

Crocodylian Behaviour: Implications for Management

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THE behaviour of crocodylians is an enigma. To the casual observer, these giant lethargic reptiles are the antithesis of "behaving" animals because, most of the time they exhibit little or no activity. Indeed, it is their immobility in the face of persistent attempts to arouse them which usually impresses onlookers. To those who live or work around alligators and crocodiles, the most notable behaviours are likely to be the sudden movements associated with feeding and with threat. Displays of strength and cunning are infrequent and unpredictable — but when seen, they are unforgettable and a constant reminder that there is more to the behaviour of crocodylians than meets the eye. In fact, crocodylian behaviour is subtle, complex and quite unlike that of other reptiles.

The overview of crocodylian behaviour provided in this chapter is intended as something of a primer on behaviour, especially on the aspects relevant to conservation and management. It is generalised, with examples from various species drawn from the literature and from my own observations and experiences. A behavioural inventory is introduced with a discussion that focuses on the characteristics of crocodylian behaviours, their significance and their species-specificity. What follows is thus a working outline of important behaviours to consider, together with suggestions for future study.

The concluding section deals with how behaviour and management are interrelated. The behaviour of crocodylians affects many aspects of their management, yet management in turn, influences how crocodylians behave and, consequently, how they grow and reproduce. In nature, habitat requirements vary with species, age, sex and season. Crocodylians respond not only to specific abiotic and biotic resources, but also to conspecifics and on occasion to other species. Information about a species' social behaviour and organization is a prerequisite for successful stocking, relocating and harvesting programmes.

GENERAL FEATURES OF CROCODYLIAN BEHAVIOUR

Understanding Behaviour

Why is the behaviour of alligators and crocodiles difficult to comprehend? Why does it seem strange and unfamiliar? Three key features need to be considered: slow response times; amphibious/aquatic settings; and, complex social systems.

Firstly, the time-scale of crocodylian responses is different — they occur in slow motion by mammalian or avian standards. Like other reptiles, crocodylians are ectotherms, which means they depend on external heat sources to regulate their body temperature. In addition, bouts of activity are powered by anaerobic metabolism, after which a long recovery period is needed. A crocodile reacts quickly and with power, but it tires easily. As a consequence, behaviour tends to be sporadic, and behavioural events are separated not by seconds, but by minutes and hours. Crocodylians are also very large reptiles. Large body size limits behaviour even further by lengthening the recovery time needed between bouts of activity. In fact, very large reptiles are effectively incapable of any sustained work; once fatigued, a large crocodylian takes many hours or even days to recover (Coulson 1984).

Inactivity itself is an important behavioural response. Just because an animal is not moving does not mean it is not vigilant. Inactivity is a poor indicator of arousal states in reptiles (Regal 1978). The ability to remain motionless yet alert, has obvious advantages to an opportunistic predator that relies on being stealthy and cryptic. Large crocodylians have very low metabolic rates which, in turn, reduce food requirements. They are able to survive for months without feeding if body temperatures remain low. Thermoregulation entails hours of heat-seeking or avoidance during most days, contributing further to an overall impression of inactivity.

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High body temperatures facilitate digestion and serve other specific functions, but many behaviours are remarkably independent of body temperature (see Lang Chapter 30). Anyone who has witnessed a crocodile's rapid lunge or sudden jawclap early in the morning can readily appreciate this. Social interactions that include chases, vocalizations and territorial displays typically occur at dawn, when body temperatures are lowest and before basking is initiated. Crocodilians forage between dusk and dawn when ambient daily temperatures are low, and they are often inactive during the middle of the day when ambient temperatures are highest. This pattern is the reverse of more familiar reptiles, like diurnal lizards, which are active during the warmest parts of day and are inactive at night.

The second unusual feature of crocodilian behaviour relates to their amphibious mode of existence — they live in both aquatic and terrestrial habitats. Crocodilians adhere to changing daily schedules of movement between land and water. They are neither exclusively nocturnal nor diurnal, but move on land and in the water as well, and between land and water, throughout the day and night. Their eyes, for example, are adapted for nocturnal vision, but the pupil can close to a vertical slit for acute vision in bright sunlight. A membrane covering the eye provides protection for seeing underwater. Many behaviours occur at the water surface or underwater, in an environment which is alien to us. Prolonged diving is facilitated by anaerobic metabolism, and large individuals often remain submerged for hours. Furthermore, some of these behaviours are subtle because life in the water involves the use of senses which are not familiar to us. Crocodilians sense aquatic sounds and vibrations, possess touch receptors on the body surface to feel movements in the water, and have a very keen sense of smell (Bellairs 1971; Johnsen and Wellington 1982). But our knowledge is still sketchy about exactly how these sensory systems work and about what crocodilians perceive, especially in the water.



Fig. 1. A male *Crocodylus palustris* carrying newly hatched young down to water (after Lang *et al.* 1986).

Perhaps the most unusual and interesting feature of crocodilian behaviour is that they are surprisingly social. They display an array of social behaviours that clearly distinguish the group from the other reptiles (Garrick *et al.* 1978). Parental care at hatching (Fig. 1) and post-hatching care of the young are probably universal traits within crocodilians. Social communication is elaborate by reptilian standards and utilizes a diverse signalling system. The variety and complexity of social behaviour have only recently been appreciated. It is now apparent that sophisticated social interactions and relationships probably occur among all age classes from hatchlings to adults. These interactions, in turn, directly affect the ways in which an individual avoids predators, feeds, grows, and reproduces.

Importance of Behaviour

Learning anything about crocodilians in the wild presents formidable challenges. However, behaviour is especially difficult to study in nature because most individuals are shy, elusive and are disturbed easily. An eminent biologist cautioned that the first lesson about watching crocodiles through the keyhole, is that they seem to be watching back (Gans 1976). Consequently, much of what we know is based on observations of captive animals in semi-natural situations. Even under these conditions, not all behaviours are obvious and it is easy to underestimate just how important some behaviours really are.

For example, consider the question: "How are crocodilians able to survive and grow in saltwater habitats?" To answer this, scientific attention focused initially on a search for physiological mechanisms that would allow salt-loaded animals to concentrate and excrete excess salt. Secretory lingual glands that performed this function were located on the tongues of some salt-tolerant species, for example *Crocodylus porosus*, the saltwater crocodile (Taplin and Grigg 1981). But other species, for example *Crocodylus acutus*, the American crocodile, also live in the sea yet appear to lack equivalent physiological specializations; they depend primarily on behavioural adjustments to regulate salt and water balance (Mazzotti 1983; Mazzotti and Dunson 1984; Taplin 1984). Water balance is maintained by feeding, by periodic movements out of salt water onto land and by drinking brackish or fresh water. Behavioural osmoregulation is particularly important for young crocodiles which have much higher rates of water loss than larger individuals. In this case, the behavioural responses for coping with life at high salinities are critical to survival.

Behaviour is also more than just a veneer of environmentally and socially appropriate responses to different stimuli. It affects brain chemistry and hormone levels that, in turn, control and regulate



Capture and handling techniques employed by researchers and managers vary with the species, habitat, size of crocodile being caught, and the degree of "wariness" the exhibit.



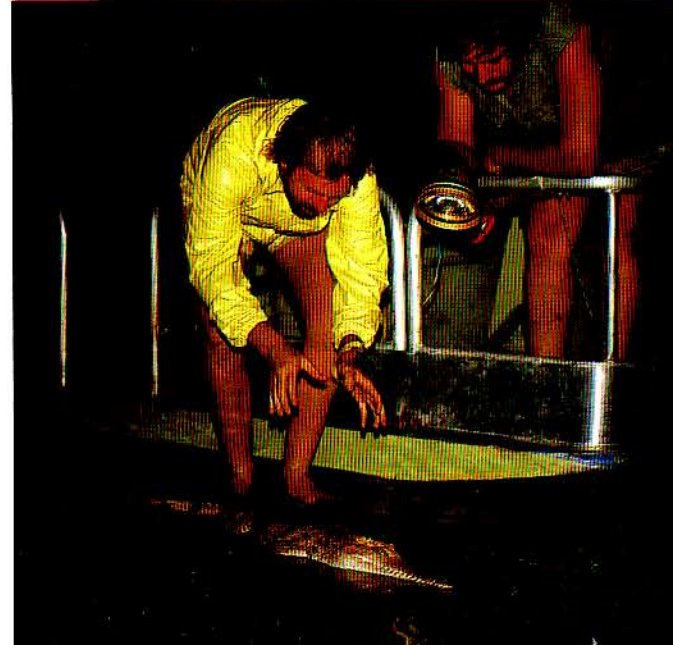
Above Left: If delays between capture and release are inevitable, crocodilians can be tethered at the water's edge. This saltwater crocodile (*Crocodylus porosus*) is being retrieved from a tether rope. (Grahame Webb)

Above Right: This saltwater crocodile (*Crocodylus porosus*) shows placement of tether ropes usually used in northern Australia. (Grahame Webb)

Centre Left: After capture, crocodilians such as this saltwater crocodile (*Crocodylus porosus*), are often transported while restrained on a stretcher. (Vicki Whelan)

Below Left: Gallamine triethiodide ("flaxedil"), has proved a cheap and efficient immobilizing agent for crocodilians. Here it is injected into a 1.1 metre long Australian freshwater crocodile (*Crocodylus johnstoni*). (Grahame Webb)

Below Right: Hand-catching is perhaps the most common method for catching crocodilians less than 1.1 metres long. With Australian freshwater crocodiles (*Crocodylus johnstoni*), the noise of an airboat often makes them "freeze". (Grahame Webb)





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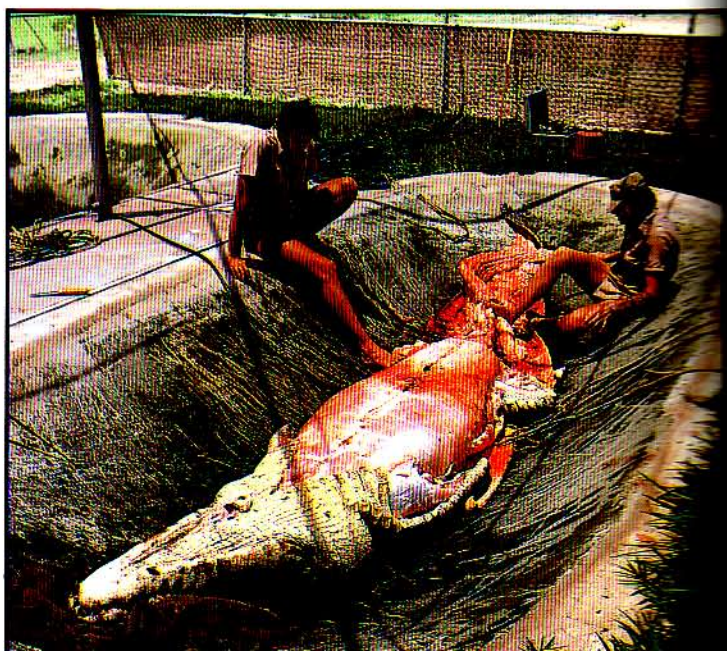
Above Left: Various types of traps are used for catching wary crocodilians. This one, constructed so that it will rise and fall with the tide, is used with saltwater crocodiles (*Crocodylus porosus*) in the Northern Territory of Australia. (Tony Forde)

Above Right: After capture, the front and hind limbs are often secured off the ground, as shown with these Indian muggers (*Crocodylus palustris*), to restrict struggling. (Jeff Lang)

Centre Left: After capture, crocodilians such as this mugger (*Crocodylus palustris*) in India, are often transported while restrained on a board or frame. (Jeff Lang)

Below Left: With large saltwater crocodiles (*Crocodylus porosus*), such as this 5.2 metre long specimen, rope traps have proved an effective capture method in northern Australia. (Grahame Webb)

Below Right: A 5.1 metre long saltwater crocodile (*Crocodylus porosus*), which died soon after capture, being skinned for a museum preparation. It is now thought that the reason very large crocodiles sometimes die soon after capture, is that their struggling to exhaustion elevates blood lactic acid levels to lethal limits. (Grahame Webb)



vital processes such as growth and reproduction. Studies on a variety of other reptiles and vertebrates point to complex organismal interactions involving behaviour (Crews and Garrick 1980; Crews and Moore 1986; Greenberg and Crews 1981). In lizards, male social behaviour has profound effects on the physiology and behaviour of females. Male-female courtship promotes egg development in females; male-male aggression inhibits normal egg development. Comparable studies have not been carried out on crocodylians, but does the sight and sound of a chorus of bellowing American alligators *Alligator mississippiensis*, help stimulate egg production in the females? Does male-male fighting during the courtship period inhibit female readiness to court, mate, and nest?

