

# Behaviour of the Australian crocodiles, *Crocodylus johnstoni* and *C. porosus*

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Behaviour associated with thermoregulation, activity, feeding and hunting, voluntary diving, responses to other animals and defensive displays are described for *Crocodylus johnstoni* and *C. porosus*.

Reactions to various animals are discussed and defensive behaviour at the intra- and interspecific levels are discussed.

## CONTENTS

Introduction	315
Methods and materials	316
Behaviour of <i>Crocodylus johnstoni</i>	318
Thermoregulatory behaviour	318
Activity and movements	319
Feeding behaviour	320
Voluntary diving	320
Reactions to other animals	321
Defensive display	322
Behaviour of <i>Crocodylus porosus</i>	322
Thermoregulatory behaviour	322
Activity and movements	324
Hunting and feeding behaviour	325
Voluntary diving	328
Reactions to other animals	328
Defensive display	329
Discussion	329
Summary	333
Sumario	334
Acknowledgements	335
References	335

## INTRODUCTION

*Crocodylus johnstoni* is restricted to longirostrine environments in northern Australia. The other Australian species is the longirostrine, estuarine *C. porosus* which inhabits much of the Old World tropics. *C. porosus* is widely distributed in India, Indochina, the Malay archipelago, New Guinea, Solomon Islands,

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northern Australia, and Fiji Islands (Cogger, 1960; Bellairs & Carrington, 1966; Sill, 1968). The fact that *C. porosus* is well adapted to salt water probably accounts for its wide distribution. In some areas, such as the Sunda Archipelago, this species has become entirely marine, living within the tidal zone (Mertens, 1960).

Although a vast amount of literature exists on reptilian behaviour, the majority concerns studies on saurians and to a lesser extent on ophidians. Few studies have dealt with crocodylian behaviour and such studies have usually been incorporated in investigations dealing with their biology, ecology and physiology. *Crocodylus niloticus* is best known from a behavioural aspect based upon important investigations such as Cott (1954, 1961) and Cloudsley-Thompson (1964).

The present study was designed to investigate both the thermoregulation and behaviour of two species of crocodiles in the free-living condition, and this paper deals with the latter aspect.

#### METHODS AND MATERIALS

The study area was located about 12 miles north of Cooktown, Cape York Peninsula, Queensland, on property owned by Charles Tanner. A small pond covering an approximate area of 147 m<sup>2</sup> and about 1.5 m deep at the deepest part was selected for study (Fig. 1). Bordering the western edge of the pond was dry sclerophyll forest. On the other edges, there was no vegetation within 5 m. Some logs and a small tree were placed at the water's edge to add shade as the pond was devoid of debris and lacked aquatic vegetation. The northern and eastern banks were steep, whereas the western and southern banks sloped gradually and provided a considerable area of shallow, muddy bottom along the edges. The pond was surrounded on all but the western side with a wire netting fence (1.4 m high), a safety precaution in case the crocodiles tried to move towards the Endeavour River (approximately 0.25 mile to the east). At no time did any of the crocodiles approach the fence at least 5 m from the water's edge.

A blind was constructed at the southern end of the pond amongst some small forest vegetation approximately 15 m from the water's edge. Observers could approach and leave the blind without being seen by the crocodiles. A dingo, *Canis dingo*, approached the pond one morning and did not appear to detect the observer's presence; similarly there was no response from the crocodiles indicating disturbance.

Environmental temperatures (electronic thermometer) and body temperature (radio telemetry) of some of the crocodiles were measured and will be reported upon elsewhere (Johnson *et al.*, in prep.).

Two *C. johnstoni* were purchased from commercial collectors, and had been in captivity for approximately four weeks before being used. One of these had a radio transmitter surgically implanted in the body cavity. Charles Tanner owned all the other crocodiles (14 *C. porosus* and 2 *C. johnstoni*); originally from the upper Herbert River (12 *C. porosus*), Endeavour River (2 *C. porosus*) and the Ham River (2 *C. johnstoni*), all in north Queensland. They ranged from 0.3 to 0.6 m at capture and had since been maintained in a fenced enclosure (47 m<sup>2</sup>) at Cooktown for three years. One of the *C. porosus* was released with

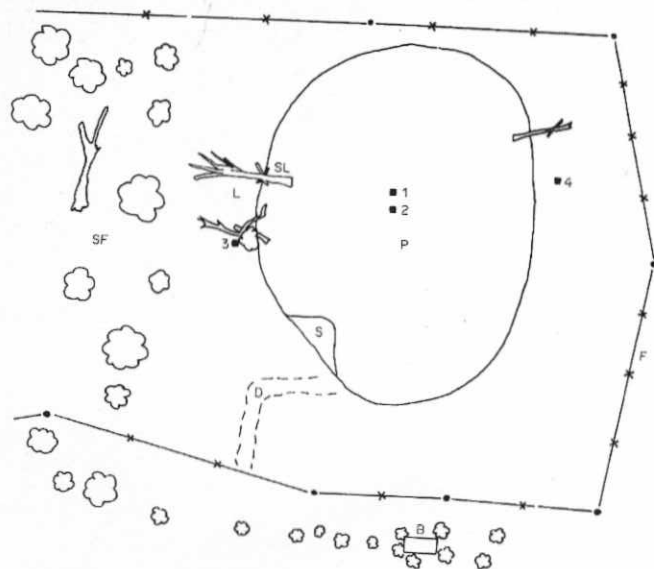


Figure 1. Map of study area. B, Blind; SF, sclerophyll forest; D, ditch; S, sand spit; L, log; SL, submerged log; P, pond; F, fence. Black squares indicate placement of probes used in measuring environmental temperatures.

a transmitter, and one of the *C. johnstoni* was released without a transmitter. A number of previous observations by Tanner are reported here.

The first *C. johnstoni*, 42 cm s-v length, was released in the pond at 10.00 hrs on 30 September, and intensively observed until 07.00 hrs, 2 October, when the transmitter failed making it necessary to remove the crocodile from the pond. The *C. porosus*, 60 cm s-v length, was released on 2 October (11.00 hrs) and intensively observed until 8 October (09.00 hrs). After this the crocodile was observed at irregular intervals until 11 October (17.00 hrs). Night observations were made when possible by the light of the moon. Human interference was minimized, however, the *C. porosus* was fed twice at dusk and the *C. johnstoni* was disturbed once when the investigator removed some cattle from the pond. After seven days of observation on the *C. porosus*, two *C. johnstoni*, approximately 48 and 52 cm s-v length, without transmitters were released in the pond. Observations on their behaviour were taken for comparison with the *C. johnstoni* which had a transmitter surgically implanted. Any interaction between the two species was noted both in the pond and in the enclosure at Charles Tanner's home.

