Insights into Crocodile Lifestyles

Crocodiles are agile hunters

Hunting

Although all crocodiles are excellent 'sit and wait' predators, positioning themselves where prey are likely to bump into them in the water or come within striking distance on the bank, they also have remarkable hunting strategies. When their attention is attracted by movement on the bank, or by vibrations such as splashing, they first orient their head toward the disturbance. Normally they slip below the surface and swim toward the disturbance, crossing rivers with remarkable precision even when the water is flowing at a few kilometres per hour, to emerge exactly where the disturbance was when they dived, followed by a rapid attack. If the prey has moved along the bank, the crocodile does not appear to be able to anticipate the lateral movement, and must emerge, reorient and try again. Waterbirds seem adept at moving fast enough along the bank to foil an attack—but not always.

Rushing Down Prey

Confronted with swimming prey in deeper water, such as rats, injured birds or even Water Buffalo, often the crocodile simply rushes it, swimming as fast as possible, head on the surface, twisting and turning as the prey changes direction, to grab it, drag it immediately below the surface, and either drown or crush it. They come back to the surface to eat.

Death Roll

In crocodile-based tourism, much is made of the legendary 'death roll'. This is for good reason. The way in which a crocodile can move its body relative to its head, and the strength of the skeletal elements joining the head and body, affords a remarkable mechanical advantage in overpowering prey larger than itself. The head of a crocodile is around 20 per cent of its body weight, and the jaws are lined with 60 to 70 interlocking teeth. The jaw muscles are designed to lock the jaws together with enormous power, relative to the weak muscles associated with opening the mouth. In the context of attacking large prey, the prime function of the head is to attach itself to the prey and *hang on*. The body and tail are thrown into an explosive, rapid, rolling action, with the torque absorbed at the powerful junction between the crocodile's head and neck. The mechanical advantage is so strong that the prey animal is normally thrown off balance, rolled and disoriented, and thus more easily dragged into deeper water and drowned. If the prey is able to withstand the rolling action, the crocodile unrolls its body, and may thrash backwards, forwards and sideways before rolling again.

So effective is the death roll manoeuvre that a fit 100kg person has great difficulty holding even a 10kg crocodile if it rolls in an attempt to escape.

Food Caches

The idea that crocodiles hide large prey items in caches beneath the water until they rot and can be eaten is accepted as true by many. In reality, little is known about this behaviour. While crocodiles do not need a lot of food to sustain themselves, and have relatively small stomachs, they take prey items well beyond their ability to consume in one sitting. At the time of capture, many prey items are torn apart by thrashing or have bits torn off, which are consumed on the spot. Efforts to hide the remainder seem likely, but this behaviour has not been well documented and may be difficult in habitats with smooth, muddy bottoms. Saltwater Crocodiles placing prey (eg snakes, turtles) on woody snags above the water's surface and taking prey (eg wallabies) onto land and returning for it later have been reported.

The other problem with the notion of caches is that when a carcass bloats, it floats. Whole communities of crocodiles will feed on a floating water buffalo carcass, where some degree of decomposition may soften the thick skin and help in separating the body into pieces. If such carcasses were cached below the surface, they would clearly attract a wide range of other potential prey, such as crabs and fish.

Crocodiles steal food from other predators

Crocodiles moving overland to return to their territory are sometimes caught in bushfires

Homing

It was long ago realised that when Saltwater Crocodiles caught in urban areas were relocated well away in the wild, there was a high probability that they would return to the same location to be caught yet again. In one experiment, 17 Freshwater Crocodiles from a single pool 75m long were caught and relocated 30km upstream to a much larger pool (180m long) containing other Freshwater Crocodiles. Despite hundreds of pools between the capture and release sites, within 14 months, 7 of them were recaptured in the original pool. This suggests considerable homing abilities, but how crocodiles navigate with such precision is unknown. At this point, it is unclear whether relocation stimulates increased movement which by chance results in some crocodiles 'finding' their original capture site, or whether they truly have the ability to set a course for 'home'.

Diving

The underwater activities of crocodiles are poorly understood, partly because many live in muddy waters where visibility is poor and they cannot be seen when they are underwater. There are, of course, spring-fed streams and rivers, and many documentaries include underwater footage of crocodiles swimming along the bottom, more often than not for short distances until they find weed beds or the like in which they can rest and hide. That is, they appear to use such underwater locations for refuge rather than as part of a normal activity cycle. Underwater holes in the bank are also used for refuge. Crocodiles in captivity will pack into such holes if they are available, to the point that their activity enlarges the holes.

Physiologically, crocodiles are well adapted for diving. The heart has unique adaptations for shunting blood away from the lungs during dives. Crocodiles go through extreme bradycardia when they dive, the heart rate slowing from around 30 beats per minute when on the surface to 1–2 beats per minute. Depending on the degree of activity before a dive, body size, and perhaps body temperature and water temperature, a crocodile can stay beneath the surface without breathing for more than one hour. The question as to how deep crocodiles can dive has never been resolved, partly because they rarely live in deep waters. They appear to have no difficulty seeking refuge on the bottom in rivers 10–20m deep.