Behaviour is commonly thought of in terms of a simple stimulus-response reaction, but in reality, to perform a particular behaviour at an opportune time, requires an integrated, whole-organism response. Juvenile *A. mississippiensis* rely primarily on an internal biological clock cued by light to time movements between land and water. However, if light cues prove unreliable, they ignore an artificial light-dark cycle and switch instead to an ambient thermal cycle for moving between land and water at appropriate times (Lang 1976). Juvenile *A. mississippiensis* navigate homeward by using cues from the sun, stars or moon, all of which vary in reliability with prevailing sky conditions. However, alternative cues, including landmarks, olfaction, magnetic guidance and vocal communication, can also be used and it is likely that no one source is used exclusively for directing movements under all ambient conditions (Murphy 1981; Rodda 1982).

Certain behaviours are stereotypic (performed in the same manner time after time), which gives the impression that behavioural responses are fixed and invariable. Nesting behaviour has been regarded as a case in point (Greer 1970, 1971). But, on closer examination, even this important reproductive activity appears to be remarkably plastic in different habitats and even within a single habitat. For example, Nile crocodiles *Crocodylus niloticus*, are characterized as "hole-nesters"; but some nests are built to near-mound proportions and may even be covered with vegetation (at Lake Rudolph; Modha 1967a). In some populations of *C. acutus*, females typically dig hole nests which are difficult to detect a day or two after nesting. In other areas, mud, sand and peat are raked into large conspicuous mound nests, several metres across. In the Florida Bay Everglades, *C. acutus* use hole nests, mound nests and forms intermediate between the two — all in the same area (Campbell 1972; Ogden 1978; Mazzotti 1983). Furthermore, individual females may construct different types of nests annually.

Bustard (1984) reported on a population of Indian gharials *Gavialis gangeticus*, that nested about 1 m above high water mark. However, he suggested the behaviour was genetically programmed, and accordingly, predicted that if females from this population were relocated into areas with greater water fluctuations, their nests would all be inundated. Evidence in support of such a rigid view of behaviour is lacking. In fact, with the exception of courtship and mating behaviours, which are stereotypic and species-specific, most behaviours are more flexible and adaptable than have previously been appreciated. Variations in behaviour are also evident within populations, and more attention needs to be focused on how such differences affect the survival and reproductive success of an individual relative to its peers. Many behaviours are age and/or sex specific and change as an animal grows and matures.

Species-specific Behaviour

Crocodylians share both a common lifestyle and many features of behaviour. Initially, detailed natural history information was only available for a few species, and generalizations about crocodylian behaviour were based on a few pioneering studies, notably with *A. mississippiensis* and *C. niloticus*. However, as more species have been examined in the wild and in captivity, significant behavioural differences between species are becoming evident. *Alligator* does not behave like *Crocodylus*; species of *Crocodylus* differ in their behaviour. Even populations of the same species may exhibit distinct behaviours in different habitats.

Crocodylus porosus and *A. mississippiensis* respond very differently to environmental temperatures, and this has direct management implications. A common technique used to census crocodylian populations is night counts, in which a prescribed route is travelled by boat with a spotlight and the reflected eyeshines of animals in the water and along the shoreline are counted. For *A. mississippiensis*, the numbers spotted along the same transect vary seasonally and are strongly correlated with water temperature. As water temperature increases, so do the number of animals sighted (Murphy 1977; Woodward and Marion 1978). In marked contrast, the numbers of *C. porosus* sighted in tidal waterways show little, if any, correlation with water temperature. But other factors, such as tidal cycles, opportunities to feed and interactions with other crocodiles, are apparently significant determinants of nocturnal behaviour (Messel *et al.* 1981). A generalization based on *A. mississippiensis* behaviour would lead to spurious predictions about *C. porosus*.

Social behaviour varies between species, and this is evident in the signalling systems used for communication. *Alligator mississippiensis* vocalize

readily, and both sexes perform many of the same movements and postures in various contexts (Garrick *et al.* 1978). Courtship and mating is relaxed, lacks conspicuous displays and involves less frequent use of appeasement and submissive behaviours than do comparable behaviours of *C. acutus* and *C. niloticus*. These species vocalize less, use sex-specific signals and show more appeasement behaviour in dominant-submissive interactions (Garrick and Lang 1977).

Social organization and reproductive patterns also differ between species, *Alligator mississippiensis* in coastal Louisiana are solitary throughout much of the year, but congregate in the spring in small groups (<10 animals) in open water for breeding. Later, females disperse to isolated nesting areas and remain near the nests with the young after hatching (Joanen and McNease 1980). *Crocodylus niloticus* in Lake Rudolf form large seasonal breeding groups (>200) dominated by a small number of territorial males (<15). Males and females remain together through the hatching period and then disperse throughout the lake (Modha 1967b, 1968). *Crocodylus porosus* in the tidal waterways of northern Australia occupy year-round territories in which breeding and nesting occur. A male's territory may encompass the nesting sites of several females. Breeding groups are not formed and adults are rarely found together at any time of year (Webb *et al.* 1977; Messel *et al.* 1981).

Such species-specific differences in behaviour need to be carefully documented and have important implications for management. There has been a tendency, particularly in manuals and pamphlets about crocodilian husbandry (de Vos 1982; National Research Council 1983), to give guidelines for the design and operation of facilities for raising and breeding crocodilians in captivity, without regard for important behavioural differences between species. While this approach may be useful in a very general way, success in breeding and rearing a species depends upon first-hand experience and information about that species' specific requirements and responses. A species' social behaviour will dictate the optimum sex ratios and densities of adults in breeding groups, as well as the stocking densities that will result in the maximum growth of young. Failure to recognize important species-specific behaviours may well mean the difference between success and failure of a management programme.

BEHAVIOURAL INVENTORY

The behaviours of crocodilians can be conveniently categorized on the basis of their primary function:

1. maintenance;

2. social interactions; and,

3. reproduction.

The important behaviours in each category are presented in Appendix 1, and selected references to them, particularly within the recent literature, are provided in the sections that follow. Additional references for many species are included in Groombridge (1982). Detailed studies are now available on the ecology and natural history of: *C. niloticus* in eastern and southern Africa; *A. mississippiensis* in southeastern United States; *Crocodylus johnstoni* (the Australian freshwater crocodile), *Crocodylus novaeuguineae* (the New Guinea freshwater crocodile) and *C. porosus* in Australasia; and, *Caiman crocodilus* (spectacled caiman) in South America.

Maintenance Behaviour

Daily and Seasonal Activity

Predictable daily movements between land and water were noted in the earliest writings about crocodiles. Daytime movement onto land, alternating with nocturnal activity in the water, is typical for some species (*C. niloticus* and *A. mississippiensis*), but not for others: in *C. porosus* and *Caiman crocodilus* the reverse pattern may be the norm with much of the daytime spent submerged, followed by prolonged periods on land at night. Daily activity varies between and within species living in different climates, particularly the tropics versus subtropics, and seasonally for a particular population. Thus, *C. porosus* in northern Australia "bask" on land during the day during the cooler parts of the dry season, and *A. mississippiensis* in Florida submerge in the daytime during the warm summer months. Even within a population, daily activity varies with size, age, sex and other individual factors. The putative function of such land-water movements is primarily thermoregulation (either heat seeking or heat avoidance), but other concerns such as osmoregulation, feeding, predator avoidance and social or reproductive activities may all determine an individual's daily activity.

In addition to changes in the daily pattern of land-water movements, some species respond to seasonal changes in temperature and water availability in more dramatic ways. In warm temperate regions, *Alligator mississippiensis* and the Chinese alligator *Alligator sinensis*, hibernate during the winter either underwater or in subterranean burrows which they construct. During brief periods of freezing weather, *A. mississippiensis* seek out shallow water and allow their snouts to freeze in ice at the water's surface (Brisbin *et al.* 1982; Hagen *et al.* 1983). In hot, periodically dry climates, some species aestivate by remaining quiescent for days buried in mud, leaf litter or in underground burrows excavated as water levels fall (Whitaker and

Whitaker 1984). Individuals exhumed from such retreats often appear comatose for a period, although they eventually assume normal alertness. The metabolic correlates of this behaviour and the cues that prompt it, are essentially unstudied.

Locomotion

Not only are crocodilians adept swimmers, but they can assume an almost infinite variety of postures at the water's surface. The extent of body exposure is controlled by altering buoyancy; intermittent respiration seems to have little or no effect on position in the water. Static postures are maintained in and out of the water for extended periods and they function in multiple ways to communicate social messages, control heat exchange and facilitate prey capture. Crocodilians are also able to dive and remain underwater for long periods — hours for larger individuals — and are able to move underwater with little surface disturbance.

On land, crocodilians walk in a semi-erect posture at a slow pace, and dash and lunge over short distances with speed and agility. Galloping has been documented in several species and may facilitate travel over obstacles (Webb and Gans 1982). Young and even adults of many species climb on occasion, even over vertical fences several metres high. Long-range overland travel is typical of some species living in areas which dry periodically (Fig. 2); salt-tolerant species are capable of long-distance movements at sea.



Fig. 2. A *Crocodylus johnstoni* moving overland between drying pools had sought refuge in the shade of an undercut bank.

Prey Capture and Feeding

Crocodilians are indiscriminate feeders, displaying catholic tastes for any available animal protein. Biochemical studies indicate that plant protein is not digested or assimilated (Coulson and Hernandez 1983). In the wild, the menu includes a diverse and challenging array of prey, ranging from dragonflies, small passerines and bats, to sharks, antelopes and buffalo. Prey size increases with body size. Hatchlings subsist primarily on insects and crustaceans;

adults actively hunt larger vertebrates as well as feeding on carrion. Cannibalism is known to occur, but is rare. Only a few species include humans in their diet.

Crocodilians exhibit definite preferences for particular foods. For example, captive *A. mississippiensis* readily eat red meat, white meat and fish. Switching from fish to red meat occurs quickly, but the reverse switch requires a lengthy fast before fish is finally accepted.

At times, feeding may involve relatively sophisticated and subtle methods of prey capture. There are reports of animals using the tail and body to corral fish trapped in shallow water, and of co-operative hunting of larger game by adults (Pooley and Gans 1976; Schaller and Crawshaw 1982; Whitaker and Whitaker 1984). Feeding also involves movement to sites where prey are concentrated; nesting colonies of birds, roosting sites for bats and narrow inlets where fish occur in dense shoals become favoured hunting areas. In some instances, social dominance is abandoned by groups of adults feeding on a large prey item. In other situations, particularly among juveniles, larger animals may exclude smaller ones from food. Social facilitation of feeding has been demonstrated in other reptiles. The sight or sound of other animals feeding nearby may be important social cues that elicit feeding (Bjorndal 1986).

Experimental studies on how various types of prey are located and captured are lacking. Tactile and/or chemosensory cues are probably important at close range, but the behavioural patterns associated with the hunting of specific prey items are not well documented. Feeding specializations, for example fish-eating, are commonly inferred from the morphology of the jaws — narrow versus broad snouts. But observations of false gavials *Tomistoma schlegelii*, feeding on primates (Galdikas and Yaeger 1984), suggest caution in accepting unqualified generalizations.

Although crocodilians hunt and feed at night, when ambient temperatures are low, appetite ultimately depends on the availability of warm temperatures to digest and assimilate food. Consequently, feeding may be curtailed or abandoned during the cooler times of year. There is also evidence from laboratory studies on *A. mississippiensis* that an internal annual clock depresses appetite during the winter, even when the animals are held on summer light and temperature regimes (Coulson and Hernandez 1983).