BEHAVIOUR OF *CROCODYLUS JOHNSTONI*

## Thermoregulatory behaviour

The following description of one day's events typified the animals thermoregulatory behaviour over the entire period of observation. Shortly after sunrise at approximately 06.20 hrs, *C. johnstoni* was in the water with its head and snout against the western bank at right angles to the edge. Shortly after the sun's rays touched the animal (06.40 hrs, approximately) it started moving up onto the bank, and remained there about 15 minutes before re-entering the water. After swimming briefly, the *C. johnstoni* again crawled out on the bank and assumed a position near the shore parallel to the water's edge. The body was curved with the inside of the arc toward the sun. He remained there for about 20 minutes, then re-entered the water and swam for about six minutes. Little increase in body temperature occurred during this whole period.

The crocodile repeatedly shuttled between water and land until about 08.00 hrs when he crawled out onto the bank and positioned himself at right angles to the sun's rays as before. This time the *C. johnstoni* was lying completely out of the water and flat against the wet mud; there was a slight curve to the body. The legs were placed back beside the body, as is characteristic of many basking lizards (Bustard, 1970; Heatwole, 1972a). After about 2.5 hours of basking in this position body temperature attains the preferred range ( $31.3^{\circ}$ - $32.5^{\circ}$ C). Once during this basking period the animal's position was changed to face the sun. Twice the head was lifted off the substrate and jerked rapidly from side to side (presumably irritated by insects). At 10.20 hrs while basking the *C. johnstoni* moved closer to the water's edge, having remained on wet soil during the entire basking period. When upper preferred temperatures were reached, head and snout were placed in the water, remaining in this position until body temperatures had increased to  $33.5^{\circ}$ C (approximately 20 minutes). After completely entering the water the crocodile immediately swam about, made several dives and then crawled out on the bank again. This procedure probably served the purpose of moistening the skin, as it did not lower the body temperature, but may have some thermoregulatory significance not shown by mere body temperature (Johnston *et al.*, in prep.). After ten minutes the crocodile re-entered the water, swam back to the bank and placed its head flat against the wet sand at the water's edge, with the rest of its body floating just under the surface. This position was kept for about 1.2 hours, after which the crocodile slowly moved up onto the bank. Body temperature decreased during this period. All of the body was exposed and again curved with the inside of the arc toward the sun (13.50 hrs). The crocodile remained basking in the sun for 20 minutes, when it became shaded by the shadow from a nearby tree. After remaining in the shade for an hour the crocodile moved into the water, dived and then floated on the surface with the head and nasal disk exposed. The crocodile made a number of dives and swam about for approximately ten minutes, after which it moved towards the shore to a shady patch of water. It remained the rest of the afternoon with its nasal disk and head against the bank, or diving and swimming and occasionally basking in the shallows.

Two other freshwater crocodiles relaxed in the pond, without temperature transmitters, behaved somewhat differently. At no time were they observed to

bask on the shore; instead they basked in the shallows with their snouts and heads against the bank or up on the mud and backs partially exposed.

Figure 2 diagrams the sequence of events which occurred in thermoregulatory behaviour.

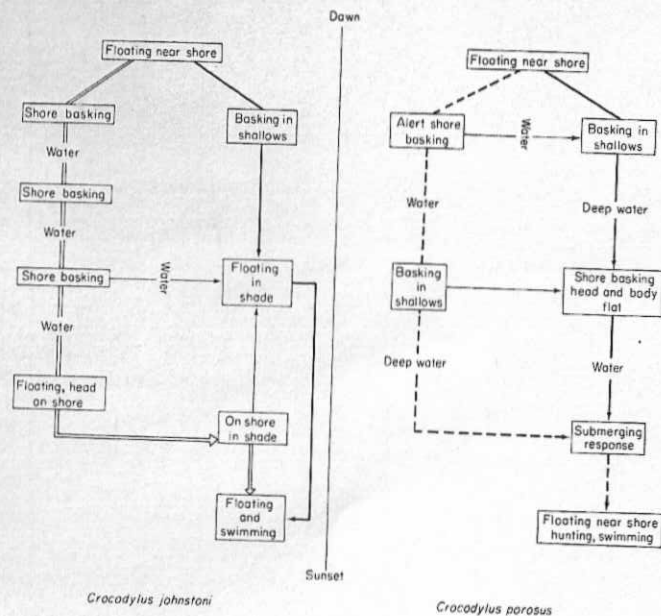


Figure 2. Sequence of thermoregulatory behaviour during daylight hours. With *C. johnstoni*, dark solid arrows indicate behaviour of crocodiles without transmitters and open arrows indicate behaviour of crocodile with implanted transmitter. Light solid arrows indicate behaviour which sometimes occurred. With *C. porosus*, dashed dark arrows indicate usual behaviour and light solid arrows indicate behaviour which may occur occasionally.

Gaping of the mouth was also observed to occur with the *C. johnstoni* when basking in the enclosure at Charles Tanner's home, but was not observed at the pond.

## Activity and movements

The movements of the *C. johnstoni* with the transmitter were somewhat restricted to shallow areas containing logs either above water or submerged (Fig. 3A). Several shore basking sites were utilized but preference was given to the area near the sand spit. When two freshwater crocodiles were released in the pond together they maintained distinct areas (Fig. 3B), although the area

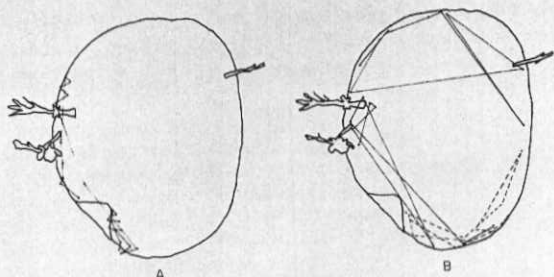


Figure 3. Activity and movements of *C. johnstoni*. A. Movements of *C. johnstoni* with implanted transmitter. B. Solid lines indicate movements of two *C. johnstoni*. Dashed lines indicate the movements of *C. porosus* which overlaps with the movement of one *C. johnstoni*. All data collected between 06.00 and 19.00 hrs on 1 October (A) and 10 October (B).

of one freshwater crocodile overlapped with that of the *C. porosus*. No interaction occurred between *C. porosus* and *C. johnstoni*, although the range of the *C. porosus* appeared to decrease after introduction of the freshwater crocodiles. Body size may play a distinct role in the area of the home range as the larger freshwater crocodiles moved over a greater area than the smaller one. It is interesting to note that when the two freshwater crocodiles without transmitters were netted from the pond at the end of the experiment, they were caught on the bottom in the deepest part of the pond. Retreat to deep water may thus be a normal escape response.

