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The Nesting of *Crocodylus porosus* in Arnhem Land, Northern Australia

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In northern Australia *Crocodylus porosus* nest between November and March, i.e. during the wet season. Mean distance between nests and permanent water was 7.8 m. Nests adjacent to more saline, lower reaches of rivers were in freshwater swamps, whereas further upstream they were beside the river.

The nests are mounds, with mean dimensions: 53 cm high, 175 cm long and 157 cm wide, constructed of vegetation and mud, collected from a mean area of 47 m². Beside the nest may be 1 to 4 wallows. Some nests are made in which no eggs are deposited.

Mean number of eggs per nest was 50 (range 40 to 62). Variation in egg size between nests was far greater than that within any one nest. Mean egg length varied from 7.2 cm to 8.1 cm, egg width from 4.7 cm to 5.4 cm and egg weight from 91 gm to 132 gm.

Flooding killed all embryos in 24 of 30 nests with eggs under study. Incubation temperature means ranged between 27.3 C and 31.4 C. Temperatures within a nest can be stable or fluctuate ± 3 C. Maximum temperatures may occur during the night. Incubation time was between 80 and 98 days. Predation on eggs was minimal. Survival rate of juveniles was high. Adult *C. porosus*, thought to be the females, remain next to the nest during incubation, excavate the nest when the young hatch, and remain with the hatchling group for up to 2½ months after hatching.

*C*ROCODYLUS porosus have been recorded from India, Indonesia, south-east Asia, Malaysia, the Philippines, Papua New Guinea and from Australia, the southern-most extreme of their distribution (Neill, 1971; Brazaitis, 1973). In Australia, *C. porosus* are restricted to the northern coastal regions. The greatest numbers are in sections of rivers under tidal influence, though breeding populations are known from freshwater sections of rivers and lagoons.

Deraniyagala (1939) presented detailed data on 4 nests in Sri Lanka and Kopstein (1929) examined 4 nests in Java. Worrell (1952) and Ogilby (1904) gave general descriptions of *C.*
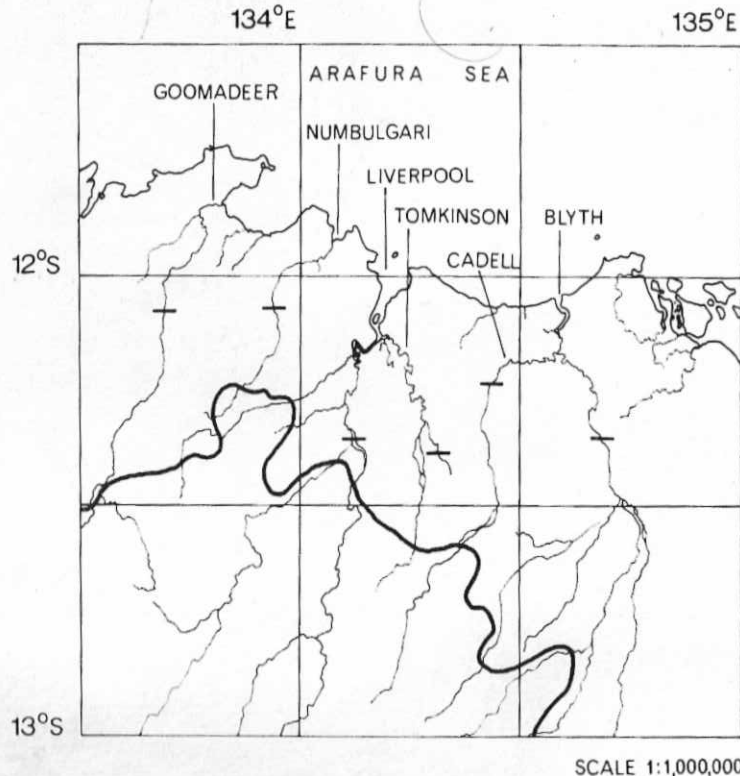
Fig. 1. North coast of Arnhem Land showing the location of rivers in which *C. porosus* nests were examined. The sandstone escarpment is represented by the heavy continuous line. The extent of tidal influence in each river is marked with a bar.

porosus nests in Australia. Smith (1931) gave general descriptions from India and Burma. Neill (1971) briefly reviewed nesting in *C. porosus* throughout its range.