Temperature Selection

As a group, crocodilians have been characterized as heat-seekers and thermoregulators, largely because initial studies focused on *A. mississippiensis*. In contrast, tropical species living in equable, warm

climates actively avoid high ambient temperatures during much of the year and are more appropriately considered to be thermoconformers.

Temperature selection (either heat-seeking or heat avoidance) within available habitats is an important daily activity of all species. Because individuals typically spend much of the day or night in the water, ambient water temperatures and seasonal changes in them strongly influence thermal behaviour and the resulting body temperatures. Solar radiation is an important source of heat, especially for large animals which are relatively independent of ambient air temperatures (Spotila *et al.* 1972; Smith 1979;). Crocodilians gape by opening their mouth for long periods, and this behaviour may function to cool the head during basking. Gaping probably has other functions as well (for example a social signal), because it also occurs in the rain and at night (Loveridge 1984).

There are clearly differences between species (and perhaps within species) in thermal behaviour and thermal preferences (= selected body temperatures) which are related to differences in the thermal regimes of respective habitats (Avery 1982; Loveridge 1984). An individual's thermal behaviour and preference is influenced by external factors, such as social milieu and climate, as well as by internal factors such as age and nutritional status (Lang 1977, 1979, 1981). Because body temperatures directly control metabolic rate and energy utilization, vital processes such as growth and reproduction are ultimately determined by thermal selection within the constraints of available thermal regimes. In tropical species, heat avoidance and especially voluntary cooling (on land at night) may result in the saving of a significant amount of energy by reducing metabolic rate. If body temperatures remain high but feeding is restricted (for example when animals are held at constant high temperatures), weight loss will eventually ensue. Features of crocodilian thermal selection and its consequences in terms of growth and health are discussed further elsewhere (see Lang Chapter 30).

Water and Salt Balance

Daily land-water movements also serve other functions, periodic submergence in water is necessary to counteract desiccation which, in small animals, may exceed 25% of body weight per day when individuals are on land. Smaller crocodilians may suffer dangerously high rates of water loss within a few days, particularly at high temperatures (Brown and Loveridge 1981). Even large animals are susceptible to appreciable water losses if forced to remain on land (Davis *et al.* 1980). Water is required for submergence and for drinking to prevent dehydration.

Some crocodilian species are salt-tolerant and live in brackish or even sea water, but recent studies indicate that periodic access to fresh water either by drinking or through food is essential (Taplin 1984). In one situation, a *C. porosus* maintained in sea water, routinely drank fresh water from a hose held by its keeper. Small individuals are especially vulnerable, presumably due to increased surface area relative to their mass. These animals decrease their exposure to high salinities by regularly moving onto land.

Site Fidelity

Adults reside in familiar areas and are active within home ranges which vary in size with species, habitat, sex, and season. In homing experiments, individuals have been displaced kilometres from capture sites and a high percentage return to home areas, often within days (Rodda 1982; Webb *et al.* 1983a). Less is known about the site fidelity and movement patterns of younger age classes. Hatchlings typically remain in the vicinity of the nest for weeks. Young *A. mississippiensis* may remain near their nest sites for several years, whereas the young of other species, for example *C. niloticus* and *C. porosus*, tend to disperse from nest areas within several months (Deitz 1979; Magnusson 1979; Hutton 1982; Rodda 1984). In a number of species the dispersal of juveniles and subadults has been inferred from their distribution; they are not found in the same areas as adults and hatchlings (Hutton 1982; Messel *et al.* 1984; Messel and Vorlicek 1985). Juvenile *A. mississippiensis* are able to orient and navigate using a variety of cues, and presumably crocodilians of all ages are able to make directed movements within familiar areas or travel over long distances (Rodda 1982).

Sometimes movements of tens of kilometres occur in response to seasonal changes in the aquatic environment (for example droughts and floods) or in response to seasonal reproduction. *Caiman crocodilus* concentrate by the hundreds at the end of the dry season in the few remaining sites containing permanent water (Schaller and Crawshaw 1982). *Crocodylus johnstoni* disperse along river channels, tributaries and out over flooded plains to reach shallow water areas at the height of wet season floods (Webb *et al.* 1983a). Adult *A. mississippiensis* congregate in small groups in open-water canals during the spring breeding period in Louisiana (Joanen and McNease 1980). *Crocodylus niloticus* in the 250 km long Lake Rudolf, travel long distances to reach breeding and nesting sites on the Central Islands in the lake (Modha 1967b, 1968).

In captivity, it is not uncommon for an escaped adult to return "home" to the facility and attempt to "break into" its pen. If animals are shifted from one pen to another, they often attempt to return to their

prior home. There are even instances of wild crocodilians entering enclosures during the breeding season, presumably to court and mate with the captive animals.

Habitat Modification

Habitat modifications by crocodilians are correlated with changes in water level, climate and/or reproductive activity. Nesting, especially the construction of a mound nest composed of vegetation gathered together at the nest site, is usually accompanied by habitat alterations that permit nest vigilance and guarding. An area around the nest is cleared, trails and runways are formed which permit easy access to the site, and shallow pools or wallows are constructed near the nest to provide cover and access to the water for the female and young (Webb *et al.* 1977). Tunnels which may extend underwater are dug into the banks of rivers and lakes, and are sometimes found closely associated with nesting sites (Mazzotti 1983; Whitaker and Whitaker 1984). Underground tunnels and burrows large enough to provide cover and shelter for adults have been documented for various species living in the tropics and subtropics. When water levels drop in southern India, mugger crocodiles *Crocodylus palustris*, dig and enlarge tunnels on land into which a number of adults may retreat (Whitaker and Whitaker 1984). During cool weather, *A. stewarti* move into elaborate, underground burrows. Juvenile *C. niloticus* seek shelter during the winter in earthen tunnels which they construct.

Digging is accomplished with co-ordinated movements of the front and hind limbs, aided by the occasional use of the snout. A similar process may be used to deepen and enlarge water holes and channels. A submerged animal will sometimes emerge with its body covered with mud, sand and debris. Some species, such as *Caiman crocodilus* in the Llanos of Venezuela, burrow into soft mud as water levels subside, and they may remain entombed in the mud for days as the surface layers dry and harden.

Shelter Seeking

Individuals of all ages seek out shelters in which to hide, but this behaviour is pronounced among young crocodilians. In the wild, hatchlings are often found beneath cover or in vegetation near the water. In captivity, young hide under available cover or pile together in groups in the corners of pens. Smaller crocodilians are vulnerable to many predators and such behaviour probably functions to reduce the risk of predation. Lack of adequate cover may disrupt normal behaviour patterns, particularly in young animals, and result in stress responses (see below).

Temperament and Stress

Temperament differs dramatically between species. *Crocodylus porosus* have a well earned reputation for belligerence whereas *A. mississippiensis* are rightly considered docile in comparison. Interspecific aggression directed toward potential predators may involve a series of escalating movements and postures intended to intimidate an enemy before an attack. Nest-guarding *A. mississippiensis* employ predictable sequences of threat behaviour before biting an intruder (Kushlan and Kushlan 1980), but other species may attack without provocation (Webb *et al.* 1978; see Blake and Loveridge Chapter 29). Even among members of the same species or population, an animal's disposition varies according to its size, age, sex, reproductive status, prior experience and other individual factors.

Vigilance does not necessitate activity, and thus an inactive crocodilian may be fully alert. Exactly what constitutes disturbance and how various species respond to unusual stimuli or disruptions in normal activity are not well understood. Response to disturbance often involves very subtle changes in physiology and behaviour which are not obvious and may be easily overlooked. Under experimental laboratory conditions, crocodilians respond to handling and even close approach with various physiological and behavioural "fear-induced" responses. It may take hours or days before normal behaviour patterns are resumed (Gans 1976; Gist and Kaplan 1976; Brown and Loveridge 1981; Weinheimer *et al.* 1982; Lewis and Gatten 1985).

Stress is an adaptive response that manifests itself in immediate physiological changes and in long-term changes in performance; for example, growth and reproduction. Confinement of wild animals or repeated disturbance to captive animals may result in stress responses with long-term effects on an animal's health and well-being (Wallach *et al.* 1967). In wild, mature, male *A. mississippiensis*, the stress of captivity results in a sharp decline in testosterone which reaches non-detectable levels within one day (Lance 1984). In *C. porosus*, marked changes in blood chemistry occur when animals are captured. These are exacerbated by large body size and may relate to the post-capture mortality syndrome often observed in large crocodilians (see Seymour *et al.* Chapter 26).

Frequent handling may depress an animal's appetite and reduce its growth. Disruptions of normal activity, such as repeated attempts to approach animals closely, may interrupt essential daily behaviour patterns, for example thermoregulation and seasonal reproductive activities. Irregular and unpredictable changes in an animal's environment or in the daily routines of feeding and care, are likely to be much more disruptive than are predictable maintenance schedules.

There are species differences in response to similar events. Young *Caiman crocodilus* kept in the laboratory showed normal "basking" behaviour only on weekends, when noise in nearby rooms was minimal; usual weekday activities in nearby rooms disrupted daily "basking" behaviour, even after weeks and then months. In contrast, the daily behaviour of *A. mississippiensis* under similar conditions was unaffected.

Habituation and Learning

Despite susceptibility to disturbance, crocodilians do become accustomed to prevailing conditions. In the wild, animals inhabiting areas which are subject to daytime disturbances, primarily from people, often become nocturnal and secretive. In captivity, individuals habituate to people and normal human activities if they are predictable and do not interfere directly with an animal's daily behaviour. In habituation, the animal's fear of humans is gradually reduced by repeated exposures in a neutral context (Price 1984). Species differences still persist, but are not well documented. For example, captive *C. porosus* defend nests repeatedly day after day without hesitation throughout incubation. In contrast, nesting *A. mississippiensis* under similar conditions, quickly become accustomed to repeated approaches and cease to defend their nests.

Learning is an important component in the habituation process (Price 1984). Crocodilians learn quickly when motivated to discriminate in appropriate environments. This ability is the basis of the numerous shows in which captive animals perform various feats on cue from a keeper. Learning may take the form of positive associative conditioning in which responses are rewarded with positive stimuli such as food and shelter. Or it may take the form of avoidance in response to aversive stimuli. The few studies in this area limit generalizations about species differences in learning ability. Rapid learning has been implicated in the demonstrated tendency of wild crocodilians to become increasingly wary when approached and/or captured (Webb and Messel 1979). Social cues influence other aspects of behaviour, and the behaviour of neighbours may affect how quickly an individual habituates and learns in certain situations. For instance, social facilitation of feeding has been demonstrated in other reptiles; a feeding animal predisposes other animals nearby to begin feeding (Bjorndal 1986).

Interspecific Interactions

Behavioural interactions between species are poorly documented, but appear to play an important role in determining the relative abundance and microhabitat distributions of crocodilians which occur together (Magnusson and Rebelo 1983; Webb

et al. 1983b; Ouboter and Nanhoé 1984; Herron 1985). For example, *A. mississippiensis* occupy coastal, saline marshes along the Gulf of Mexico, but are limited to freshwater marshes in the south-eastern Everglades of Florida. In this region, *C. acutus* inhabit available saltwater environments — *A. mississippiensis* are absent (Mazzotti 1983). When both species are housed together in large enclosures, adult *C. acutus* dominate *A. mississippiensis* and limit their access to food, but are not overtly aggressive towards them. More information is needed about interspecific behavioural interactions between sympatric species of crocodilians in both wild and captive situations.

Social Behaviour

Social behaviour includes communication, gregarious behaviour, dominance interactions and territorial activities (Appendix 1). The following is based in part on previous studies [Garrick and Lang (1977); Garrick *et al.* (1978)], although additional references are in Groombridge (1982) and Ferguson (1985).

Communication

Social interaction has a major influence on crocodilian behaviour. Communication begins in the egg, perhaps even prior to hatching, and continues throughout the life of an adult. Social messages are conveyed by a communication system composed of vocal, visual and non-vocal acoustic signals, all of which are suitably adapted to an amphibious life-style.

