship between crocodilians and birds, experimental observations, based perhaps on attempts at colour training, would be welcome.

Q. 13.

Ear and Hearing

The outer and middle ears of crocodiles show many interesting features, but it is questionable how far these are significantly related to the function of hearing. The outer ear structure is considerably more elaborate than that in other groups of reptiles (see Fig. 3A). Behind the eye there is a well developed superior ear-flap or 'pinna'; this is covered with scaly skin and conceals a fairly shallow meatal space at the bottom of which lies the tympanic membrane. Beneath and in front of the superior ear-flap is a less well defined inferior flap continuous with the tissues of the 'cheek' region. At the front of the ear region there is a slit-like opening between the upper and lower ear-flaps which is generally dilated when the head is in air and closed when it is submerged. These movements are effected by muscular action and appear to constitute the normal method whereby the tympanic membrane is exposed to sound waves. The whole superior ear-flap can also be moved up and down by a further pair of muscles situated near its posterior edge. Wever and Vernon (1957), in their valuable study of the crocodilian ear, state that the superior ear-flap is often raised slightly when the animal is on land, but pronounced movements of this flap can seldom be observed. They can be elicited, however, if a few drops of water are squirted under the flap on to the tympanic membrane; while an author on big-game hunting (Lake, 1953) has written that if a crocodile is frightened or angry its superior ear-flaps move up and down like hummingbirds' wings, an apt description. One would like further observations on the use of these ear-flaps in nature.

Wever and Vernon suggest that the main function of the ear-flaps is to exclude water from the auditory meatus, but they do not seem to be completely water-tight; there may be some seepage between them when the head is submerged (Shute & Bellairs, 1955). Since the pressure of the water would tend to close the superior flaps more tightly during diving, it is possible that they may to some extent protect the delicate tympanic membrane from pressure; they would certainly guard it from injury against underwater snags. The auditory sensitivity is reduced considerably when the flaps are tightly closed, but hardly reduced at all if they are even slightly opened.

The conducting apparatus of the middle ear is of the usual reptilian type; there is a single ossicle, the stapes or columella, and a cartilaginous extrastapes, part of which is applied to the tympanic membrane. The middle ear cavities and Eustachian tubes are remarkably complicated, for there are both lateral and median tubes; the membranous tympanic system eventually communicates with the pharynx by a common opening in the midline behind the internal nostrils (see Fig. 3B). There is also a connection across the midline from one tympanic cavity to the other, and an extension from each cavity into the lower jaw through a membranous tube called the siphonium.

It would seem that a rather similar though less elaborate type of tympanic pneumatisation occurs in many birds, and it is possible that this feature is part of a common archosaurian heritage. Its function is obscure, though it has been suggested that the branched air passages of crocodilians, with their transverse communication, provide a method of very rapidly equalizing the pressures within the two middle ear cavities (Colbert, 1946; Simonetta, 1956). Wever and Vernon (1957) have shown that sounds are conducted very readily through the transverse passage so that vibrations stimulating one ear stimulate the other 'about equally well'. The benefits, if any, of this crosspassage are not clear, since it would apparently make it more difficult for the animal to localize the source of sound impinging on both ear drums on the basis of differences in their intensity. We know that alligators can localize sounds, however (Beach, 1944), and it is possible that there is some very sensitive mechanism for detecting a minute time-lag between the stimulation of one ear and the other.

The cochlea or lagena of crocodiles is extremely well developed by reptilian standards, and though not coiled like the mammalian cochlea, is bent halfway along its length, as in some birds (Baird, 1970). Wever and Vernon investigated the auditory capacities of caimans by recording electric potentials set up in the ear when this is exposed to sounds of different frequency. It was found that auditory sensitivity was greatest for sounds with a range of 100 to 3000 cycles per second and fell off rapidly for lower and higher tones. These figures are comparable with those obtained by Wever and his colleagues for certain lizards, and it is not really clear whether the Crocodilia have better powers of hearing than lizards such as geckos, which also have a well developed cochlear apparatus.