Activity at night consisted mainly of swimming about on the surface and considerable periods of time floating on the surface several metres offshore facing shoreward.

#### Feeding behaviour

Long-term observations have shown that *C. johnstoni* prefer to eat fish (dead or alive) rather than meat (Tanner, pers. comm.). However, *C. johnstoni* was not observed to feed in the study pond, although it contained an abundant supply of fish up to 13 cm long. They spent considerable time diving (presumably fishing) and it is possible that they do not have to surface to swallow, although this is commonly thought (Pope, 1956; Cogger, 1960; Cott, 1961).

#### Voluntary diving

Dives were classified into four main categories: (1) swimming underwater from one place to another, (2) short submergences made after basking probably serving to moisten the skin and possibly to reduce head temperature (not to be confused with the submerging response of *C. porosus*), (3) feeding dives (assumed), and (4) escape dives. Figure 4 shows the time in seconds of each type of dive. Post-basking dives lasted the shortest amount of time whereas escape dives were the longest. Freshwater crocodiles appear to have longer

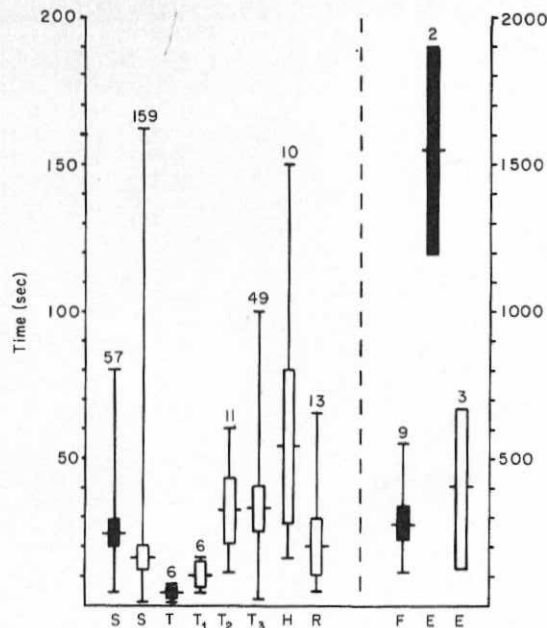


Figure 4. Voluntary diving times in seconds observed in the field on *C. johnstoni* (dark rectangles) and *C. porosus* (open rectangles). All data right of dashed line refer to times on right axis and data to the left refer to left axis. S, Swimming underwater from one place to another; T, thermoregulatory; T<sub>1</sub>, head bobbing; T<sub>2</sub>, submerging of nasal disk during submerging response; T<sub>3</sub>, total submergence during submerging response; H, hunting; R, skin conditioning; F, fishing; E, escape dives. Vertical lines, ranges; horizontal lines, means; rectangles, 2 S.E.'s; numbers above vertical lines refer to sample sizes.

diving times than estuarine crocodiles; this is probably due to the need to remain submerged for long periods during fishing. Diving does not appear to play such an important thermoregulatory role in freshwater crocodiles as it does in estuarine crocodiles.

#### Reactions to other animals

The *C. johnstoni* showed no visible reaction to the distant approach of three cows on the opposite side of the pond (13.20 hrs). When the cows circled the pond, approached the edge to drink and came within 6 m of the freshwater crocodile, it dived and swam towards the opposite end. He surfaced about 9 m away from where the cows stood at the water's edge. The crocodile then swam slowly continually watching the cows from about 12 m away. As the cows

circled the pond to leave, the crocodile turned and dived, surfacing in the middle and watched them depart.

A different reaction was elicited when approached by the investigator and colleague (07.00 hrs). The *C. johnstoni* submerged when we were 12 to 15 m from him. On arriving at the spot where he had last been seen, we saw him lying on the bottom in about 20 cm of water a metre from shore. The crocodile was easily captured by slowly moving a snake stick toward its neck and quickly grabbing it. The crocodile proved more wary on subsequent encounters, as has also been shown with *C. porosus* (Bustard, 1968).

A pair of mudlarks, *Grallina cyanoleuca*, landed a metre away from a *C. johnstoni* which had its head against the shore (07.20 hrs). The mudlarks entered the water, bathing and splashing. The crocodile paid no attention to them, nor to any other birds coming to the pond to drink or feed during the study.

#### Defensive display

When an investigator approached to within 1.5 to 1.8 m the freshwater crocodiles opened their mouths and on occasions raised their bodies from the ground. If approached closer they would sometimes make short lunges, in several instances actually running towards the investigator in a series of short lunges. They kept their bodies high off the ground and mouths open during these attacks. They could be bluffed by yelling and counter-attacking, hitting them lightly with a broom on the back or hitting the ground hard in front of them (Tanner method). Occasionally while on retreat, the animals would suddenly whip around, lunging back at the attacker. This response was seldom elicited in the freshwater crocodiles when they were threatened by the *C. porosus* sharing the enclosure; they usually retreated without defensive displays.

#### BEHAVIOUR OF *CROCODYLUS POROSUS*

##### Thermoregulatory behaviour

The following description is typical of an average day's events. At 07.10 hrs the *C. porosus* was near the eastern shore floating in the sun with head, snout and back partially exposed. The crocodile remained in this position until 08.22 hrs when he crawled out on shore, along the steep bank and began basking at right angles to the sun's rays. The *C. porosus* lay on the dry ground about 1.8 m from the water's edge. Two minutes later the crocodile shifted position to about 2.4 m above the water line. The head was held high (about 0.3 m) off the substrate with the body flat and legs in a normal position. This posture is subsequently referred to as the "alert basking posture" (Fig. 5A). Three minutes later the crocodile again shifted position with its head facing downward toward the water. The basking posture otherwise remained the same. Eight minutes from the time he first moved to land he re-entered the water. During this brief basking period body temperature only rose slightly (less than 0.5° C increase). The *C. porosus* swam along the shore, for about 20 minutes then entered the shallows at the south end to bask there, with his head

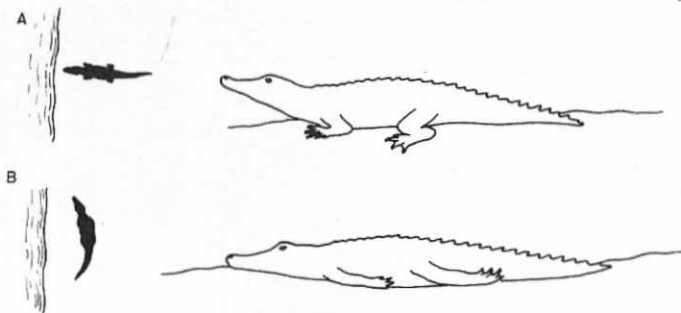


Figure 5. Shore basking postures of *C. porosus*. A. Alert basking posture. B. Shore basking in flat basking posture. Black crocodiles show posture from above and their relative position to the water's edge.

on the mud and most of his back and tail exposed. He remained so, occasionally moving about in the shallows either submerging to wet his body or occasionally splashing water onto his back with the forelimbs and onto his lower back and tail with the hindlimbs.