Young crocodilians vocalize spontaneously, or when they are disturbed or handled. Adults approach calling young and respond to intruders and potential predators by threatening and attacking. In some species, juveniles vocalize readily in response to hatchling calls. For example, the single calls of a hatchling *C. novaeguineae* were answered on repeated occasions by a chorus of vocalizations from juveniles in a nearby pen. Spontaneous vocalizations are often produced when mixed groups of young of various sizes are put together. Novel conditions, such as being introduced into a new pen, frequently elicit vocalizations from young.

Vocalizations between adults, such as bellowing or roaring, are associated with establishing and maintaining social relationships and are most obvious during seasonal reproductive activities. Body postures in and out of the water and specific movements, such as tail-thrashing or snout-lifting, are also used to convey information about an individual's social status and intent. Headslapping and bubbling and other non-vocal acoustic sounds are also important signals in a species' repertoire. Of particular interest are sub-audible vibrations (Fig. 3); these low frequency signals are produced by a



Fig. 3. *Caiman crocodilus* asserting dominance by arching the tail and producing sub-audible vibrations, which make the water on the flanks bubble.

number of species in conjunction with roaring and bellowing and appear to be transmitted through the water to animals at the surface as well as to those underwater.

Tactile cues and chemosensory messages may also be employed, but much less is known about how such signals are sent and received, or what they mean. Crocodylians possess chin and cloacal secretory glands; their secretions may function as defensive compounds to repulse potential predators and/or be employed as pheromones in intraspecific interactions (Wright and Moffat 1985). Yearling *A. mississippiensis* respond differentially to adult male glandular secretions (Johnsen and Wellington 1982). *Caiman crocodilus* also exhibit behavioural responses to glandular secretions (S. Gorzula, pers. comm.).



Fig. 4. Snout-lifting is a common submissive display of crocodylians as shown here by a young, male *Gavialis gangeticus*.

All of the species examined so far use various combinations of these signals in social contexts. Many are performed in a stereotypic manner, particularly courtship and territorial displays, and have meanings which are species-specific. Silent snout-lifting (Fig. 4), for instance, is a submissive

behaviour performed by female *C. acutus* when approached by a dominant male. In *C. porosus*, a similar movement accompanied by sex-specific vocalizations has the same meaning when performed by females in the same context (Fig. 5). Headslaps and sub-audible vibrations are incorporated into courtship sequences in *C. niloticus* and *C. acutus*. However, in *C. porosus* headslaps are not part of courtship. In all three species, headslaps also function as an assertion display when performed by dominant males.

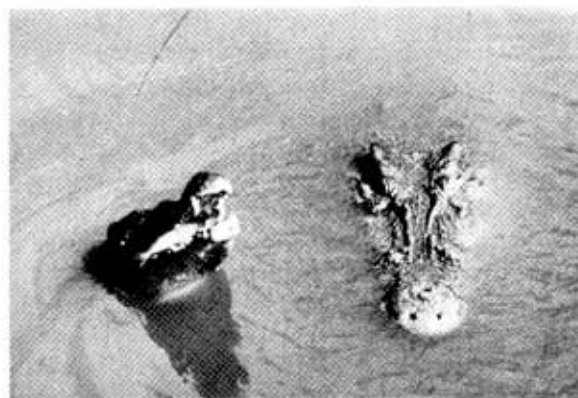


Fig. 5. During courtship female *Crocodylus porosus* snout-lift and vocalize to signify submission to the male.

Species differ in the relative use of signal modalities. *Alligator mississippiensis* are more vocal than several species of *Crocodylus*. These differences appear to be correlated with particular habitat features, for example vegetated marsh versus open water. In *C. porosus*, a headslap is a contagious behaviour that elicits headslaps from other animals; in *A. mississippiensis*, bellowing evokes bellows from nearby individuals.

Each species' repertoire is composed of discrete, graded and complex signals. Graded responses are evident in certain vocalizations and postures; complex signals are composites of vocal, visual and acoustic elements. It is apparent that adults living together recognize each other and respond accordingly. Individual recognition may be incorporated into some signals and displays, particularly vocalizations which are individually distinct. This feature awaits further documentation, and would be a worthwhile area for experimental studies. The signalling system of *A. mississippiensis*, and probably that of other crocodylians, shows a complexity similar to that reported for some birds and mammals (Garrick *et al.* 1978).

Gregarious Behaviour

Hatchlings tend to form social groups and they frequently remain in the vicinity of a nest site in pods, creches or nurseries. Although this behaviour is usually associated with the presence of a parent or

other adults nearby, hatchling groups assemble and persist even when adults are not present. For example, *A. mississippiensis* hatchlings remain together in sibling groups for one or more seasons. Individuals spend the daylight hours together, typically basking on land or moving back and forth from the water, but individuals or small groups disperse at night to forage, and then reassemble the next morning. Vocalizations play an important role in maintaining group cohesiveness, and occur more frequently at dawn and dusk when animals are moving. No obvious agonistic behaviours are apparent and there is no evidence of social dominance or hierarchies in these groups (Deitz 1979).

Presumably, group living decreases an individual's risk of predation, and thus it is not surprising that the behaviour is pronounced in hatchlings which are especially vulnerable to predation. The young of other species exhibit similar behaviour, but there are differences between species in the length of time hatchlings remain together; there may also be intraspecific differences in such behaviour that are related to different habitats and/or seasonal regimes. In at least one population of *C. acutus*, hatchlings apparently disperse within days of hatching (Mazzotti 1983).

Juveniles and adults are less gregarious than hatchlings, but may also associate in loosely-organized social groups. Individuals of some species, for example *A. mississippiensis* and *C. niloticus*, frequently assemble in basking groups on land at particular times of day. In habitats subjected to periodic drought, individuals may aggregate in mixed-age groups or groups segregated by age and/or size, at sites where there is permanent water. Social encounters, particularly agonistic behaviour associated with the maintenance of territory or dominance, are often suspended or diminished when such groups form.

Dominance Hierarchies

Systematic studies of captive groups of subadults and adults indicate that dominance hierarchies are a regular feature of social life. Dominance relationships are most obvious during seasonal reproductive activities, but typically persist throughout the year. Dominant individuals control access to mates, nest sites, food and living space. Challenges may occur on occasion, but combat involving physical contact is rare. Large body size and aggressive temperament appear to be the most consistent characteristics of dominant animals. Dominance is asserted and maintained by social signals that vary between species. Dominant animals are conspicuous and typically expose the head, body and tail when approaching other individuals (Fig. 6). Submission is indicated by lifting the head (Figs 4 and 5), submerging the body, retreating underwater or moving away upon approach.



Fig. 6. Male *Crocodylus acutus* contesting territories by using displays which maximize the size of the body.

Large males dominate breeding groups and females normally display submissive behaviours in the presence of a dominant male. Females may also form dominance hierarchies, but challenges among females are usually associated with access to suitable nesting sites or defence of nesting territories, rather than with access to mates. Subadult males and small females occupy low ranking positions in hierarchies. Less is known about dominance relationships among wild crocodylians, but hierarchies based largely on size and sex are formed when individuals congregate at breeding sites or in areas of permanent water during seasonal droughts. In captive groups, particularly when densities are high, low ranking animals may be denied access to food, water, shade and places to bask and nest. Dominant animals attack submissive individuals by grabbing and biting at the base of the tail, behind the legs. In captive groups, scarring or injuries in this area are indicative of low ranking animals that are unable to avoid repeated attacks.

Groups of larger juveniles and subadults may form hierarchies in which larger animals control access to available food and shelter, but such behaviour appears to be species-specific and density-dependent. In captive groups, dominance relationships may contribute to the often marked differences in growth rates among pen mates; such disparities can be minimized by periodically sorting according to size.

Territorial Behaviour

Territorial behaviour is an expression of site-dependent dominance behaviour. In wild populations dominant males defend territories from which they exclude other males. The defended resource(s) varies with species and includes access to mates, nesting sites, nurseries, foraging areas, basking locations, overwintering sites or some combination of these factors. Territorial defence intensifies during the reproductive season, but often persists throughout the year. In some species, for example *C.*

porosus, territories are defended throughout the year, although they vary in size with seasonal changes in aquatic habitat and with seasonal reproductive activities. In *C. niloticus*, males maintain home ranges with little overlap along sections of river throughout the year. Territorial behaviour is evident during the breeding season. Females maintain overlapping home ranges which include nesting sites (Hutton 1982). In other areas, for example Lake Rudolf, breeding territories are established by dominant males near nesting sites, but only during the reproductive season. Females of some species defend territories within which they nest. In other species, females nest together, but usually defend specific nest sites on colonial nesting grounds.

In captive breeding groups, territorial defence appears to be density-dependent as well as species-specific. When densities are low, dominant animals maintain separate territories which may vary in size and location with social status. Females and sub-adult males may be tolerated within a male's territory, but other adult males are prohibited. In high density situations, maintenance of exclusive territories becomes increasingly difficult. Dominant individuals may continue to limit access to defended resources while permitting subordinates to remain nearby. Under such conditions, dominance hierarchies typically form.

Reproductive Behaviour

Crocodylians construct nests in which they lay hard-shelled eggs that take 2-3 months to incubate. Reproductive behaviours include courtship, mating, nesting, incubation, hatching and post-hatching care of young (Appendix 1). There are differences between species, but the basic behaviours are universal and complex. Reproductive behaviours require a major investment of time and energy during each season. The following sections are based in part on previous studies [Garrick and Lang (1977); Garrick *et al.* 1978)], with additional information from Groombridge (1982) and Ferguson (1985).

General

Body size at sexual maturity varies with species and sex. Larger species (adult lengths 3-6 m) mature at larger sizes and older ages than smaller species (1-3 m). Size is age related, but populations of the same species with different resource bases grow at different rates and, consequently, mature at different ages and sizes. Larger species mature at older ages (10-15 y) relative to smaller species (4-10 y). Maturation is size dependent and may be accelerated by rapid growth in captivity. Sexual dimorphism is marked, with males being up to twice as large as females in all but the smallest species. Females mature at smaller sizes and apparently slightly

younger ages than males. Adults are long-lived (20-40+ y), and the length of the active reproductive period is extended (10-30+ y). Adult females of several species have reproduced successfully after 40 y in captivity. Reproductive effort increases with size and/or age, and then eventually declines. As females mature, they lay more eggs that are larger and more viable. Senescent females have been noted in some wild populations. Large males are able to inseminate many females, probably 15-20+ in some species. A single male *Crocodylus palustris* sired 15 clutches, numbering over 300 viable eggs, in a single season.

Reproduction is seasonal, and the major reproductive events can be restricted to a short season or temporally extended over much of the year. In environments with extremes in thermal or hydric regimes, nesting typically occurs within a contracted period; 2-3 weeks in *A. mississippiensis* and *C. johnstoni*. In more equable climates, nesting is extended over 3-4 months, as occurs in *C. porosus*. In some localities, two distinct nesting periods are evident within a year (*C. niloticus* in Lake Victoria, Africa, and *C. porosus* on the Sepik River in Papua New Guinea). In general, females nest once per season, but biennial and triennial nesting occur in *A. mississippiensis*, apparently in response to prevailing water conditions. In contrast, captive *C. palustris* regularly produce two clutches per season. Multiple clutch production by a single female within one reproductive season may also occur in other species with extended reproductive seasons (*Crocodylus mindorensis*, *C. porosus* and *C. siamensis*), but the trait is poorly documented.

For all species studied to date, the mating system is polygynous, with single males mating with a number of females. In some species, aggregations of adults form during the breeding season. In others, breeding takes place within territories occupied throughout the year. The operational sex ratio (reproductive males to females), varies with the size of the breeding group from about 1:20 in *C. niloticus* within Lake Rudolf, to 1:1-3 in some territorial species. In seasonal aggregations of crocodylians, breeding territories are established by large males; dominance hierarchies may also be formed, principally among adult males. Territorial defence in all species intensifies during the breeding season.