Masters of Anaerobic Metabolism

Athletes pushing themselves to the limits of endurance in competitive events maximise the energy that can be produced through aerobic pathways (breathing), burning the oxygen they inhale during exertion. They also call on energy derived through anaerobic pathways which do not require oxygen, but which result in lactic acid levels building in the blood, and carbon dioxide in the lungs, creating an 'oxygen debt'. When the exertion is over, deep breathing repays this debt, flushing the excess carbon dioxide from the lungs and bringing blood acidity back to normal levels.

Crocodiles fighting, struggling with prey or trying to escape capture, are capable of an explosive switch from resting to maximum activity, an integral part of their evolutionary make-up. They usually do not need to struggle for long, but they do need maximum power and to be able to call on that power immediately. This is achieved

When capturing very large crocodiles, the first priority is to prevent struggling. Once the crocodile is secure, flushing the excess carbon dioxide from the lungs may be needed to avoid death by acidosis. In most captures involving large crocodiles, immobilising drugs are used at the earliest opportunity to prevent struggling.

The safe capture of large crocodiles is a challenge for authorities

almost exclusively through anaerobic pathways. A 3m-long crocodile can struggle intensely for about 15 minutes, by which time it is completely exhausted and has a very significant oxygen debt, with blood lactic acid levels induced through activity that are higher than recorded in all other animals. Blood pH levels decline to as low as 6.6, the most acidic blood measured in other animals without being lethal. After perhaps 15 minutes recovery time, a crocodile can struggle again, but for less than a minute before exhaustion overcomes it once more. Very large Saltwater Crocodiles, more than 5m long and weighing over 600kg, can struggle for upwards of an hour. By the time they are exhausted, however, serious physiological damage and death can result from blood acidosis.

Fear of People

The effects of long-term hunting on the degree of wariness that crocodiles exhibit are poorly understood. Many Freshwater Crocodiles from the upper reaches of rivers in the Arnhem Land Plateau—where food is scarce and where Aboriginal people rarely venture—although stunted in size, show little fear of people. They respond to any loud noise with an answering growl, approach canoes with aggressive displays, and sometimes engage in a tug-of-war with a fish on a line (without actually being caught on the hook), allowing themselves to be pulled right up onto the bank and even then not letting go of the fish. When crocodiles with such a limited history of contact with people are introduced into captivity, they settle down within days and start eating immediately.

Crocodiles need time to recover after capture

These behaviours are not seen in Freshwater Crocodiles from areas with a long history of Aboriginal occupation or where there was intensive commercial hunting after 1950, so it seems that wariness has been selected for areas with a history of hunting. Hatchlings from eggs collected in different areas, and placed in identical pens, side by side, can demonstrate vastly different behaviours. Hatchlings from some areas are extremely wary and opt to remain hidden if there is any human disturbance, whereas others readily come up and feed together, despite people being present.

Immediately after protection, virtually all adult Saltwater Crocodiles were wary, diving and hiding at the sound of people or boats. No wild females encountered in the 1970s ever defended their nests, which virtually all captive female crocodiles do. Nest defence in the wild started to return in the 1980s and is now reasonably widespread. In a wild crocodile population, being excessively wary is probably not normally conducive to fast growth or normal social interactions. But hunting is lethal, and can obviously drive evolutionary selection at the fastest rate. Hunting of crocodiles by Aboriginal people for food had occurred for at least 30,000 years before the commercial hunting began. Under intense hunting pressure, extreme wariness may have been the only trait dictating survival.

The often-heard comment that Saltwater Crocodiles are 'more cheeky' now than they were in the hunting period is almost certainly true, and may represent a combination of genetic and environmental factors. It is probably much safer to have 'cheeky' crocodiles that can be easily seen than to have wary crocodiles whose presence is unknown because they are hidden.

Nest defence by females has increased since protection

Crocodile Nests, Eggs, Embryos and Babies

Saltwater Crocodile eggs in an opened grass mound

Eggs

Crocodile eggs are white, hard-shelled, smooth and not unlike duck eggs. Alligator and caiman eggs are similar but are rough-surfaced. Unlike birds, which form individual eggs and lay them day after day until the clutch is complete, crocodiles, like turtles, keep the clutch inside their bodies and lay all the eggs at the one time.

Egg size varies quite significantly. Among Australian Saltwater Crocodiles the average egg is 8cm long, 5cm wide and weighs 113g. Hatchling size is dependent on egg size, with the average egg producing a hatchling 28cm long and weighing 71g. Before laying, the average adult female is about 2.7m long and weighs 80kg,. They carry about 6kg of eggs, or about 7.5 per cent of body weight. Australian Freshwater Crocodiles present a different picture. Using the McKinlay River population as an example, the average egg is 6.6cm long, 4.2cm wide and weighs 68g. The average hatchling is 24cm long and weighs 42g. Before egg laying, the average adult female, about 1.7m long and weighing 14.4kg, carries 900g of eggs (13.2 eggs at 68g), or about 6.3 per cent of body weight.