At about 10.00 hrs body temperature had risen several degrees (29.5° C) and the crocodile entered deeper water for a short swim. Sometimes a second shore basking period took place at this time. This second basking period varied in posture from the alert basking posture in that the crocodile remained near the water's edge with the head and body close to the substrate and with the legs back along the sides of the body (Fig. 5B). After about five minutes he again entered the shallows and exposed most of his body. Basking lasted until 11.00 hrs, when the crocodile had another swim, returning to the shallows four minutes later placing his head on the mud. By 11.25 hrs his skin appeared dry and body temperature had increased 3.0° C ( $T_B = 32.5^\circ C$ ). He remained so until 12.00 hrs ( $T_B = 34.5^\circ C$ ). Often the crocodile covered his back and head with mud during long periods of basking in the shallows. At 12.00 hrs he entered the water and started undergoing a "submerging response", which lasted all afternoon until 18.00 hrs by which time his body temperature had only decreased 2.0° C (32.5° C). Even though shade was present on both water and shore, the crocodile made no attempt to enter it, but continued the submerging response. This response can be described basically as follows: The *C. porosus* was usually floating on the surface about 1.2 to 3 m offshore with only the nasal disk, eyes and occiput exposed (Fig. 6A). He then closed his nares and kept the nasal disk underwater with his eyes above the surface for a period of time lasting from 11 to 60 seconds (Fig. 6B), then raised it above water for a breath (Fig. 6C), then immediately submerging into a dive for a period lasting from 2 to 99 seconds (Fig. 6D). The crocodile then surfaced, breathed, and again submerged the nasal disk. Sometimes he made repetitious dives without the nasal disk submerging sequence taking place. He did not shift his position, but remained in one place during submerging and surfacing.

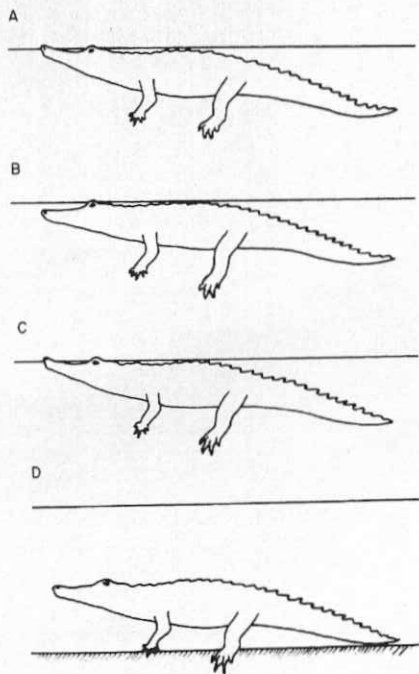


Figure 6. Sequence of submerging response in *C. porosus*. A. Normal floating posture. B. Submergence of nasal disk. C. Taking a breath. D. Total submergence to bottom.

Figure 4 compares data on the times of these dives and this submerging response. The significance of the submerging response and other thermoregulatory behaviour will be discussed elsewhere (Johnson *et al.*, in prep.). Sometimes the alert basking sequence does not take place (Fig. 2). Gaping of the mouth was observed often with basking *C. porosus* in the enclosure but not in the study pond.

#### Activity and movements

In *C. porosus* activity appears to vary considerably from day to day (Fig. 7A, B). Activity appears to depend upon the amount of time spent hunting. Most of the crocodile's movements across the pond involved stalking prey. Other activity usually involved swimming around the edges. In contrast to the freshwater crocodile's movements the entire pond was utilized. Alert basking took place usually on the steeper banks and with this coupled with posture

(head held high off substrate and legs normal) the crocodile had a substantial view of its surroundings and was alert to any impending danger; shallow water basking usually occurred in the gradually sloping areas. The submerging response always took place in the southern end of the pond immediately offshore from the shallow areas.

Activity at night occurred both in shallow and deep areas (Fig. 7C). Actual observations showed *C. porosus* making rapid short dives from 2 to 15 seconds and swimming about rapidly at times on the surface. Considerable time was also spent (up to several hours) in one area usually 0.6 to 2 m offshore, facing shoreward. *C. porosus* was less frightened at night by the approach of the investigator and would actually come out of the water and chase the investigators at dusk or after dusk if they ventured too close to the water's edge. Their eyesight appears to be somewhat limited after dark.

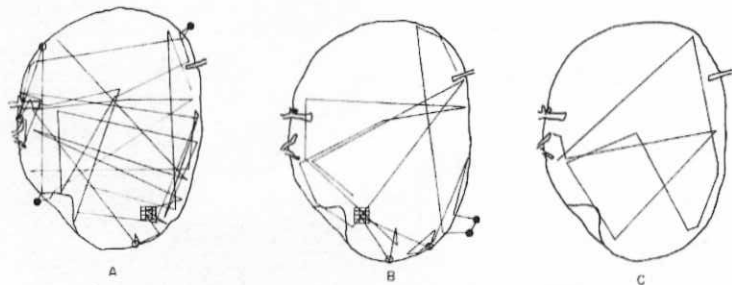


Figure 7. Activity and movements of *C. porosus*. A. Movements of *C. porosus* on 4 October, 06.00 to 19.00 hrs and B, on 5 October, 06.00 to 19.00 hrs. Cross-hatched squares indicate areas used for submerging response, open circles indicate areas used for shallow water basking and dark circles indicate areas used for shore basking. C. Movements of *C. porosus* on 5 and 6 October, 21.00 to 04.00 hrs.

#### Hunting and feeding behaviour

The following is a description of observed events and encounters with various types of animals. It is presented in sequential order so that an estimate of feeding intensity can be determined.

On 2 October at 17.25 hrs a pair of mudlarks, *Grallina cyanoleuca*, flew to the water's edge for a drink. The *C. porosus* was floating about 4.5 m offshore at the time. It noticed them immediately, dived and surfaced about 0.3 m from the birds and lunged up on the bank, but missed them. It quickly swam out with only his eyes exposed and waited offshore. The birds now alerted, cautiously approached the water's edge for a second time. The crocodile again dived and came up exactly where the birds had been when it had last seen them, they having moved further along the shore. When the crocodile surfaced, the birds, frightened flew to the opposite shore. The crocodile watched them land on the bank at the water's edge about 12 m from him. He immediately dived and came up in the exact spot that they were standing when he dived.