Courtship and Mating

Establishment of territories and gaining dominance precede courtship and mating. A large male advertises its dominance by swimming conspicuously within its territory with much of its body exposed at the water surface, and periodically engaging in species-specific assertion displays. Headslapping, an explosive jaw clap performed at the water surface, is often accompanied by audible vocalizations, exhalations and/or sub-audible vibrations (Fig. 3). Large

males dominate breeding groups by patrolling territorial boundaries and by approaching other animals. Subdominant males are actively challenged and excluded by vigorous chases and open-mouth lunges. Combats between males contesting dominance involve head-to-head physical contact, often sparring with the jaws or head ramming, and posturing with raised, inflated bodies (Fig. 6).

Females are tolerated within territories, and when approached, indicate submission by snout-lifting, (Fig. 5) vocalizing with sex-specific calls, and/or by submerging. In some species, females tolerate other females at this time, but dominance hierarchies may be formed. In other species several females may defend exclusive territories within a male's territory.

Receptive females typically initiate courtship with available mates and tolerate the presence of other females nearby during both courtship and mating. Dominant males interrupt courtship attempts by subdominant males. An interrupted female often resumes courtship with the dominant male after he has displaced a subordinate. In large aggregations, females move with impunity between territories and may court and mate with several dominant males in succession. In captive breeding groups, dominant males often court and mate with receptive females in serial sequence, repeatedly courting with one female for days and subsequently consorting in a similar fashion with others. Although female-female aggression is subdued during courtship (relative to nesting), social hierarchies among females are evident in some species and may affect when and how often a female mates with the dominant male.

Courtship and mating consist of a sequence of attraction/advertisement behaviours followed by pair formation, precopulatory behaviours and copulation. Dominant males approach females to initiate courtship; or females approach a dominant male, frequently after a male-male aggressive interaction or an advertisement display. During pair formation and precopulatory activity, males and females engage in a variety of species-specific behaviours which include snout contact, snout-lifting, head and body rubbing and riding, conspicuous male displays, vocalizations, exhalations, narial and guttural bubbling, circling and periodic submergence and re-emergence. Mating occurs when the male mounts the female by moving onto her back and positioning his tail and vent underneath the female's tail; the anteriorly curved penis is then inserted into the female's cloaca. Copulation is difficult to observe because it occurs underwater, but successful copulation appears to take at least several minutes and may last 10-15 minutes or longer. In captive groups, a pair may copulate on repeated occasions for several days.

Differences among species in courtship and mating behaviours are readily apparent. In some species, there is a determined order to the sequence;

copulation predictably follows precopulatory behaviour. In others, sequences are interchangeable. Precopulatory behaviour may occur repeatedly, but many sequences terminate before copulation is attempted. These behaviours probably enable individuals to assess the attributes of potential mates and to synchronize reproductive activity. Behaviour may also serve as a premating mechanism to prevent interbreeding and ensure reproductive isolation. However, hybridization has been reported in some mixed-species groups in captivity [*C. porosus* x *C. siamensis* and *C. acutus* x *Crocodylus rhombifer* (Groombridge 1982)]. These observations suggest that differences in these behaviours are not sufficiently distinct to prevent interbreeding between related species.

In *A. mississippiensis* and *C. niloticus*, the time interval between copulation and egg deposition is approximately one month. Intervals of 3-6 weeks appear typical of most species, but intervals of 2-5 months have been reported in some. In *C. palustris* that nest twice in a single season, individual females court and mate for 2-8 weeks prior to the first nesting. Mating continues after the first nesting and before the second nesting. Mating by individual females peaks about 4-5 weeks before each nesting.

Nesting and Incubation

Crocodylians nest by scraping together available vegetation and/or soil into a mound, or by excavating a cavity in the substrate. The entire clutch is laid at once, usually within 1-2 hours at night, and the nest is reshaped or covered. A female visits her nest frequently during incubation and guards it against potential predators. The type of nest constructed, a mound versus a hole, is species-specific, but variations in nest type are evident in different habitats and even within habitats. The same nest sites are utilized year after year; mound nests may be reconstructed for use in successive years. Nest spacing also varies widely between and within species. Colonial nesting occurs in some hole-nesting species, but mound nesters also construct nests in close proximity to each other in some habitats. Females defend nests and exclude other females from the immediate nest sites or from territories within which nests are located. In captive situations, there is a marked increase in aggressive interactions between females during the nesting period, often in contrast to more tolerant behaviour among females prior to nesting.

The cues used by females in selecting nest sites are not well understood. In the light of recent studies, which indicate that incubation temperatures determine embryonic growth rates and sex, it is probable that the thermal characteristics of the nest site influence where it is located as well as its manner of construction. Features such as available

nesting material, adjacent vegetation, exposure to sunlight, soil moisture, proximity and height above water and the locations of nearby nests, may all play significant roles in nest site selection. In captivity, the social status of a female appears to be a major determinant of where she nests.

Nest site selection may begin several months prior to nesting, but actual nest construction typically takes place 1-2 weeks before egg deposition. Hole nesters scrape and dig in potential nest sites with co-ordinated movements of the front and hind limbs. Mound nesters use similar movements to gather material into a central pile and frequently walk across it, compacting and shaping the nest with treading movements of the hind feet. The head is laid on the substrate at frequent intervals, and at times the snout is used to probe into the material being excavated or collected. Trial or false nests are sometimes constructed before eggs are laid, and these are usually located in the vicinity of the eventual nest. However some mound nests are constructed within several days of laying, without trials, and some hole nests are laid in areas where there is no evidence of prior digging.

Immediately before laying eggs, the female excavates a cavity by digging and scraping nest material out of the chamber with co-ordinated movements of the hind legs. During egg-laying, the hind legs are positioned within the nest chamber and the tail is used as a support. Eggs emerging from the female's cloaca are directed forward and compacted in the nest chamber with periodic forward movements of the hind legs. Females are typically quiescent during egg deposition and are sometimes approachable at close range. In some instances, other females, males and subadults, move near to nesting females and are tolerated at close range. When all of the eggs are laid, the female covers the nest opening by scraping material back over the nest and periodically packing it down with the hind feet.

After egg-laying, females defend their nests and may remain near their nests for much of the 2-3 month incubation period. In some species, for example *C. niloticus*, some females reportedly fast during all or much of this period. The nest may be reshaped or covered periodically during incubation, particularly if it is disturbed. A nesting female may void cloacal fluid on the nest during construction and while eggs are incubating, but the frequency of this activity and its significance are poorly documented.

Vigorous nest defence is a good indication that eggs have been laid, but not all females defend nests. Intruders or potential predators are confronted with a sequence of threat behaviours which include close approach, lunging with open mouth and biting, or they are attacked without hesitation. The frequency of nest attendance and the intensity of nest defence

seem to vary among species, but comparisons are difficult because of the varied histories of hunting and/or disturbance in most wild populations. In captivity, aggressive species such as *C. porosus* are tenacious nest defenders; some females threaten and attack intruders continually, several times a day, for the entire three month incubation period. In less aggressive species, nest defence toward humans wanes quickly, particularly if nests are approached repeatedly. Within a species, individual differences are also readily apparent. Within a single enclosure, some females may vigorously defend their nests whereas others rarely do so. Increased threat and attack behaviour toward humans in captive versus wild nesting females has been noted in several species (see Blake and Loveridge Chapter 29).

In general, female-female aggressive interactions diminish during incubation. In some species, such as *C. porosus*, females continue to exclude other females from the nest vicinity throughout incubation. However, in other species, aggression between females subsides after egg-laying. In captivity, dominant males may also participate in nest attendance and nest defence. The dominant male in a breeding enclosure of *C. palustris* sometimes approached a female on her nest during egg-laying or immediately afterwards, and moved around the nest and contacted her head and body.

Hatching and Post-hatching Care

When crocodylian eggs hatch, the female excavates the nest and assists the young to emerge. The hatchlings and eggs are picked up in the female's mouth and transported to the water (Fig. 1). Hatchlings remain together as a group near the nest and associate with one or both parents and other adults, who defend the young from predators.

Nest excavation has been observed in many species and consists of scraping and digging movements of front and hind legs, to open the nest cavity. Hatchling vocalizations appear to be an important proximate cue directing adults to the young, but nests which do not contain viable hatchlings may sometimes be opened as well. In one instance, a captive *C. palustris* excavated her empty nest (the eggs had been removed three months previously) after hatchling vocalizations were played on a tape recorder at the opposite end of a large enclosure.

Movements of the young in the nest and/or chemosensory cues may also play a role in initiating and directing nest excavation. During the process, the female frequently rests her lower jaw and head on the substrate and places her snout into the nest as it is opened. As young and eggs are encountered, they are picked up in the jaws and shifted into the mouth. Eggs are manipulated by rolling and by gently crushing the shell between the tongue and palate, which facilitate hatching (Fig. 7). Mouth



Fig. 7. A female *Crocodylus noronhaiensis* manipulating an unhatched egg in her mouth. Assisted hatching by parents appears to characterize most crocodylians.

transport of hatching eggs and young from the nest to the water appears to be universal among crocodylians with the possible exception of one or two species with very long, slender snouts.

Dominant or territorial males in the vicinity of a nest may respond when hatching commences. In captive breeding groups, the male is usually attentive in the water or at the nest. In some species, the male has been observed to participate in nest excavation and in mouth transport of the young and eggs. In a captive group of *C. palustris*, a dominant male opened a nest and transported the hatchlings to the water without assistance from the nesting female, who remained vigilant in the water near the nest. This male exhibited all of the behaviours normally performed by females when opening nests (Lang *et al.* 1986).

During hatching, the young vocalize readily. These calls attract the attention of nearby adults and also evoke vocal responses from, and elicit close approach by, siblings and other adults. While on the nest, hatchlings may also posture and move in the direction of the adult. These behaviours probably aid the parent in locating and picking them up. In some species, adults may vocalize during nest opening, whereas in others, adults appear to be silent. Group cohesiveness is maintained by frequent vocalizations of hatchlings, and a nursery or creche is established near protective cover in shallow water. Young disperse to forage but regroup during inactivity. Parents remain near groups of hatchlings and defend the young from potential predators. Feeding of young by attending adults has been suggested, but has not been documented.

Young crocodylians remain in loosely organized groups with adults for variable lengths of time. In *A. mississippiensis*, females remain near nesting areas, with groups of young, for 1-2 years. In *C. porosus* and *C. niloticus*, young disperse much earlier — within a matter of months. The cohesiveness of groups of young may depend on the presence of the female

and/or on seasonal changes in available habitat. When males remain near nesting sites, they may also be associated with hatchling groups, in some areas. In *A. mississippiensis*, males do not regularly remain near the female during the nesting, hatching or post-hatching periods.

Hatchling vocalizations attract other adults, sub-adults and even juveniles. Large males (especially dominant males in captive breeding groups) and females respond demonstratively by approaching, threatening and attacking intruders. Intraspecific defence of young has also been observed. In captivity, juveniles, subadults and other adults may be actively excluded from the vicinity of hatchling groups by protective parents. In one captive situation, juvenile *Crocodylus moreletii* were repeatedly threatened and attacked by a female guarding young. This behaviour typically resulted in juveniles fleeing the nursery area. If retreat was not immediate, the female grabbed the juvenile, held it between her jaws and shook it before releasing it.

BEHAVIOUR AND MANAGEMENT

Management in Nature

Habitat

Effective habitat management requires detailed information about how and when crocodylians utilize various habitats. Critical habitat includes physical features, such as water availability and protection from extreme temperatures, and biotic factors such as food availability, protection from predators and interactions with conspecifics. In all species, social behaviour is varied and complex. Consequently, the social environment plays a prominent role in determining how an individual uses available resources and how a population is distributed within habitats. Two complimentary techniques, mark-recapture and radiotelemetry, have been used successfully to collect relevant data on species living in various habitats. In particular, radio tracking has provided detailed information about the movements, activities and behaviours of representative individuals (e.g. Mazzotti 1983).

The behavioural responses outlined in the preceding sections clearly indicate that species' requirements differ. When the distributional range of different species overlaps (for example *C. porosus* and *C. johnstoni* in Australia, *Melanostictus niger* and *Caiman crocodylus* in Brazil), each species occupies distinct areas and utilizes available habitats differently. Thus, the initial focus of any management strategy must be on the species of interest (Magnusson and Rebelo 1983). Furthermore, populations living in different habitats, for example lakes versus rivers, respond in different ways to critical environmental factors. For instance, knowledge about seasonal movements and behaviours

associated with hibernation or aestivation are necessary to ensure that suitable habitats are available throughout the year.