Crocodile Nests

Crocodilians are divided into *hole-nesters*, which include the Australian Freshwater Crocodile, and *mound-nesters*, which include the Saltwater Crocodile. Freshwater Crocodiles nest in the dry season. Adult females with developing eggs begin digging test holes in sandbanks or a variety of other substrates, including gravel and humus, on occasion up to 100m from permanent water. The function of test holes is not well understood, but over a 3–4 week period, typically in August–September, all the females nest in a pulse. Digging a hole around 20cm deep, in a half-hour period, they deposit the typically small clutch of around 10–15 eggs, then cover the hole and retreat to the water.

Saltwater Crocodiles nest in the wet season, over a prolonged 6–7 month period. The females select secluded sites in vegetation 1–3m tall, in swamps, on floating mats of vegetation or on river banks, using feet and teeth to clear a site from 10 up to 50m2. They pile vegetation, litter and often soil, in a mound averaging 53cm high and 1.6m base diameter. Egg-laying occurs almost exclusively at night. Excavating a 30cm diameter chamber in the mound with the hind feet, the female deposits the clutch of an average of 53 eggs. The top egg generally lies around 20cm below the surface. The chamber is covered and the female retreats to the water, typically within 10m.

Mothers on Guard

Crocodiles are the only living reptiles that exhibit a high degree of parental care to hatching stage, although it appears likely that similar behaviour characterised some of the giant reptiles known from the fossil record. Female Saltwater Crocodiles often reside in wallows or water channels next to the nest, from where they can launch attacks on predators. Their goal seems to be to chase the predator away rather than eat it. Nest defence was rarely observed in the wild immediately after the hunting period, but has become much more common. In captivity, virtually all female Saltwater Crocodiles defend their nests; occasionally the males get involved as well.

Among Freshwater Crocodiles, nest defence occurs rarely in the wild, but is common in captivity. Females play a role in excavating the nest at hatching time, and in caring for the hatchlings, as described below. Males are sometimes seen at nests, but it seems to be a matter of self-interest—the nest clearing may be a convenient secluded basking site.

Incubation Period

The driver of the incubation period is nest temperature, which tends to be more stable in the large mound-nests of Saltwater Crocodiles than in the shallow hole-nests of Freshwater Crocodiles. Mean temperatures in wild nests of both species are 31–32°C, and remain reasonably constant in Saltwater Crocodile

A Saltwater Crocodile guarding its nest

A Freshwater Crocodile nest in the sand

nests. It is much more variable in Freshwater Crocodile nests, where it is not unusual for temperatures to be 26–29°C at the time of laying, and to increase to 33–35°C by the time of hatching. For both species, the average incubation period in the field is about 80–85 days, but varies greatly with prevailing ambient temperatures. In captivity, constant temperature gives highly predictable mean incubation times, which at 30°C and 33°C are 90 days and 68 days respectively for Freshwater Crocodiles, and 92 days and 75 days respectively for Saltwater Crocodiles.

Temperature-dependent Sex Determination (TDSD)

In the early 1980s scientists discovered that the sex of a developing crocodile embryo is determined by incubation temperature (TDSD) rather than sex chromosomes. This was a profound finding, in the sense that it explained why sex ratios in the wild were often biased away from 50 per cent each of males and females. Until then it was assumed that such biases resulted from sex-specific patterns of movement or mortality after hatching.

In Saltwater Crocodiles, incubation at constant temperatures of 28–30°C gives 100 per cent females; at 31°C around 50 per cent males and 50 per cent females; at 32°C it gives 100 per cent males; but at 33–34°C swings back to 50–100 per cent females respectively.

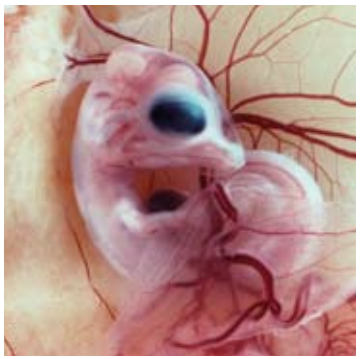
A similar relationship occurs in the Freshwater Crocodile, although it has been found that to get 100 per cent males, the eggs need a fluctuating daily temperature (31–33°C) or an escalating temperature over the incubation period (29–34°C), rather than any constant temperature.

Advantages in TDSD?

The most plausible explanation so far advanced for TDSD in crocodiles is that temperature affects growth rate, and TDSD allocates sex on the basis of growth potential. If the optimum temperature for producing a hatchling with the ability to grow fast is 32°C, and if temperatures higher or lower

than this compromise growth, there are clearly selective advantages in a sex-determining mechanism that allocates maleness to those animals with the potential to grow fast. This implies that femaleness is the default sex, which makes sense in a crocodile context. Females whose growth is compromised will still mature and mate at some time, but males with compromised growth rates are unlikely to be able to compete.