The birds had kept moving along the shore. The crocodile repeated this performance five times, each time surfacing exactly where the mudlarks had been.

At 18.45 hrs a live black and white rat, *Rattus norvegicus* was thrown into the water approximately 4.5 m from the *C. porosus*. Upon hitting the water the rat began swimming toward the opposite shore. The crocodile immediately saw it, pursued it on the surface, caught it and dived. The crocodile did not surface for several minutes, and did not appear to have swallowed the rat as swallowing would probably have to take place on the surface (Cogger, 1960; Cott, 1961; Tanner, pers. comm.), although Pope (1956) stated that very small food items may be swallowed when the crocodile's head is submerged.

On 3 October at 06.30 hrs, a mudlark landed on the shallow bank near the water's edge. The crocodile observed it and moved slowly along the shore on the surface for about 3 m. When within about 4.5 m of the bird the crocodile dove. The bird was wary and possibly noticed the ripples made by the crocodile submerging, and he moved up the bank away from the water 0.6 m. The crocodile surfaced about 0.3 m from the shore, near where the bird had been. Seeing the bird had moved away, the crocodile backed off and stirred up the mud with his body and tail. This manoeuvre appeared to be deliberate and might possibly have been to aid in cover or camouflage. At this moment another mudlark landed on the opposite shore about 15 m from the crocodile, arousing his attention. The crocodile submerged and surfaced about 1.5 m off the bank from where the bird was standing. The alerted bird remained about 0.6 m up the bank from the water's edge. The crocodile remained floating offshore about 1.5 m with only his eyes exposed, occasionally lifting his nasal disk for a breath. He remained so until 06.55 hrs, when the mudlark from the other side of the pond landed and began slowly moving along the bank. The crocodile began diving and surfacing, surfacing each time where the bird had been when he observed it before each dive. When the bird became alerted and moved away from the water's edge, the crocodile swam right up to the shoreline and appeared to hide his head behind a partly overhanging section of bank. The bird saw the crocodile, displayed by extending its wings and alarm calling, and then flew off.

At 07.50 hrs the crocodile while floating about 1.5 m offshore swam quickly shoreward, crawled up onto the bank about 0.6 m, turned his head sideways and caught a small frog in his jaws and ate it. He then quickly backed off the bank, into the water. The distance was too great for species identification, although *Litoria nasuta* and *L. latopalmata* (formerly *Hyla*; see Tyler, 1971) were often seen around the pond during early morning and evening.

At 08.11 hrs, two peaceful doves, *Geopelia striata*, landed on the shoreline and started to drink. The crocodile moved toward them on the surface. As the crocodile submerged the birds saw him and moved up the bank about 0.6 m. When the crocodile surfaced it remained motionless about 1.2 m from the birds. One obviously curious dove approached cautiously but stayed about 0.5 m from the water. The crocodile submerged all but his eyes and slowly moved closer. The doves flew off.

At 15.07 hrs, the crocodile swam very close to the water's edge and appeared to watch several large wasps (Sphecidae) that frequented the muddy edge

around the pond. The crocodile watched them for a few seconds then backed off into deeper water.

Later at 15.58 hrs, a pair of mudlarks landed between the logs on the western shore. The crocodile's behaviour was similar to his previous hunting behaviour with birds, except that this time he used one of the partly submerged logs for cover. Several dives put him near the logs and he surfaced with only his eyes exposed next to one of the logs. He remained motionless waiting for the birds to advance to the water's edge near the log. After about 10 minutes, the birds moved further along the shore and the crocodile followed diving and surfacing as described before, but without success.

On 4 October at 06.20 hrs, the crocodile attempted to catch two drinking common bronzewings, *Phaps elegans*, using the same tactics as previously described, but without success.

Later in the morning (09.00 hrs) while the *C. porosus* was basking in the shallows at the southern end of the pond, he stirred up the mud and leaves in about 15 cm of water. He then surfaced with the *Rattus norvegicus* in his jaws; the same black and white rat which he had caught after it was thrown into the pond approximately 40 hours before. Apparently the crocodile had buried it in the muddy bottom in the shallows. He held it in his jaws above the water and flicked his head violently from side to side several times until the rat was torn in half. He then swallowed the half still in his mouth. The crocodile then swam over to the other half, floating in the water, picked it up, spending some time positioning the rat lengthwise in his jaws, before lifting his head out of the water and swallowing. He then returned to basking until 09.48 hrs at which time he swam out into the water about 20 to 23 cm deep to moisten his skin. After working his jaws around in the mud and leaves, he caught a fish about 10 cm in length. The crocodile held it up in the air and swallowed it tail first with far less difficulty than he had swallowing the rat.

In the afternoon at 16.32 hrs, a pair of mudlarks arrived at the pond. They were definitely attracted to the crocodile. They landed on the bank about 0.6 m from the water's edge directly in front of where the crocodile was floating about 1.8 m out from the bank. As soon as the birds landed they displayed their wings extended and called. They refused to approach closer than about 0.6 m from the water's edge. The birds repeated their display a number of times. Then one of the mudlarks took off and flew directly over the crocodile's head, and began hovering and displaying (mobbing behaviour). It then flew to the opposite shore. The crocodile dived and headed towards the bird that had landed using the same tactics as described before. The bird took several drinks but remained alert. As the crocodile surfaced the bird flew back across the pond. The crocodile followed diving and surfacing 1.5 m offshore from where the bird had landed. The bird was alert and had moved 1 to 1.2 m back up the bank. The mudlark displayed as the crocodile surfaced.

Later in the evening (18.38 hrs) a dead, black and white *Rattus norvegicus* was left on the shore near the water. The crocodile took it off the bank and backed off into the water. Again the crocodile was not seen to swallow it.

On 5 October at 06.48 hrs the crocodile entered the shallows on the southern end of the pond. Within seconds he had dug up the same black and white rat fed to him some 12 hours before. Again the crocodile flicked it in

half, but only ate the part that remained in his jaws. At 09.32 hrs he returned to the piece of the rat which was floating but did not eat it. He then returned to his basking in the shallows.

At 09.35 hrs a mudlark arrived at the pond and displayed at the basking crocodile. The bird remained about 0.6 m from the water's edge and repeatedly displayed but elicited no reaction from the crocodile.

At 11.02 hrs the crocodile swam over to the piece of floating rat and bit at it, but did not eat it. The piece still remained uneaten at 11.30 hrs the following day.

On 7 October at 22.36 hrs, as the crocodile was swimming along the south bank about 2.4 m offshore he saw a large *Bufo marinus* near the water's edge. The toad's movement probably attracted the crocodile's attention. Upon seeing it he immediately turned and headed straight for it, but stopped and turned at about 0.3 m from the toad and continued along the shore, taking no further interest in it.