In addition, in any given population, young, juveniles and adults may all occupy distinct habitats which are appropriate for age or sex-specific activities. Adult males and females require deep, open water for mating; females require adequate sites for nesting. Young require shallow water and abundant cover in which to feed. All of these requirements must be met if healthy, viable wild populations are to be maintained. Habitat features associated with reproduction are especially critical. Reproductive activities occur over many months and are behaviourally complex; eggs and hatchlings are particularly vulnerable to mortality should conditions not be adequate.

The quality and quantity of critical resources within habitats differ. These features alter behavioural responses and ultimately affect growth and reproduction. In a number of species, growth rates vary with habitat and are correlated with differences in food resources and thermal regimes. Reproductive success also varies with habitat. For example, the nesting success of *C. porosus* in northern Australia is high in some tidal river systems and freshwater swamps, but is low in adjacent habitats. Given adequate information about how populations respond in different habitats, it is feasible to make decisions about which habitat is most suitable from a range of possible habitats and to outline appropriate actions to maintain vital resources.

Even though certain resources are essential, crocodilians are surprisingly adaptable and fortunately do not require pristine environments. Some species are able to survive and even thrive in disturbed habitats. Examples include *A. mississippiensis* living on suburban golf courses and *Caiman crocodilus* living in drainage ditches in large cities. The behaviours of a species provide important clues about which features of its habitat are critical for its survival. This information, in turn, is useful in making wise management decisions with the goal of establishing and maintaining suitable habitats for wild populations.

Animals

Various strategies have been used to conserve and manage crocodilian populations, which include:

1. Stocking habitats by releasing young animals raised in captivity;
2. Relocating animals from one habitat to another; and,
3. Removing or harvesting animals, usually juveniles or adults rather than a random cull.

In the light of the behavioural differences between species, management decisions pertaining to these options need to be tailored to the species and habitats of concern. Behaviour may affect the outcome of different potential strategies.

Because eggs and young are vulnerable to mortality, "head-start" programmes have been established for some species. Young are reared in captivity and are later released in the wild. Little is known about the optimum size and/or age for release, nor how successful such strategies really are from the points of view of survivorship and movement out of the release area. In general, crocodilians appear to be more adaptable, more social and less site-specific when they are young. As they reach subadult size, there is evidence of increased social interaction, especially agonistic behaviour (e.g. dominant-submissive interactions), and a greater tendency for movement and dispersal. Thus the optimum age or size for released animals to remain in their release site is probably at the younger ages, when animals are capable of behavioural adjustments to their new surroundings and before competitive social interaction and/or dispersal occurs. However, against this must be balanced the general trend towards increased probabilities of surviving with increasing age and size.

The influence of conspecifics becomes increasingly important as animals mature, and the success of release programmes involving subadults and adults may depend on whether or not the habitat is already occupied by individuals of comparable size and upon the social organization of the population. Relocation of wild animals from one habitat to another will similarly be affected by the presence of resident animals. In addition, older animals exhibit site fidelity to a greater extent than younger animals and this tendency will influence whether an animal stays in the release area or attempts to move home-ward. One of the difficulties in dealing with nuisance animals, particularly large adults, is that simply moving them from one area to another results in the eventual reappearance of the animal where it was originally captured. The tendency to home is strong and adults are capable of moving long distances. Overall, release and relocation programmes will be most effective when younger animals are released into vacant or depleted habitats.

Should harvest programmes be designed to minimize effects on reproduction? Crocodilians are long-lived and consequently the reproductive potential of each breeding adult is high. Reproduction is seasonal and extended over many months, culminating in hatching and post-hatching care of young. Social organization favours breeding by larger animals, particularly large males, and the removal of these animals destabilizes long-standing social relations. If continued over a long enough

period, overall reproductive success could decrease. Even if some of the adult males are not breeding, these animals have the highest probability of breeding in future years. In this sense, they are not "surplus" animals, as is sometimes maintained. On the other hand, a harvest that targets younger non-breeding segments of the population, notably sub-adult males, will result in minimal disruption to the existing social order.

Multi-species Interactions

Behavioural interactions between sympatric species may influence the distribution and abundance of one or both species. Possible scenarios include competitive exclusion or predation, but there is little available information on this aspect at present. For example, in areas subject to recent intense hunting, *C. intermedius* and *M. niger* have been extirpated, and *Caiman crocodilus*, formerly rare in these habitats, are now abundant. Prior to hunting, the larger crocodylians presumably excluded the smaller *Caiman crocodilus* from these areas. If a programme were established to restock depleted habitats with young *C. intermedius* or *M. niger*, the now established populations of *Caiman crocodilus* may successfully exclude or even prey upon the young. Such potential interactions, might be alleviated by releasing the introduced species at larger sizes and/or reducing the *Caiman crocodilus* populations in the release areas.

Management in Captivity

General

Crocodylians are relatively easy to maintain in captivity if provided with certain basic requirements, such as access to water, suitable food and adequate temperatures. Management programmes involving captive animals have focused on maintaining adults for breeding, rearing young, or a combination of these. Although it is possible to achieve both objectives by housing animals together, most facilities have breeding adults separated from younger animals. Success in breeding and rearing has been accomplished in diverse settings, ranging from expansive fenced enclosures in natural habitats to concrete pens in zoos. The ultimate goals of these programmes differ and include public display, species conservation and/or commercial utilization.

The species on which a programme focuses is usually determined by geographic location or the availability of animals. Nevertheless, it is of primary importance to recognize how species-specific differences in life history and behaviour affect the design and operation of breeding and rearing facilities. If breeding is a primary objective, the minimum size and/or age at which a female reproduces is a critical variable. Size and age at first nesting will determine

how quickly a captive population increases, and has obvious implications if animals are being produced for release or commercial harvest. Similarly, if rearing is a primary objective, the species-specific growth rate becomes a prime consideration in predicting how quickly an individual animal will be ready for release or harvest.

Many captive breeding and rearing facilities have been stocked initially with wild-caught animals, but there may be distinct advantages in using captive-reared animals whenever possible. There are indications in a number of species that an animal's prior experience affects its subsequent behaviour in captivity. Animals raised in captivity exhibit less avoidance behaviour and become "tame" or, at least, are less disturbed by humans, which facilitates feeding and maintenance. Presumably, these animals experience less stress and, as a consequence, grow faster and are more likely to breed than their wild counterparts brought into captivity.

Captive-reared crocodylians not only habituate to humans, but also appear to be more tolerant of conspecifics. Social conditioning in the high density situations typical of most facilities, results in reduced aggression and fewer injuries among pen mates. This effect is probably augmented by segregating animals into similar size groups because there is less opportunity for size-related dominance behaviours. Comparisons are most obvious in the behaviour of wild-caught versus captive-reared adults, particularly with respect to breeding requirements and behaviour. Studies on *A. mississippiensis* in Louisiana have demonstrated that captive-reared adults breed successfully in one-tenth of the area required by wild-caught animals (Joanen and McNease 1980). When densities were increased in breeding pens, increased agonistic behaviour between wild-caught animals resulted in subordinates being excluded or even killed by dominant animals.

Differences in the levels of agonistic behaviour are likely to be most apparent when wild-caught animals are introduced into high-density enclosures or pens that are stocked with captive-reared individuals. If wild-caught adults are being introduced, then it is advisable to first isolate these animals for an interim period, then introduce them gradually into low density pens or enclosures. These precautions will minimize stress and reduce the risk of injury or death to either introduced or resident animals. Experience in Papua New Guinea with *C. novaeguineae* indicated that wild-caught juveniles are better able to adapt to captive conditions if they were initially isolated from captive-reared animals and held at low densities.

These changes in the behaviour of captive crocodylians, (habituation to humans and tolerance of conspecifics), are presumably learned responses which are acquired and reinforced by an individual's

experience during its lifetime. Such changes occur relatively quickly in young animals and much more slowly in adults. Because behavioural changes induced by captivity are learned and are not inherent, such changes are likely to diminish or disappear in captive-raised animals when they are released into the wild.

The point here is that captive and wild animals behave differently toward humans and toward each other. Detailed documentation of these differences is lacking, but this feature of crocodylian behaviour is relevant to management. How does experience in captivity affect the subsequent survival of released animals? How does age or length of prior experience affect the acquisition and loss of "captive" traits? Certain behavioural changes are obviously beneficial. Captive-reared animals may be preferred for intensive breeding in commercial operations because, as adults, they breed more readily and require less space. If time and space are limiting, purchasing captive stock when starting or expanding an operation may be a wise move — even if wild animals are available at little or no cost.

Breeding

Nearly all of the 21 species of crocodylians have bred in captivity, and many of these species have bred within different types of facilities (Honegger 1982; Tryon and Behler 1982). Geographic location has little influence if ambient conditions are favourable; *A. mississippiensis* have nested successfully at zoos and tourist exhibits in northern Europe, the Middle East and southeastern Australia. In *A. mississippiensis*, reproduction is triggered by seasonally increasing temperatures. Relocated animals adjust their reproductive activities to conform to this pattern even when seasons are reversed, as occurs in Australia, or when favourable moisture regimes do not coincide with increasing temperatures, as in Israel (see Ben-Moshe Chapter 35). Less is known about the cues utilized to initiate reproduction in tropical species, although seasonal changes in temperature and/or moisture appear to determine when breeding occurs.

Social behaviour associated with reproduction is a dominant factor in captive propagation. Breeding success is very sensitive to the sex ratio and to the density of adults in enclosures. The optimum composition and size of a breeding group depends on the social behaviour and social organization of the species of interest. Species differ in these features, and such differences are particularly evident during reproductive activities in captivity. Territorial and dominance behaviours are intensified among males during courtship and mating, and among females during nesting.

Species comparisons are difficult because holding conditions, prior history of the animals, feeding regimes and many other variables affect breeding

success. In most species, isolated pairs have bred successfully, if the male is larger than the female. In *C. porosus*, pairing of males with females of the same size may result in the female killing the male. Small groups, composed of 1-2 males with 2-10 females, constitute the optimum breeding unit for most species. Some species (*A. mississippiensis*, *Caiman crocodilus*, *C. johnstoni*, *C. novaeguineae*, *C. siamensis*) continue to breed at high densities, but with others (*C. porosus*), aggressive interactions in both sexes increase with group size, and at least some females fail to nest in group enclosures. If proper management is available for pairing potential mates, *C. porosus* may breed more successively by isolating pairs in small pens (<100 m²) rather than by grouping animals in larger enclosures.

Information about a species' social organization in nature appears to be a useful indicator of its ability to tolerate conspecifics at close range, which is typical of high-density captive conditions. Territorial species tend to be antisocial and exhibit aggressive behaviour toward conspecifics. These species require more space in breeding enclosures and/or are best isolated in pairs or small groups (single male with several females). On the other hand, species which form seasonal aggregations for breeding, or in response to periodic droughts or other factors, tend to be more social and to tolerate conspecifics at closer range and higher densities. At present, data are inadequate to make definitive statements for most species about this behavioural feature. Nevertheless, some interspecific differences are obvious (*C. porosus* versus *A. mississippiensis*), and species can be ranked approximately with respect to tolerance of conspecifics (Fig. 8).

Because territorial and dominance behaviours intensify during the breeding period, the spatial arrangement of land and water within a breeding enclosure should be designed to provide natural boundaries and retreats for subordinates. Water areas may be subdivided, and isolation pools or ponds are advisable. In addition, suitable nesting sites should be distributed throughout the enclosure and visual barriers should be provided to reduce aggression among nesting females. In one captive facility, nesting stalls are provided for females in high-density enclosures in order to reduce interference among nesting females.

Breeding success tends to be highest in enclosures where the animals are long-term residents and when they have had opportunities to establish the social order well in advance of the breeding season. When new animals are introduced into an enclosure, it is advisable to do this several months before breeding begins and to introduce them gradually by initially partitioning the newcomer in a corner of the enclosure. Behaviour should ideally be monitored during and after the introduction, as aggression can lead to injury and death.