Dynamic Embryos



Sex is determined by temperature when embryos are about 35 days old

Unlike turtles and birds, in which there is limited embryological development in the eggs before laying, crocodile embryos develop considerably before laying. When the eggs are exposed to air in the nest, the embryo may only be small in size (about 5mm long), but already has a distinct head, heart, spinal column and muscle blocks. Dramatic changes occur immediately after laying in the allocation of fluids within different compartments of the egg. Progress in this process is reflected in a chalky white band on the surface of the shell, which starts as a spot (exactly above the embryo), extends as a band, and by two-thirds of incubation extends around the whole egg. Inside the egg, this chalky white band is covered by a remarkable embryological structure, the allantois. This bag-like structure contains the waste products of the growing embryo, and on the outside, pressed against the inner surface of the shell, is covered in blood vessels. The allantois also serves as the embryonic lung, exchanging oxygen and carbon dioxide with the atmosphere through small pores in the shell.

The Big Challenge—Survival to Hatching

Survival rates of crocodile eggs vary from site to site, and at any one site from year to year. The survival challenge for embryos is clearly monumental. The clutch of eggs sits in a mound of vegetation and dirt, or in a hole in the ground, but is otherwise unprotected from the elements. Within each egg is a sensitive and delicate embryo, complete with rations of food in the yolk and

A chalky white band indicates a live embryo

water in the albumen, changing in structure while it develops. A great deal can go wrong.

Among Freshwater Crocodile nests, predation by large varanid lizards (goannas) can reach remarkable proportions, exceeding 95 per cent at some sites. Predation is more extreme in colonial nesting banks than in single nests in isolated banks and sandbars. The general lack of nest defence by wild Freshwater Crocodiles may contribute to the loss. Varanid lizards use a keen sense of smell to locate freshly laid eggs.

Predation on Saltwater Crocodile eggs is slight. Only if the eggs die and rot, and the female leaves the nest site, is there a rise in varanid predation. On the other hand, perhaps 70 per cent of all Saltwater Crocodile nests are lost to inundation. Wet-season deluges, nests sinking through floating rafts of vegetation, nests being flattened by females basking on them in cooler weather, unusual combinations of spring tides and rainfall, all mean that the eggs can become inundated and the embryos drown. The embryos depend on being able to exchange oxygen and carbon dioxide through the pores in the shell, which is impossible if the eggs are submerged. Flooding can also be a problem for Freshwater Crocodiles because the dry-season nesting period results in hatching at the start of the wet season. The sandbanks in which they nest are often deposited by wet-season water flow, and early wet-season heavy rains can result in the sandbanks being severely eroded or washed away, inundating the eggs or washing them out into deep water.

Overheating can be another important cause of mortality. Some nests dug by Freshwater Crocodiles are so shallow that they overheat. The vegetation that Saltwater Crocodiles use to construct their nest mounds is sometimes energy rich, generating high levels of heat from decomposition. If nest temperatures reach 36–37°C, the embryos of both species can be killed, and those not killed typically display severe spinal abnormalities.

Additionally, a Freshwater Crocodile excavating a nest in a colonial nesting bank can inadvertently dig up another nest, exposing the eggs to the sun. This rarely if ever happens with Saltwater Crocodiles, which are solitary nesters, keeping out of sight of other nesting females.

The Hatching Process

One of the last steps before hatching is that the remainder of the yolk, the food supply for the developing embryo, is drawn inside the abdomen. This ensures that the new hatchling will have food sufficient to sustain itself for a few weeks.

Flooding is the main cause of Saltwater Crocodile egg mortality

The hatchling's movements within the egg weaken the connection between the shell membrane and shell, and it slices through the membrane with a tooth-like structure on the tip of its snout—the *caruncle*. Once through the membrane, the caruncle breaks the shell itself and the tip of the snout protrudes through the shell. The hatchling may remain in the egg with snout protruding for a few days, or burst out almost immediately. Regardless, it begins to make the hatchling call—a sort of *gnrrr, gnrrr*—within the nest. Mechanical or vocal disturbance at this time can stimulate other eggs to hatch. But here one of the great examples of parental care in reptiles is exhibited. The female crocodiles respond to the call by digging into the nest and releasing the hatchlings, often carrying them down to the water in their mouths.

Crocodile Crèches

Saltwater Crocodile hatchlings move immediately from the nest to the nearest water, or are carried there by the female, often forming a crèche, or pod, in the wallow next to the nest. The female remains with the hatchlings, and they may crawl up on her head and body to bask in the sun. Some instances have been described in which hatchlings escape the nest without parental assistance, and simply disperse over time—but this is the exception.

The *gnrrr, gnrrr* hatchling sound plays a role in keeping the crèche together. A whole crèche on a riverbank can appear on the opposite

Saltwater Crocodiles hatching

bank, at least 50m away, indicating that the hatchlings can move as a unit. In captivity, a *pecking order* is established in a hatchling group within the first few weeks of life, and this may also occur in the wild. Individuals begin to drift away within two months, but they may join crèches further downstream, perhaps older or younger, and thus come under the guardianship of unrelated adult females. Freshwater Crocodiles exhibit similar behaviour in the wild. Once in the water, especially in smaller billabongs, crèches coalesce and appear to come under the guard of a single adult female which, if her own nest was taken by predators, may be unrelated to any of them.