Evidence for the importance of sounds in daily life is much better documented for crocodilians than for other reptiles. Young Nile crocodiles croak as a signal for maternal help before or after hatching, while older individuals may hiss or growl in threat. During the breeding season male (and at least in some species, female) crocodilians roar; Cott suggests that this may be a mating call rather than a threat directed towards rivals, but it is very possible that it has some territorial significance. The roar or bellow of the American alligator has been described as 'one of the great animal voices of the world' (Carr, 1963). Some people have apparently been able to attract wild crocodilians by making noises of various kinds, which may perhaps simulate sounds made by the animals themselves, or even by potential prey. Joy Adamson (1961, p.38) writes that crocodiles in East Africa invariably respond to a certain man-made sound which can be roughly represented by 'imn, imn, imn'; if there were any crocodiles within 400 yards they would come to the water's edge "as though drawn by a magnet ... If we moved, and our noises then came from a different place ... (the crocodiles) would follow them". The Adamsons learnt the trick from African fishermen on Lake Baringo. In the laboratory, Beach (1944) studied the reactions of captive male alligators to sound and elicited roaring, hissing and aggressive display by blowing a French horn to them at a frequency of 57 Hz. Other noises such as thunder, blasting or gunfire which perhaps resemble the roars made by rivals, may also provoke a vocal response from an alligator.

It therefore seems clear that crocodilians have good hearing, at least by reptilian standards, and that auditory stimuli are important in their social behaviour; such stimuli may well play a part also in predatory and defensive activities.

Other Senses

Taste buds are present in the mucous membrane covering the pterygoid region of the palate (Wettstein, 1931-54).

The scales of the upper and lower jaws are furnished with conspicuous pigmented elevations. These have a rich nerve-supply, and are organs of touch (Laidlaw & Murray, 1933); organs of this type are not uncommon in the integument of reptiles, but seem particularly well developed in the Croco dilia. Perhaps they have some special significance here—for instance the detection of disturbances under water made by fish.

An interesting idea, mentioned during the course of this meeting, is that crocodilians might possess some system of underwater echolocation comparable with that of cetaceans. Could the complexities of the middle ear play any part? I do not know of any evidence for anything of this kind, and Dr R.H. Chabreck has told me that a blind alligator which he kept bumped repeatedly

into obstacles in its tank until it learnt its way around.

Our ignorance about so many aspects of the biology of these impressive and fascinating reptiles is one of the best reasons for ensuring that they do not become extinct.

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Figure 1

- A Diagram showing action of crocodilian narial muscles, the external nostril being shown open on the left, and almost closed on the right. The muscles are shown as if in horizontal section, the arrows indicate direction of pull or thrust.
- B Diagram of head of crocodilian in longitudinal section to show masal cavity (lateral wall) and conchae, internal nostrils and flaps or valves guarding them. (Partly based on Parsons.)

CM, circular muscle (closes nostril). CO, concha. IN, internal nostril. LA, region of larynx. LM, longitudinal muscle (opens nostril). N, (external) nostril. NT, nasopharyngeal tube. OE, oesophagus. PC, preconcha. PO, postconcha. R, recess of nasal cavity (others also present). T, tongue. TR, trachea. V, valvular flaps (upper and lower) guarding airway when mouth is open under water.

Figure 2

Visual cells from retina of American alligator, from near centre of tapetum. A, single cone. B, double cone. C, rod. (After Underwood.)

Figure 3

- A Diagram of external ear structures of a crocodilian. The superior earflap has been turned up to show the tympanic membrane, and its muscles have been dissected out; the action of the levator muscle is not obvious from the figure. Arrows show movements of inferior ear-flap. (After Shute & Bellairs.)
- B Diagram of membranous Eustachian tube system in a crocodilian. The broken lines indicate the position of the skull base. (After diagram in Wettstein.)

DM, depressor muscle of superior ear-flap. E, extension of tympanic cavity which leafs into quadrate and ultimately into lower jaw. IEF, inferior ear-flap. LM, levator muscle of superior ear-flap. LT, lateral Eustachian tube. MT, median tube. O, anterior, slit-like opening of outer ear. OP, common opening of membranous Eustachian tube system into pharynx. SEF, superior ear-flap. T, transverse communication between tympanic cavities. TC, tympanic cavity. TM, tympanic membrane.