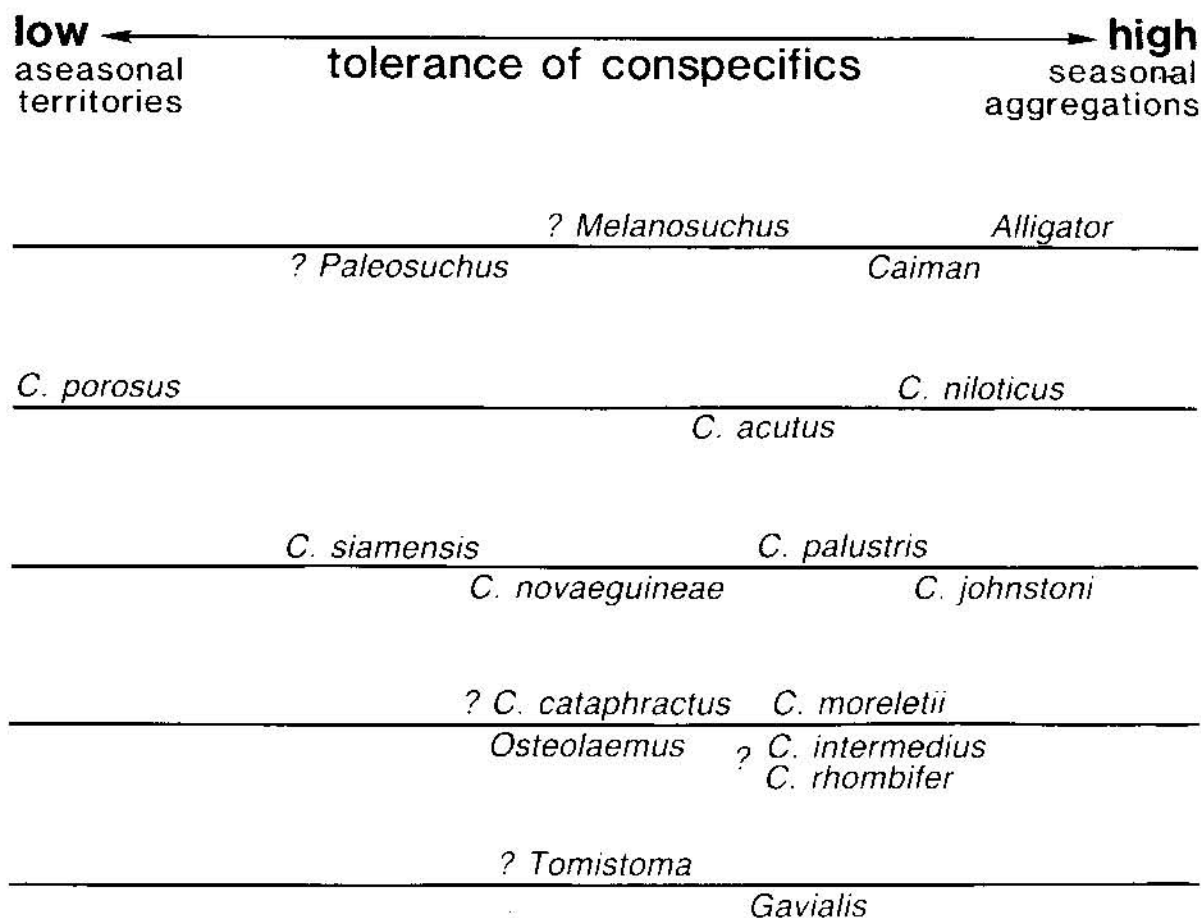


Fig. 8. Tolerance of conspecifics in crocodilian species on a continuum from low (frequent and intense aggressive interactions; right side of diagram) to high (less frequent and intense aggressive interactions; left side of diagram). Tolerance of conspecifics is correlated with social organization, ranging from aseasonal territoriality (left of diagram) to seasonal aggregation (right of diagram). The position of each species is based on behavioural observations of social interactions among adults living in captivity (*A. mississippiensis*, *Caiman crocodilus*, *Crocodylus acutus*, *C. niloticus*, *C. porosus*, *C. johnstoni*, *C. palustris*, *C. novaeguineae*, *C. siamensis*, *C. moreletii*, *Osteolaemus tetraspis*, *Gavialis gangeticus*) and/or on published information on wild populations.

Introductions of adults, either males or females, results in an immediate restructuring of the social relations within a group. If introductions occur during the breeding season when territorial and dominance interactions are heightened, then aggressive encounters are likely to intensify which may, in turn, interfere with normal reproductive activities such as mating and/or nesting. Similarly, removal of animals from social groups, particularly dominant or high-ranking members, temporarily disrupts the social organization of a group and may be detrimental to reproduction.

Extensive pen maintenance during the breeding period is likely to disrupt reproductive activities. Regular maintenance, including water of sufficient depth (>1 m) and frequent feeding, is necessary before and during the breeding period. In at least one species (*A. mississippiensis*), viable egg production has been linked to female diet. Animals fed exclusively on fish produced fewer viable young than those fed on meat (see Joanen and McNease Chapter 32).

Rearing

Growth in hatchlings and juveniles depends primarily on adequate space, abundant and varied food and a suitable range of ambient temperatures. In addition, young animals seek out shelter in which to hide and are also gregarious. Thermal behaviour is well developed in hatchlings and depends on access to temperature gradients in suitable environments. Newly-hatched young, feeding young and young with infections all select relatively high temperatures (31-35°C); at other times, lower temperatures are preferred (25-30°C). If natural or artificial gradients are incorporated into a pen design, then each animal is free to select the appropriate temperature at any time. Constant high temperatures result in weight loss unless the animals are continually fed; low temperatures inhibit feeding and increase susceptibility to disease (see Lang Chapter 30).

Young crocodilians seek out shelter and will pile on top of one another (especially in pen corners) if cover is not available. Young animals also spend a considerable portion of each day out of the water

under cover if it is provided. Presumably, exposed animals are subject to stress and are also more susceptible to climatic extremes and/or disease. Regular maintenance of pens minimizes disturbance, but handling has varied effects and may result in temporary loss of appetite.

Most hatchlings feed readily when provided with suitably-sized food and given access to heat. Hatchlings which are reluctant to feed may be stimulated by other animals feeding nearby. Varied diets are preferable to monodiets, and live food, if available, is often taken more readily than dead food. Diet may alter certain behaviours. Young *A. mississippiensis* fed on fish were shy, whereas those fed on meat were aggressive.

The normal social behaviour of young animals is to associate closely with one another, and lone individuals seek out companions when isolated. Consequently, isolation may be stressful, particularly for hatchlings. Agonistic social interactions are not evident among hatchlings, but they become increasingly apparent as animals grow and are usually obvious in juveniles > 1 m long. Aggressive interactions among pen mates this size or larger may limit feeding and growth in smaller animals; periodic sorting into groups of similar sized animals reduces this effect.

REFERENCES

- AVERY, R. A., 1982. Field studies of body temperatures and thermoregulation. Pp. 93-166 in "Biology of the Reptilia" Vol. 12 ed by C. Gans and F. H. Pough. Academic Press: London.
- BELLAIRS, A. d'A., 1971. The senses of crocodilians. Pp. 181-91 in "Crocodiles". IUCN: Gland, Switzerland.
- BJORNDAAL, K. A., 1986. Effect of solitary vs group feeding on intake in *Pseudemys nelsoni*. *Copeia* 1986: 234-5.
- BRISBIN, I. L. JR., STANDORA, E. A. AND VARGO, M. J., 1982. Body temperatures and behaviour of American alligators during cold winter weather. *Amer. Mid. Nat.* 107: 209-18.
- BROWN, C. R. AND LOVERIDGE, J. P., 1981. The effect of temperature on oxygen consumption and evaporative water loss in *Crocodylus niloticus*. *Comp. Biochem. Physiol.* 69A: 51-7.
- BUSTARD, H. R., 1984. Breeding the gharial *Gavialis gangeticus*: captive breeding a key conservation strategy for endangered crocodilians. Pp. 385-406 in "The Structure, Development and Evolution of Reptiles" ed by M. W. J. Ferguson. Academic Press: London.
- CAMPBELL, H. W., 1972. Ecological or phylogenetic interpretations of crocodilian nesting habits. *Nature Lond.* 238: 404-5.
- COLLISON, R. A., 1984. How metabolic rate and anaerobic glycolysis determine the habits of reptiles. Pp. 425-42 in "The Structure, Development and Evolution of Reptiles" ed by M. W. J. Ferguson. Academic Press: London.
- COLLISON, R. A. AND HERNANDEZ, T., 1983. "Alligator Metabolism: Studies on Chemical Reactions *in vivo*". Pergamon Press: London.
- CREWS, D. AND GARRICK, L., 1980. Methods of inducing reproduction in captive reptiles. Pp. 49-70 in "Reproductive Biology and Diseases of Captive Reptiles" ed by J. B. Murphy and J. T. Collins. Contributions to Herpetology No. 1. Society for the Study of Amphibians and Reptiles: Lawrence, Kansas.
- CREWS, D. AND MOORE, M. C., 1986. Evolution of mechanisms controlling mating behaviour. *Science* 231: 121-5.
- DAVIS, J. E., SPOTILA, J. R. AND SCHEFLER, W. C., 1980. Evaporative water loss from the American alligator, *Alligator mississippiensis*: the relative importance of respiratory and cutaneous components and the regulatory role of the skin. *Comp. Biochem. Physiol.* 67A: 439-46.
- DE VOS, A., 1982. A manual on crocodile conservation and management in India. FAO Field Document No. 10 (FO:IND/74/046), Crocodile Breeding and Management Project, Dehra Dun, India. 69pp.
- DETZ, D., 1979. Behavioural ecology of young American alligators. Unpublished Ph.D. Thesis, Univ. Florida, Gainesville. 151pp.
- FERGUSON, M. W. J., 1985. Reproductive biology and embryology of the crocodilians. Pp. 329-491 in "Biology of the Reptilia" Vol. 14 ed by C. Gans, F. S. Billett and P. F. A. Maderson. Wiley and Sons: New York.
- GALDIKAS, B. M. F. AND YAEGER, C. P., 1984. Crocodile predation on a crab-eating macaque in Borneo. *Amer. J. Primatology* 6: 49-51.
- GANS, C., 1976. Questions in crocodilian physiology. *Zoologica Africana* 11: 241-8.
- GARRICK, L. AND LANG, J. W., 1977. Social signals and behaviours of adult American alligators and crocodiles. *Amer. Zool.* 17: 225-39.
- GARRICK, L., LANG, J. W. AND HERZOG, H. A. JR., 1978. Social signals of adult American alligators. *Bull. Mus. Nat. Hist.* 160: 153-92.
- GIST, D. II AND KAPLAN, M. L., 1976. Effects of stress and ACTH on plasma corticosterone levels in the caiman *Caiman crocodilus*. *Gen. Comp. Endocrinology* 28: 413-9.
- GREENBERG, N. AND CREWS, D., 1981. Physiological ethology of aggression in amphibians and reptiles. Pp. 469-506 in "Hormones and Aggressive Behaviour" ed by B. B. Svare. Plenum: London.
- GREER, A. E., 1970. Evolutionary and systematic significance of crocodilian nesting habits. *Nature Lond.* 227: 523-4.
- GREER, A. E., 1971. Crocodilian nesting habits and evolution. *Fauna* 2: 20-8.
- GROOMBRIDGE, B., 1982. "IUCN Amphibia-Reptilia Data Book, Part 1: Testudines Crocodylia Rhynchocephalia". IUCN: Gland, Switzerland.
- HAGAN, J. M., SMITHSON, P. C. AND DOERR, P. D., 1983. Behavioural response of the American alligator to freezing weather. *J. Herpetol.* 17: 402-4.
- HERRON, J. C., 1985. Population status, spatial relations, growth, and injuries in black and spectacled caimans in Cocha Cashu. Unpublished Honours Thesis, Princeton University, New Jersey.
- HONEGGER, R. E., 1982. Breeding crocodiles in captivity, a retrospect 1960-1980. Pp. 286-97 in "Crocodiles, Proceedings of 5th Meeting of Crocodile Specialists". IUCN: Gland, Switzerland.
- HUTTON, J. M., 1982. Home range and territoriality in the Nile crocodile. *Zimbabwe Science News* 16: 199-201.
- JOANEN, T. AND MCNEASE, L., 1980. Reproductive biology of the American alligator in southwest Louisiana. Pp. 153-9 in "Reproductive Biology and Diseases of Captive Reptiles" ed by J. B. Murphy and J. T. Collins. Contributions to Herpetology No. 1. Society for the Study of Amphibians and Reptiles: Lawrence, Kansas.
- JOHANSEN, P. B. AND WELLINGTON, J. L., 1982. Detection of glandular secretions by yearling alligators. *Copeia* 1982: 705-8.
- KISTILAN, J. A. AND KUSHIAN, M. S., 1980. Function of nest attendance in the American alligator. *Herpetologica* 36: 27-32.