Surviving to One Year of Age

Hatchling Saltwater and Freshwater Crocodiles, averaging 71g and 42g respectively, are almost perfect replicas of their parents. They are small and rather defenceless, and are assumed to be taken by a wide range of predators, particularly fish and birds, but possibly also varanid lizards, snakes, crabs and freshwater turtles, depending where they live. In one study in tidal rivers, about 50 per cent of hatchlings were lost within the first year, with no evidence indicating that larger crocodiles were the main predator, despite becoming significant predators later. This is not the case with all crocodilians. Stainless-steel webbing tags used for marking hatchling American Alligators have been recovered from the stomachs of older, larger alligators.

With Saltwater Crocodiles at least, survival to one year of age is related to the number of hatchlings recruited to the population—*density-dependent survival*. In years with a lot of hatchlings, a relatively high proportion is lost relative to years in which there are few hatchlings. It is an important phenomenon allowing a depleted population to recover more rapidly.

Among Freshwater Crocodiles, mortality in the McKinlay River area may exceed 95 per cent in the first year, mostly in the first two months after hatching. Freshwater turtles, particularly the Northern Long-necked Turtle (*Chelodina rugosa*) and Snapping Turtle (*Elseya dentata*) are known to eat hatchlings. Cannibalism may well be implicated in this high rate of hatchling mortality but has not been demonstrated.

Surviving from 1 Year to 5 Years

Given that it takes 12 to 16 years for crocodiles to reach maturity in the wild, juvenile survival rates ultimately dictate the rates at which depleted populations recover. In one large population of Freshwater Crocodiles, studied over a number of years, annual juvenile rates of survival appeared to average around 85 per cent. The figure could obviously vary greatly among different populations. The reasons for the 15 per cent annual loss are largely unknown, although cannibalism and injuries inflicted through social interaction are probably involved.

Among Saltwater Crocodiles in tidal rivers, the proportion of 1-year-olds retained to the next year is highly correlated with the number of larger crocodiles in the same river, and cannibalism is the most likely reason. Juveniles 1–2 years old have been recovered from the stomachs of large Saltwater Crocodiles, and sightings of large crocodiles eating smaller ones are increasing. From 3 to 5 years, the numbers of juveniles retained in a river from year to year appear to depend on social 'exclusion': the rivers seem to have the capacity to sustain only a set number. Crocodiles in this age group are often involved in dispersal around the coast. However, the numbers arriving at outside sites do not equal the numbers dispersing out of rivers. so mortality appears high.

Overall, in a recovered crocodile population it seems unlikely that more than 1 per cent of hatchlings would survive to maturity. In a depleted population, without cannibalism and social exclusion by larger crocodiles, survival to maturity is likely to be much higher.

Body weight increases exponentially with length, such that a 10cm increase in length in a 1m-long crocodile (body weight 2.5kg) adds 0.9kg, but a 10cm increase in length in a 5m-long crocodile (body weight 500kg) adds 34kg.

Crocodiles Outside and Inside

The heavily muscled tail propels the crocodile along

General Proportions

Approximately half the length of a crocodile is the tail. The main organ of propulsion, the tail is packed with muscle and serves as a site for fat storage in times of plenty. The length of the head, measured from the tip of the snout to the back of the cranial platform on the upper surface, is about one-seventh of the total length of a crocodile from the tip of the snout to the tip of the tail. In a 2m crocodile in good condition, the body weight is subdivided approximately into head 10 per cent, trunk 63 per cent and tail 27 per cent. Body weights per unit length are about 20 per cent heavier in captivity than they are in the wild, reflecting more food and larger fat deposits.

The Scaly Skin and Armour

The skin of a crocodile comprises multiple layers of fibrous material that affords it great strength, both in the living animal and as cured leather. Crocodiles are often caught with small harpoon heads that utilise straightened fishing hooks with a 5mm wide barb to penetrate the skin. The full weight of the crocodile can be drawn to the surface without the skin tearing at the site of the small barb, demonstrating the immense strength of the skin. The surface of the skin is covered in scales, each with a thick protective outer layer made of keratin. The scales tend to be squarish on the belly and sides of the tail, and roundish on the sides of the body and the top surfaces.

Bone strengthens the dorsal armour

In both Australian species, each belly scale has a clearly defined pit which is highly innervated and appears to be a sensory organ. The pits, called 'integumentary sense organs' (ISO), are not present on the scales of alligators or caimans. Along the back of the body, the scales contain *osteoderms*, large, thick, sculptured bone plates, comprising a bony armour that makes it very difficult for the teeth of other crocodiles to penetrate during conflict. Along the tail, the upper scales are converted to vertical fins that greatly increase the surface area. The dorsal scales all contain a rich blood supply, and during basking play an important role in trapping heat subsequently distributed to the inner body by the circulating blood.