#### Voluntary diving

Diving has been divided up into five basic categories as follows: (1) swimming underwater from one place to another, (2) thermoregulatory, (3) hunting and feeding, (4) skin conditioning and (5) escape. Within the thermoregulatory category there are three subcategories: (i) head bobbing or ducking the head under the surface rapidly, (ii) submerging the nasal disk (submerging response) and (iii) complete submergence of entire head and body (submerging response). In *C. porosus* no significant differences were found (overlap of two S.E.'s) at the 5% level between times of submerging and submergence of nasal disk, but a significant difference was found between these categories and that of head bobbing, although low numbers of observations within some categories limit these comparisons (Fig. 4). The widest range in time was found within the swimming underwater category. The skin conditioning category fell within the normal swimming underwater range and consisted of the crocodile rubbing his skin against submerged logs presumably to scrape off old skin. Large differences were found when comparing escape response between those of freshwater and estuarine crocodiles. *C. porosus* stayed under once for 11 minutes after being frightened whereas times of 23 and 28 minutes were recorded for the *C. johnstoni*.

#### Reactions to other animals

The *C. porosus* during shallow water basking at 11.00 hrs observed three cows approaching the pond and moved off into deeper water, dived and surfaced on the opposite side of the pond. As the cows approached close to the water's edge to drink, the crocodile dived and surfaced beside one of the partly submerged logs taking cover behind it. As they moved several metres closer around the edge of the pond the crocodile actually moved under a overhanging log next to the bank, keeping out of their sight. He continually watched the cows until they had left the pond and had moved at least 40 m away from the water's edge.

No aggression was noticed in the pond between the *C. porosus* and the *C. johnstoni* that were later released, although occasionally aggression occurred

within Charles Tanner's home enclosure between the two species. With *C. porosus*, intraspecific aggression was far more the case.

As mentioned previously all the *C. porosus* had been raised from individuals ranging from 0.3 to 0.6 m in size in the enclosure, but one individual became dominant and obtained more food; it reached a total length of 1.8 m. This individual has taken over the pond (2.5 m<sup>2</sup>) in the enclosure and will not allow the other *C. porosus* to enter it. If they do they are immediately attacked and repelled violently from the pond. The same aggression is not shown toward the *C. johnstoni* and on numerous occasions they were observed to enter the pond even when this dominant individual occupied it; no aggression was shown. To date sex has not been determined for this dominant individual. Each evening the dominant *C. porosus* harasses the other *C. porosus* in the enclosure by chasing them about the enclosure and biting their tails in a display of dominance. This dominant crocodile is particularly aggressive at feeding time. This individual has also made several attempts at attacking Charles, by submerging in the pond when Charles entered the enclosure and waiting for him to come near, then lunging up and out onto the bank in an attempt to grab him.

#### Defensive display

The defensive display appears to be the same for that described for *C. johnstoni* except that *C. porosus* is more aggressive and persistent in attacking situations. Smaller individuals are easily bluffed by counter-attacking and even the dominant *C. porosus* can be bluffed if the counter-attack is vigorous enough.

#### DISCUSSION

Thermoregulatory behaviour varied considerably between *C. porosus* and *C. johnstoni*. Shore basking was observed in both species, although in *C. porosus* shore basking only lasted for short intervals. The *C. johnstoni* with the transmitter spent long periods of time shore basking while the two without transmitters spent most their basking time in the shallows. It is possible that the presence of the radio transmitter may have affected the behaviour of this particular animal. Basking postures were similar in both species. A submerging response was observed and described in *C. porosus* whereas no such or similar response was observed in *C. johnstoni*. The *C. johnstoni* instead used shuttling between the shade-sun interface to maintain preferred temperatures. Similarities between thermoregulatory behaviour and the general diurnal rhythms of both *C. johnstoni* and *C. porosus* can be found with those of *C. niloticus* as described by Cott (1961) and Cloudsley-Thompson (1964). All species are nocturnally aquatic. All three species undergo a morning shore basking period. Cott (1961) stated that early morning basking in *C. niloticus* served to restore the heat lost during the night. This did not appear to be the case with *C. porosus* as shallow water basking appears to be the main behaviour for raising the body temperature to the preferred range in the morning. The results were less consistent with *C. johnstoni*, although larger individuals



without transmitters appeared to prefer shallow water basking over shore basking as opposed to the shore basking used by the smaller, transmitter carrying individual. Cott (1961) found two main shore basking periods to occur in *C. niloticus*, between 07.00 and 09.30 hrs and between 14.30 and 17.30 hrs. During the heat of the day *C. niloticus* returned to water or to shade. During cloudy weather, *C. niloticus* did not return to water in the heat of the day. Cloudsley-Thompson (1964) found under experimental conditions a weak 24-hour periodicity of activity and rest and a peak in activity in the early evening hours, but activity appeared to be highly dependent upon weather conditions, being less marked in hot than in cooler weather. Both *C. johnstoni* and *C. porosus* were highly active in the early morning and late evening hours and at irregular periods throughout the night. *C. johnstoni* spent the heat of the day mostly inactive basking or in the shade, whereas *C. porosus* was highly active throughout the afternoon while undergoing the submerging response. *C. niloticus* had a greater tendency to shore bask when the weather was hot than during colder conditions. Both *C. porosus* and *C. johnstoni* waited till the sun was on them before they moved onto the shore and began basking. If the weather was overcast *C. porosus* did not shore bask, but if intermittent sun appeared the *C. porosus* would move ashore or quickly into shallow water and began basking.

Gaping of the mouth was observed by both species in the enclosure but was never observed to occur in the pond. Cott (1961) reported that *C. niloticus* usually gaped when lying ashore or partly submerged, but its effect on body temperature was not demonstrated. It is known that if some crocodiles are restrained in direct sunlight with their jaws roped together their temperature rises beyond the normal activity range and death ensues (Shelford, 1916), but this would probably occur even if the crocodile were permitted to gape, although gaping would probably forestall death for a longer period. Cott (1961) found that gaping increased progressively during the morning hours when external temperatures were rising and that a higher percentage of crocodiles in the sun gaped than those in the shade. Gaping has been mentioned by Bellairs & Carrington (1966) as a method of temperature control by evaporative cooling and was pictured in a basking *C. palustris*. Mertens (1960) presented a photograph of *C. cataphractus* gaping while basking. Gaping probably also acts to reduce head temperature during basking and is probably widespread among crocodilians. Although no data were collected on head temperature some of the thermoregulatory behaviour observed suggests that it was functioning to reduce head temperature. Both head bobbing and the submerging response of *C. porosus* and the short submergences made by *C. johnstoni* after basking may act to reduce head temperature, especially since some of these did little to lower body temperature. The significance of the thermoregulatory behaviour observed here will be discussed in greater detail elsewhere (Johnson *et al.*, in prep.).