- LANGE, V., 1984. Endocrinology of reproduction in male reptiles. Pp. 357-83 in "The Structure, Development and Evolution of Reptiles" ed by M. W. J. Ferguson. Academic Press: London.
- LANG, J. W., 1976. Amphibious behaviour of *Alligator mississippiensis*: roles of circadian rhythm and light. *Science* 191: 575-7.
- LANG, J. W., 1977. Studies of the thermal behaviour and body temperature of crocodilians. Unpublished Ph.D. Thesis, Univ. Minnesota, Minneapolis, Minnesota.
- LANG, J. W., 1979. Thermophilic response of the American alligator and the American crocodile to feeding. *Copeia* 1979: 48-59.
- LANG, J. W., 1981. Thermal preferences of hatchling New Guinea crocodiles: effects of feeding and ontogeny. *J. Therm. Biol.* 6: 73-8.
- LANG, J. W., WHITAKER, R. AND ANDREWS, H., 1986. Male parental care in mugger crocodiles. *Nat. Geog. Res.* 2: (in press).
- LEWIS, L. Y. AND GATTEN, R. E. JR., 1985. Aerobic metabolism of American alligators, *Alligator mississippiensis*, under standard conditions and during voluntary activity. *Comp. Biochem. Physiol.* 80A: 441-7.
- LOVERIDGE, J. P., 1984. Thermoregulation in the Nile crocodile, *Crocodylus niloticus*. Pp. 443-68 in "The Structure, Development and Evolution of Reptiles" ed by M. W. J. Ferguson. Academic Press: London.
- MAGNUSSON, W. E., 1979. Dispersal of hatchling crocodiles (*Crocodylus porosus*) (Reptilia, Crocodylidae). *J. Herpetol.* 13: 227-31.
- MAGNUSSON, W. E. AND REBELO, G. II., 1983. Brazilian crocodiles: problems of conservation in a multispecies system. *Zimbabwe Science News* 17: 56-7.
- MAZZOTTI, F. J., 1983. The ecology of *Crocodylus acutus* in Florida. Unpublished Ph.D. Thesis, Pennsylvania State University, University Park, Pennsylvania. 161pp.
- MAZZOTTI, F. J. AND DUNSON, W. A., 1984. Adaptations of *Crocodylus acutus* and *Alligator* for life in saline water. *Comp. Biochem. Physiol.* 79A: 641-6.
- MESSEL, H. AND VORLICEK, G. C., 1985. Population dynamics of *Crocodylus porosus* — a ten-year overview. Pp. 71-82 in "Biology of Australasian Frogs and Reptiles" ed by G. C. Grigg, R. Shine and H. Ehmann. Surrey Beatty and Sons, Sydney.
- MESSEL, H., VORLICEK, G. C., WELLS, A. G. AND GREEN, W. J., 1981. Surveys of tidal river systems in the Northern Territory of Australia and their crocodile populations. Monograph 1. Pergamon Press: Sydney.
- MESSEL, H., VORLICEK, G. C., GREEN, W. J. AND ONLEY, I. C., 1984. The continuing and mysterious disappearance of a major fraction of sub-adult *Crocodylus porosus* from the tidal waterways in northern Australia. Pp. 33-83 in "Crocodiles: Proceedings of the 6th Meeting of Crocodile Specialists". IUCN: Gland, Switzerland.
- MODHA, M. L., 1967a. The ecology of the Nile crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. Unpublished M.Sc. Thesis, University of East Africa, Nairobi, Kenya.
- MODHA, M. L., 1967b. The ecology of the Nile crocodile (*Crocodylus niloticus* Laurenti) on Central Island, Lake Rudolf. *E. Afr. Wildl. J.* 5: 74-95.
- MODHA, M. L., 1968. Crocodile research project, Central Island, Lake Rudolf: 1967 breeding season. *E. Afr. Wildl. J.* 6: 148-50.
- MURPHY, T. M., 1977. Distribution, movement, and population dynamics of the American alligator in a thermally altered reservoir. Unpublished M.Sc. Thesis, Univ. Georgia, Athens, Georgia. 58pp.
- MURPHY, P., 1981. Celestial compass orientation in juvenile American alligator (*Alligator mississippiensis*). *Copeia* 1981: 638-45.
- NATIONAL RESEARCH COUNCIL, 1983. "Crocodiles as a Resource for the Tropics". National Academy Press: Washington.
- OGDEN, J., 1978. Status and nesting biology of the American crocodile, *Crocodylus acutus* (Reptilia: Crocodylidae) in Florida. *J. Herpetol.* 12: 183-96.
- OUBOTER, P. E. AND NANHOE, L. M. R., 1984. An ecological study of *Caiman crocodilus* in northern Surinam. Dept. Animal Ecology, Catholic University of Nijmegen, Netherlands.
- POOLEY, A. C. AND GANS, C., 1976. The Nile crocodile. *Sci. Amer.* 234: 114-24.
- PRICE, E. O., 1984. Behavioural aspects of animal domestication. *Quart. Rev. Biol.* 59: 1-32.
- REGAL, P. J., 1978. Behavioural differences between reptiles and mammals: an analysis of activity and mental capabilities. Pp. 183-202 in "Behaviour and Neurology of Lizards" ed by N. Greenberg and P. D. MacLean. Nat. Inst. Mental Health: Washington.
- RODDA, G., 1982. The orientation and navigation of *Alligator*: evidence of magnetic sensitivity. Unpublished Ph.D. Thesis, Cornell Univ., Ithaca, New York.
- RODDA, G., 1984. Movements of juvenile American crocodiles in Gatun Lake, Panama. *Herpetologica* 40: 444-51.
- SCHALLER, G. B. AND CRAWSHAW, P. G., 1982. Fishing behaviour of Paraguayan caiman (*Caiman crocodilus*). *Copeia* 1982: 66-72.
- SMITH, E. N., 1979. Behavioural and physiological thermoregulation of crocodilians. *Amer. Zool.* 19: 239-47.
- SPOTILA, J. R., SOLLE, O. H. AND GATES, D. M., 1972. The biophysical ecology of the alligator: heat energy budgets and climate spaces. *Ecology* 53: 1094-102.
- TAPLIN, L., 1984. Drinking of fresh water but not seawater by the estuarine crocodile (*Crocodylus porosus*). *Comp. Biochem. Physiol.* 77A: 763-7.
- TAPLIN, L. AND GRIGG, G. C., 1981. Salt glands in the tongue of the estuarine crocodile *Crocodylus porosus*. *Science* 212: 1045-7.
- TRYON, B. W. AND BEHLER, J. L., 1982. An update of crocodilian breeding in United States zoos. Pp. 328-36 in "Crocodiles: Proceedings of the 5th Meeting of Crocodile Specialists". IUCN: Gland, Switzerland.
- WALLACH, J. D., HORSSLE, C. AND BENNETT, J., 1967. Hypoglycemic shock in captive alligators. *Jour. Amer. Vet. Med. Assoc.* 151: 893-6.
- WEBB, G. J. W., BUCKWORTH, R. AND MANOLIS, S. C., 1983a. *Crocodylus johnstoni* in the McKinlay River area, N.T. IV. A demonstration of homing. *Aust. Wildl. Res.* 10: 403-6.
- WEBB, G. J. W. AND GANS, C., 1982. Galloping in *Crocodylus johnstoni* — a reflection of terrestrial activity? *Rec. Aust. Mus.* 34: 607-18.
- WEBB, G. J. W., MANOLIS, S. C. AND SACK, G. C., 1983b. *Crocodylus johnstoni* and *C. porosus* coexisting in a tidal river. *Aust. Wildl. Res.* 10: 639-50.
- WEBB, G. J. W. AND MESSEL, H., 1978. Wariness in *Crocodylus porosus*. *Aust. Wildl. Res.* 6: 227-34.
- WEBB, G. J. W., MESSEL, H. AND MAGNUSSON, W. E., 1977. The nesting of *Crocodylus porosus* in Arnhem Land, Northern Australia. *Copeia* 1977: 238-49.
- WEBB, G. J. W., YERBURY, M. AND ONIONS, V., 1978. A record of a *Crocodylus porosus* (Reptilia, Crocodylidae) attack. *J. Herpetol.* 12: 267-8.
- WEINHEIMER, C. J., PENDERGAST, D. R., SPOTILA, J. R., WILSON, D. R. AND STANDOORA, E. A., 1982. Peripheral circulation in *Alligator mississippiensis*: effects of diving, fear, movement, investigator activities, and temperature. *J. Comp. Physiol.* 148: 57-63.

- WHITAKER, R. AND WHITAKER, Z., 1984. Reproductive biology of the mugger (*Crocodylus palustris*). *J. Bombay Nat. Hist. Soc.* 81: 297-316.
- WOODWARD, A. R. AND MARION, W. R., 1978. An evaluation of factors affecting night-light counts of alligators. *Ann. Conf. Southeastern Assoc. Fish Wildl. Agencies* : 302.
- WRIGHT, D. E. AND MOFFAT, I. A., 1985. Morphology and ultra-structure of the chin and cloacal glands of juvenile *Crocodylus porosus* (Reptilia, Crocodylia). Pp. 411-22 in "Biology of Australasian Frogs and Reptiles" ed by G. C. Grigg, R. Shine and H. Ehmann. Surrey Beatty and Sons, Sydney.

APPENDIX 1

A SYNOPSIS OF CROCODILIAN BEHAVIOUR

Maintenance Behaviour

Daily and seasonal activity: land/water movements; circadian rhythms; hibernation; aestivation.

Locomotion: adept swimmers; prolonged diving; walking, dashing, galloping, climbing on land.

Prey capture/feeding: indiscriminate feeders; range of prey types/sizes; sophisticated prey capture.

Temperature selection: heat seeking/avoidance; species-specific preferences; directly affects growth.

Water and salt balance: dehydration without periodic access to water; behavioural osmoregulation.

Site fidelity: familiar home ranges; navigation/homing capabilities; seasonal dispersal/migration.

Habitat modification: digging with front/hind limbs; nest clearings/wallows; tunnels/burrows.

Shelter seeking: evident in all ages/sizes; pronounced in hatchlings; piling and stress if no cover.

Temperament and stress: aggressive versus docile species; stress from capture/handling/disturbance.

Habituation and learning: habituate to humans; associative/avoidance learning; social facilitation.

Interspecific interactions: poorly documented; habitat segregation by competition or predation.

Social Behaviour

Communication: vocal, visual, acoustic signals; movements, postures; chemosensory/tactile modes.

Gregarious behaviour: hatchling/juveniles; species-specific response to seasonal breeding/drought.

Dominance hierarchies: size/sex dominance; favours large males; disrupted by introduction/removal.

Territorial behaviour: intense during breeding; defence of mates, nests, young; seasonal versus aseasonal.

Reproductive Behaviour

General: maturity, reproduction is size/sex dependent; breeding seasonal, extended 6-9+ months/year.

Courtship and mating: large males dominate; species-specific courtship; polygynous mating system.

Nesting and incubation: mound versus hole; solitary versus colonial; nest attendance/guarding by female.

Hatching and post-hatching: adults excavate hatchlings; mouth transport; lengthy defence of young.