In the Freshwater Crocodile and most other crocodilians, small osteoderms form in many of the belly scales, giving them increased strength, but this does not occur in the Saltwater Crocodile. The number and configuration of scales is set permanently in the embryo and varies from species to species. Saltwater Crocodiles have the highest number of rows of scales on the belly skin of the trunk, from neck to the cloaca (27 to 37; most have 30 to 33), whereas Freshwater Crocodiles have one of the lowest numbers of rows (22 to 24).

The Eyes

Crocodiles' eyes are adapted to their nocturnal and semi-aquatic lifestyle. They have upper and lower scaly eyelids and a more or less transparent inner third eyelid or *nictitating membrane* that moves horizontally across the eyeball.

Underwater, the surface of the eyeball is protected by the nictitating membrane, through which light can penetrate, although the degree to which visual acuity is affected is unknown. The retina has rods and cones, which indicate that crocodiles can discern colour. In some captive environments, different coloured buckets are used to signal to the crocodiles whether they are going to be fed or their pen cleaned, and they alter their behaviour accordingly.

The retina, as in many nocturnal animals, contains a layer of crystals that magnify the available light at night and in low light levels. Because of this *reflective tapetum*, crocodile eyes shine red in the beam of a torch at night.

Like the pupil of a cat, the crocodile pupil closes to a vertical slit during the day, restricting the amount of light that enters the eyeball, and opens completely at night to maximise the amount of light entering.

The Ears

The ears are located at the back of the head on either side of the square *cranial platform*. The external ears are long flaps of tissue that fit tightly against the skull to form a watertight seal—they do not protrude like the ears of mammals. The inner ear is associated with a canal that runs from one side of the skull to the other, with the eardrums on either side. This arrangement is thought to be related to the crocodile's very acute ability to pinpoint the source of vibrations in the water.

Crocodile communications tend to be low-frequency growls in the air or low-frequency vibrations generated in the water by slapping the head on the surface or vibrating their sides. In cases such as the Northern Territory's famous 'Sweetheart', a large old crocodile which started attacking fishing boats at night, and in particular the propellers of outboard engines, it is thought that the animal's eyesight may have failed with age but its ability to receive and interpret vibrations had not. The low-frequency vibrations from a propeller are very similar to the low-frequency growls of a rival male, and so they are attacked. In the Sweetheart example, the crocodile tipped the boat over but remained fighting the boat while ignoring the fishermen who swam in the dark to the nearest shore...in record-breaking time!

The Nose

The nose of a crocodile is essentially the elongated snout. The crocodile breathes through two nostrils on the elevated dome on the snout tip, the *nasal disc*, when the mouth is underwater or closed. Within the snout are channels that take air through to the inside of the throat, next to the opening of the windpipe or *trachea*. Within the snout also are enlarged *olfactory chambers* where smell is sensed. The crocodile brain lies encased in bone beneath the square *cranial platform* on the back of the head, but the parts of the brain associated with smell, the *olfactory lobes*, are relatively large, and extend well out in front of the brain next to the olfactory chambers. Crocodiles essentially have a *smell brain*, their sense of smell playing a major role in their daily lives. It enables them to locate the carcasses of dead animals at some distance from the water, and to locate prey such as flying foxes, which have a strong odour. Their sense of smell may also play a significant role in chemical communications, a subject yet to be investigated in any depth.

Nostrils on a raised crocodile

Prying open a crocodile's jaws is no easy task

The Head, Skull and Jaws

The head of a crocodile is dominated by the flat upper surface, designed to present a low profile at the water surface, and the greatly elongated snout, which is in essence an elongated palate with the top jaws along its length. The lower jaws are equally elongate, are hinged at the back of the cranium but extend further posteriorly. The large, powerful muscles that operate the jaws are attached to the rear of each lower jaw at one end of the muscle bundle, and at the other end to the top of the skull through two openings, the *mandibular fenestra*. Opening the jaws can be achieved passively by tilting up the skull and upper jaw—the lower jaw falls open. Rubber bands are normally used to keep the jaws closed. In contrast, from the open position the jaws can close with enormous power, 2000–3000 pounds per square inch in larger crocodiles (9–10kN). Trying to open the jaws of even a small crocodile against the muscles keeping them closed requires significant effort with sturdy levers.

The Teeth

Saltwater Crocodiles on average have 64 teeth, 34 in the upper jaws and 30 in the lower jaws. Freshwater Crocodiles have more teeth, usually 70, with 38 in the upper jaws and 32 in the lower. A crocodile's teeth are all in place at the time of hatching, whereas an alligator's teeth

Only 25–35 per cent of the full tooth length is exposed. The long shaft of each tooth, firmly embedded in the jawbone, provides the strength needed to penetrate struggling prey or other crocodiles. With the exception of the oldest crocodiles, the teeth are replaceable throughout life.