The food of crocodilians appears similar among most species, but has been shown to depend upon size of the individual crocodile (Schmidt, 1924; Welman & Worthington, 1943; Cott, 1954; Corbet, 1960; Cott, 1961). Young *C. porosus* feed upon insects and frogs (Worrell, 1964; Tanner, pers. comm.) and their diet changes with increased size consisting most likely of birds, small mammals and amphibians in larger animals. Stomach contents of *C. porosus*

have disclosed birds, turtles, turtle eggs, smaller crocodiles, snakes and wallabies (Worrell, 1964). Numerous accounts exist of predation upon large animals by *C. porosus* and it is rated in the same class as *C. niloticus* as a man-eater (Deraniyagala, 1939; Ditmars, 1944; Pope, 1956; Cogger, 1960, 1964; Heatwole, 1972b, in press). Fishes have been reported as the main diet of *C. johnstoni* as well as *Gavialis gangeticus* (Smith, 1931; Ditmars, 1944), *Tomistoma schlegeli* (Pope, 1956), *Crocodylus cataphractus* (Pope, 1956), *Paleosuchus trigonatus* (Medem, 1952), *C. palustris* (Pope, 1956), *C. siamensis* (Pope, 1956), *C. rhombifer* (Pope, 1956), *Caiman fuscus* (Medem, 1952), *C. novae-guineae* (Cogger, 1964), the young of *C. acutus* (Schmidt, 1924). Fishes have been reported as important in the diet of *C. niloticus* (Cott, 1961) and *C. porosus* was seen to feed on them in this study. *C. moreletii* and *Alligator mississippiensis* both feed heavily upon crustaceans, insects and snails with the latter also taking large numbers of fishes, snakes, turtles, birds and small mammals (Schmidt, 1924; Kellogg, 1929). Schmidt (1928) found the remains of one *Bufo marinus* in the stomach of *Caiman latirostris*, but *C. porosus* in this study was observed to avoid eating them.

Cott (1961) classed the various types of feeding behaviour into various methods of attack as follows: (a) lurking offshore near game trails and watering places, then on sighting the prey, the *C. niloticus* submerges, cruises underwater to the precise spot from which the fatal upward rush can be made; (b) feeding ashore by lying in ambush along game trails and using the tail stroke or sledge-hammer-blow to take effect and (c) feeding on land by moving about and feeding on insects as a lizard feeds. He described the classes (a) and (b) as used by adults and (c) as used by juveniles. A fourth class of feeding behaviour was also described by Cott for crocodiles when feeding on fishes. When feeding on small fishes inshore, *C. niloticus* lies submerged and motionless, with the mouth open and awash and snap up their prey as the shoals swim within reach (Stevenson-Hamilton, 1954). *C. niloticus* have often been observed fishing in open water (Hubbard, 1927; Carpenter, 1928; Pitman, 1929; Graham, 1929, Salmon, 1932); they also have been known to sieze plug-baits of fishermen (Kinloch, 1956). The procedure appears similar in most accounts, the crocodile disappears underwater, hurls itself at its prey, then surfaces, thrusts its head out of water, kills the fish in its jaws, then manipulates it until it can be swallowed head first (Cott, 1961). In all cases *C. porosus* when stalking prey used the first method as described by Cott (1961), of lurking offshore, then upon spotting the prey, submerging and swimming underwater to the precise spot and then lunging at it. The incident with the fish being preyed upon by *C. porosus* was almost identical with the accounts of *C. niloticus*.

Although Bellairs & Carrington (1966) mentioned that well fed crocodiles hide their prey in holes until it is partly rotten, they regard this behaviour as questionable. Neill (1946) provided an account of *C. novae-guineae* burying its food in mounds of dried grass and numbers of crocodile shooters have proclaimed that they have witnessed such behaviour in Australia with *C. porosus*. This behaviour was further substantiated in the present study.

According to Tanner (pers. comm.) *C. porosus* kept in captivity in Victoria would refuse to eat pieces of meat that were flicked off when feeding, whereas in this study the *C. porosus* in one instance ate the flicked off piece of rat and in another did not. Worrell (1964) reported that *C. porosus* in the wild state

have been seen to eat the decaying flesh of other crocodiles which had been shot 14 days previously. Probably well fed individuals do not bother with discarded pieces of meat. Tanner (pers. comm.) further stated that he never witnessed these captive crocodiles hiding or burying their food. According to Cott (1961) *C. niloticus* does not hide or bury prey for later use as popularly believed and that they prefer fresh meat to that which is decomposed. *C. niloticus* fill the same role as scavengers as vultures and hyaenas and often have been observed feeding on freshly killed carcasses of large animals such as buffaloes, zebra and waterbuck (Cott, 1961). If the carcase is on shore they often drag it into the water and Pitman (1939) reported that shot crocodiles were often dragged by other crocodiles as much as 30 to 40 yards through the forest to the water. Attwell (1959) reported that *C. niloticus* will often travel considerable distances inland to feed from a kill.

Cott (1961) reported several instances of *C. niloticus* in the wild state remaining submerged for periods up to an hour, during which time they lay quietly on the bottom. Under experimental conditions he found that maximum submergence varied in relation to size. Two newly hatched *C. niloticus* survived 30 minutes of forced submergence and one was still moving after 57 minutes. In observing 57 dives of four individuals *C. niloticus* of varying sizes (290 to 992 mm), Cott found mean submergences ranging from 7 minutes 10 seconds to 18 minutes 17 seconds. Cott (1961) stated that if this trend extended into larger size groups the maximum for adults would be in excess of the hour periods that have been observed in the field. The maximum escape dive reported for *C. porosus*, in this study, was 11 minutes, whereas *C. johnstoni* stayed under during such escape dives on two occasions 23 and 28 minutes. Normal dives for feeding and thermoregulation accounted for far less time in both species and usually were less than those reported by Cott (1961) for *C. niloticus*. No information on maximum survival times were determined under laboratory conditions for either of the Australian species.

Rapid learning ability has been shown in several crocodylians. Davidson (1966) in a study of escape conditioning response in *Alligator mississippiensis* with the use of a simple maze, showed that in relatively few trials, *A. mississippiensis* learned to reverse an unconditioned turning preference. Similar results were obtained by Northcutt & Heath (1971) in a study of learning ability in *Caiman sclerops*. Although such a study has not been done on *C. johnstoni*, its increased awareness of approach and subsequent difficulty in capture with successive encounters, suggests that this species also has a rapid learning capacity. Bustard (1968) demonstrated rapid learning in *C. porosus* by studying approach distances in free-living individuals.

Similar defensive display behaviour was noted in both *C. johnstoni* and *C. porosus*. A number of accounts of attack behaviour on crocodylians have been published; most of these accounts are concerned with *C. niloticus*. Some of these instances involve attacks by *C. niloticus* on small boats; these attacks appear to be territorial in nature (Jackson, 1962; Richardson & Livingston, 1962). These attacks have all taken place in remote areas where crocodiles are unfamiliar with boats and outboard motors and thus were assumed to be defending their territories against an unknown and possibly potentially dangerous intruder. In most of these attacks, the crocodiles swam on the surface, with the mouth wide open and accompanied with much splashing,

taking on a threat display attitude. Fighting during the breeding season has been reported in *C. niloticus* (Pitman, 1931, 1941, 1942), *Alligator mississippiensis* (Bartram, 1791; Clarke, 1891) and in *C. porosus* (Deraniyagala, 1939). Fighting in defence of territory (basking ground or feeding places) has been reported for *C. niloticus* (Pitman, 1931; Stevenson-Hamilton, 1954) and Cott (1961) stated that fighting in defence of territory in *C. niloticus* occurred at any time of the year and in all cases the crocodiles were males or believed to be males. *C. johnstoni* and *C. porosus* both attacked with their mouths wide open in a typical threat-display posture. *C. porosus* was far more aggressive than *C. johnstoni*. With the large *C. porosus* in the enclosure the threat-display was definitely involved in territorial defence (food, basking space and water tank), although the sex is not known for this individual.

#### SUMMARY

The present study was designed to investigate both the thermoregulation by radio-telemetry, and the behaviour of two species of Australian crocodiles in the free-living condition; this paper deals with the latter aspect. Behaviour associated with thermoregulation, activity, feeding and hunting, voluntary diving, responses to other animals and defensive displays are described for *Crocodylus johnstoni* and *C. porosus*.

Thermoregulatory behaviour varied between the two species, although basking postures were similar. Shallow water basking was used extensively by *C. porosus*. Inconsistent results were obtained with *C. johnstoni* as shore basking was used to a greater extent by an individual with an implanted transmitter than those without such transmitters; the presence of the transmitter may have influenced the behaviour. An early morning alert basking posture was described for *C. porosus* which differed from the shallow water posture of *C. porosus* and the shore basking posture of *C. johnstoni*. Likewise a submerging response was described for *C. porosus*, whereas no such nor similar response was observed in *C. johnstoni*. *C. johnstoni* maintained preferred temperatures by shuttling between sun and shade. Gaping of the mouth was observed in both species and although no data on head temperature were collected some of the thermoregulatory behaviour observed suggested that it may function to cool the head.

When two freshwater crocodiles were introduced to the study pond together, they maintained distinct areas, although the area of one overlapped with the area of *C. porosus*. No interaction occurred between the species, although the size of the home range of *C. porosus* appeared to decrease after introduction of the freshwater crocodiles.

*C. johnstoni* was not observed to feed in the study pond, although long term observations have shown that they prefer to eat fish, either dead or alive. *C. porosus* was observed to feed on fish and amphibians in the study pond and made numerous unsuccessful attempts at catching birds. In two cases *C. porosus* was observed to bury food and uncover and eat it at a later date.

Dives were classified into various categories and their significance was discussed. *C. johnstoni* appear to have longer diving capabilities than *C. porosus* and this is probably a reflection of their feeding behaviour. Diving plays a more important thermoregulatory role in *C. porosus* than it does with *C. johnstoni*.

Reactions to various animals are discussed and defensive behaviour at the intra- and interspecific levels are discussed.

## SUMARIO

El presente estudio fue diseñado a fin de investigar la termoregulación, por medio de radio telemetría, y el comportamiento de dos especies de cocodrilos australianos viviendo en condiciones de semi cautividad. Este artículo trata particularmente el último de los aspectos citados y describe el comportamiento de *Crocodylus johnstoni* y *C. porosus* asociado con otros factores tales como termoregulación, actividad, caza y alimentación, sumergimiento voluntario, respuestas a otros animales y manifestaciones defensivas.

Los procedimientos adoptados para regular su temperatura, varió en las dos especies, aún cuando las posturas de asoleamiento fueron similares. *C. porosus* prefirió frecuentemente lugares con aguas poco profundas para su asoleamiento, mientras que en *C. johnstoni* las observaciones fueron inconsistentes. Así, un ejemplar de *C. johnstoni*, al que le fue implantado un trasmisor, usó mas frecuentemente la playa como lugar de asoleamiento que otros animales sin trasmisores, sugiriendo que el trasmisor pudo haber afectado el comportamiento del animal. Otra posición de asoleamiento durante horas de la mañana es también descripta para *C. porosus*, la cual difiere de la posición en aguas superficiales para esa misma especie y de la posición en la playa adoptada por *C. johnstoni*. Se describe también una particular respuesta a sumergimiento de *C. porosus* la cual no fue observada en *C. johnstoni*. *C. johnstoni* mantiene su temperatura preferida moviéndose alternativamente de los lugares sombreados a pleno sol. En ambas especies se observó una característica posición entreabierto de la boca y aún cuando no fueron tomados datos de temperatura de la cabeza, ciertos procedimientos de termoregulación observados, sugieren que se debe a cierta función para enfriar la cabeza.

Cuando dos cocodrilos que habitan en aguas frescas fueron introducidos en la laguna de ensayo, mantuvieron áreas separadas. Sin embargo, el área de uno de ellos se superpuso con el área habitada por *C. porosus*. Ninguna interacción ocurrió entre las especies, aunque el tamaño del radio de acción de *C. porosus* pareció reducirse después de la introducción de los cocodrilos de agua fresca.

*C. johnstoni* no fue observado alimentándose dentro de la laguna, aún cuando observaciones de larga duración demostraron prefieren comer peces, ya sea vivos o muertos. *C. porosus* fue observado comiendo peces y animales anfibios y al mismo tiempo realizando infructuosos intentos de cazar pájaros. En dos oportunidades *C. porosus* fue observado enterrando su alimento, el cual fue desenterrado más adelante y comido.

Los sumergimientos voluntarios fueron clasificados en varias categorías y sus distintos significados discutidos. *C. johnstoni* parece tener mayor capacidad de buceo que *C. porosus* y éste es probablemente un reflejo de su forma de alimentación. Los buceos juegan un papel de mayor importancia en el proceso de termoregulación en *C. porosus* que en *C. johnstoni*.

La reacción ante varios animales es también discutida como así también las actitudes defensivas intra e interespecificas.

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