Freshwater Crocodile teeth

develop afterward. The teeth of Freshwater Crocodiles are finer and sharper than those of Saltwater Crocodiles. In both species, the teeth in the front of the jaw tend to be long, conical and interlocked, designed for penetrating prey and holding them. The teeth in the very front of the lower jaw often penetrate completely through two holes in the upper jaw, creating an extremely strong locking mechanism. The back teeth are short, blunt and robust, designed for crushing prey once it has been caught and moved backwards in the mouth by rapid opening and closing of the jaws with the snout held high.

Legs and Feet

The legs of a crocodile are small relative to the mass of body trunk and tail, which reflects in part that they are often simply tucked in beside the body when the animal is swimming with undulations of tail and body. The back legs are much more strongly constructed than the front legs and are able to lift and support the body mass when the crocodile high walks. The hind feet have four digits, three of which have large claws, with strong skin webbing between the digits. The claws are not very sharp and are used mainly to dig into the substrate when climbing up a bank: not for tearing food apart or grasping prey. The hind feet are often used as underwater paddles to maintain postures in the water. The front feet are reasonably small—about 40 per cent of the mass of the hind feet. They have five digits, with slight webbing between them, and three of the digits have small claws.

The hind feet have four digits

Growth and Growth Rings

Growth rates in wild crocodiles, in terms of increase in length per year, decline with increasing length of the crocodile. Yet because the animal's volume increases greatly as length increases, growth rates in body weight increase with increasing size. A small increase in length in a large crocodile involves a substantial increase in mass.

Within any one year, most growth occurs in the summer, particularly in the wet season when productivity of surrounding lands and waterways is maximised. Indeed, during the dry season many Freshwater Crocodiles not only do not grow, but lose a great deal of weight, relying on fat reserves built up during the previous wet season. These variations in growth rate, as in trees, means that growth rings are often laid down in the bones, with periods of rapid growth separated by arrest lines. Growth rings can be used in younger animals, which are still growing relatively fast, to give an indication of age. In older crocodiles whose growth has essentially ceased the rings are no longer of value for ageing. The use of growth rings can be confounded by remodelling of the inside of long bones as age progresses, or by the withdrawal of bone calcium for the formation of eggshells in females.

The heart has four chambers

Mouth, Throat, Lungs and Heart

Crocodiles have a fleshy, yellowish tongue, that is fixed along its length between the lower jaws and acts more like a pad than a manipulating organ. Modified salivary glands in the tongue pump out excess salt, allowing survival in sea water. At the back of the throat, a large fleshy pad, the *palatal valve*, seals the throat, allowing the crocodile to hold a prey item in its open mouth underwater without water rushing down its throat. Just inside the palatal valve is the opening of the trachea, which leads to two lungs in the anterior of the chest.

The heart is not positioned anteriorly between the front legs, but rather more posteriorly, between the anterior lobes of the liver. The crocodilian heart is unique. It is four-chambered like the heart of birds and mammals, and thus considerably advanced over the three-chambered heart of other reptiles. A remarkable connecting hole between the major blood vessels, the *foramen of Panizza*, allows the oxygenated and deoxygenated bloodstreams to mix when it is advantageous for this to occur, as in diving and perhaps when fully active using anaerobic metabolism.

The Digestive Machinery

The oesophagus, leading from the mouth to the stomach, is thin-walled and very distensible — if a food parcel can fit between the crocodile's jaws, it seems to be able to pass all the way into the stomach. The stomach is a bag-like structure with the entry and exit points next to each other at one end, and usually contains a number of deliberately ingested stones. Food items stay in the highly acidic stomach until they are completely ground up and/or broken down by enzymes. Digestion is remarkably efficient: in the wild more than 80 per cent of what is eaten appears to be utilised, whereas in captivity food conversion rates of 25 per cent are commonly reported.

What's in a Stomach?

The stomachs of many animals, including virtually all other reptiles, are designed to deal with a steady flow of food—but not the stomach of the crocodile, which is designed to extract the maximum amount of nutrition from food that is not necessarily available daily. In the wild, crocodile feeding is opportunistic, often a 'boom and bust' affair. Crocodiles can live for months without feeding.

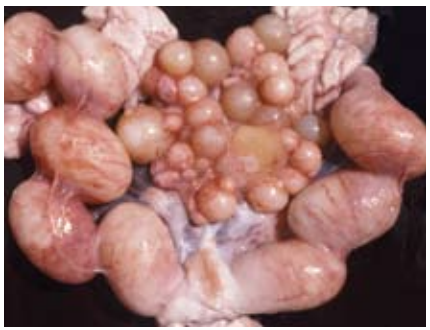
The bag-like stomach retains any heavy and non-digestible items, and can sometimes be full of surprises. Miniature acrylic-covered electronic sensing devices fed to a crocodile can be recovered from its stomach, intact, after more than a year. In crocodiles feeding on wild pigs, the pigs' bristles may form into hairballs up to 10cm in diameter, which are occasionally regurgitated. A very common finding is bullets and lead shot, not an indication that the crocodiles themselves have been shot, but rather that they have eaten animals such as wild pig and waterfowl that have been shot and lost by hunters.

Stomes from the stomach of a 5.1m crocodile

Crocodiles that have attacked people have been identified through items such as rings and watches found in the stomach. In India, where funeral ceremonies often involve placing bodies in or near rivers, crocodile stomach contents can reveal an array of metal bracelets and ornaments.

On Disease and Immunity

In the wild it is unusual to find animals that are obviously sick or diseased, and sick wild crocodiles are even less likely to be found. They have an ability to recover from horrific injuries, such as amputations, without the sterile conditions and medical treatment humans need. They can apparently eat rotting carcasses without being compromised. Part of the reason for this is now known — they have a powerful antibiotic substance in their blood that seems particularly well suited to fighting infections.



Ovaries and eggs in the oviducts

The Hidden Reproductive Organs

Other than large size, and the largest crocodiles are always males, there are no clear external indicators of whether a crocodile is male or female, for all reproductive apparatus is hidden within the body cavity. Ovaries and testes are located where they form in the embryo, next to the kidneys.

The male's penis is hidden inside the butt of the tail, and is everted through the cloaca. During mating, the penis delivers sperm into the oviducts, where it is present to fertilise the ova when ovulation occurs.

Abnormalities

When one considers the highly controlled environment in which mammalian embryos develop, and that even minor irregularities can cause birth defects, it is truly remarkable that almost identical embryological processes occur in crocodile eggs with relatively few birth defects. Because their food supply is the yolk, rather than provided through a placenta, crocodile embryos are not as vulnerable to factors linked to the mother's diet and behaviour.

Twins

Crocodile eggs sometimes produce twins. Twins can come from the odd very large egg, when two yolks and two developing embryos have been pressed

A light-coloured Freshwater Crocodile hatchling

close together in the oviduct, and packed into a single egg membrane and shell. They sometimes hatch and survive, but often one twin is large relative to the other, having dominated the space inside the egg, and both are smaller than the average hatchling from the average egg in the clutch. These 'double-yolked' eggs appear to be chance events, and more than one in a clutch is rare. On other occasions twins come from normal-sized eggs with a single yolk, and within one clutch there may be a number of eggs containing sets of twins. A wild saltwater crocodile nest, located in a similar part of the same swamp over a few years, and assumed to belong to the same female, had multiple eggs containing twins each year.. Where they share the same yolk, which must be internalised prior to hatching, they do not survive.

Albino Crocodiles

True albino crocodiles, with no pigment and pink eyes, have rarely if ever been found, despite hundreds of thousands of wild and captive-laid eggs having been incubated and hatched. The occasional albino American Alligator has been found, with some coming from the same female's nest year after year. However, the eyes are dark rather than being colourless or pink. Around 1 in 5000 hatchling Saltwater and Freshwater Crocodiles are considered *leucistic*, in which the background colouration and pattern lack intense pigment, so that they are extremely light in colour relative to the average animal. These animals can survive in the wild and grow to large sizes, but they are encountered only rarely.

Light and Dark Crocodiles

In the muddy tidal rivers of northern Australia that cross floodplains and contain high levels of suspended silt, resident juvenile Saltwater Crocodiles tend to be light and yellowish in colour. In clear freshwater areas, they tend to a darker olive colour. Similarly with Freshwater Crocodiles: in muddy turbid waters they tend to be light in colour and very dark in clear, spring-fed waters, fully exposed to the sun. There seems to be a degree of colour adaptation to the amount of light to which they are exposed in their natural environments.

Injuries

Most injuries to wild crocodiles are inflicted by other crocodiles, either during conflict between rivals or attempts at cannibalism. Almost all Saltwater Crocodiles over 3m have scars or injuries. There are often puncture marks on the snout or injuries to the tip of the snout. Severe amputations of the snout are fatal, as are major breaks in the rear of the lower jaws, which can no longer function. Perhaps the most common injuries are mutilation of the feet and partial or complete amputations of fore and hind limbs. Many larger males and some adult females have one or more limbs amputated, but there is no real evidence to indicate how many crocodiles die from such injuries. Injuries to the tail tip are common. In Freshwater Crocodiles, the tail is a common site of rake marks obtained in the process of establishing dominance and territory. Both deep and shallow puncture marks and rake marks caused by the teeth are common on the belly surfaces of larger crocodiles. Sometimes hatchlings are injured by the sharp teeth of females when they are carried to the water after hatching.

Parasites

A number of obvious parasites are associated with crocodiles. The most commonly detected is a nematode worm of the genus *Paratrichasoma*. The worms traverse the belly skin under the thick keratin layer. Leeches attached in the armpits or groin are common on Freshwater Crocodiles in some habitats, but tend to be small (1–2cm long). Barnacles are found on some Saltwater Crocodiles that live extensively in the sea, but rarely.

All crocodiles can become infected with an aberrant genus of worm-like arthropods, pentastomids, which migrate to the lungs and can be fatal. Microscopic flukes, emanating from freshwater snails, can also cause chronic illness and death.

Parasite trails in the skin