This study reports on *C. porosus* nesting on the north coast of Arnhem Land. Most observations were made in the Liverpool/Tomkinson river system, where the total population in 1974 was thought to be less than 500 individuals; 10% to 20% of these being adults. Additional observations come from the Cadell/Blyth river

system (similar population size to the Liverpool/Tomkinson system), the Goomadeer River and Numbulgari Creek (both with less than 100 individuals). The location of these rivers and creeks is shown in Fig. 1. There has been no hide hunting of *C. porosus* in these rivers since 1972, though the eggs of some nests are taken by aborigines.

In the Liverpool, Tomkinson, Goomadeer, Blyth and Cadell rivers and Numbulgari Creek, *C. porosus* are mainly found in the meandering

sections under tidal influence (70 km, 100 km, 50 km, 55 km, 37 km, 16 km, respectively). The rivers have muddy banks, are lined with either mangrove or grass/sedge floodplains and contain water discoloured with fine suspended sediments. All have long, narrow, upstream drainages, usually with rocky substrates and occasional expansions into lagoons which may contain *C. porosus*.

Our nesting study was initiated in 1973, the first nesting season being the 1973/74 wet season (November to May; no nests found after the end of March). In the 74/75 wet season, observations were made largely by Magnusson. In all, 56 nests have been examined. Individual nests are referred to by the river initial and a number, e.g. L1, Liverpool River nest 1.

MATERIALS AND METHODS

Nests were located using boats or aircraft, or by walking along the river banks. Some were found by local aborigines searching areas known to have previously contained a nest. The extent to which the nests located reflect the total number of nests is not known. Measurements were made of nest dimensions, area cleared of vegetation during construction of the nest, distance from the nest to the water and size of any wallows. Plants used in nest construction were collected for identification and the site was described.

During the 1973/74 season the nests were checked every 7 to 10 days. Notes were made of predator damage and flooding. Evidence of the presence of a crocodile (tracks, sightings, fresh disturbance in wallows) and secondary work on the nests were also noted. Temperatures of the interior (10 cm deep) of the nest, the external substrate and the air, were taken. Water temperature was recorded if the nest was fully or partly inundated. During the 1974/75 season, nests were checked less frequently. A simple flood height gauge (float pulling cotton from a reel) was erected at each nest to indicate whether the nest had been flooded since a previous visit.

During 1973/74, care was taken not to disturb eggs unnecessarily. One egg was removed from each nest initially, checked for signs of life and the embryo, if present, measured. Eggs from G1 were removed, counted, weighed, measured and replaced carefully at the same angle as they were found. When, after flooding, it was suspected that embryos had died, an additional egg was examined. If the embryos were dead, all eggs were measured and weighed and notes taken on cracks in the eggs, fungal infections and the size of the dead embryos; weights of eggs swollen or with seeping cracks were discarded. During the 1974/75 season, all eggs were weighed and measured as soon as the nest was found.

A hide was erected approximately 50 m from L1 and thermocouples (read on a Comark "Electronic Thermometer") were inserted in various positions within the nest. Temperatures were measured each half hour during the day and at less regular intervals during the night for 21 days. At T14 a Grant multitemperature recorder was used with 9 thermistors positioned in and around the nest. Temperatures were automatically recorded each half hour for 29 days. At T12 and T14 sounds made by the hatchlings within the nest were recorded on a National RQ-158S tape recorder. The microphone was buried in the nest and the recorder left on "voice control."

Notes were taken for each successful nest on the extent of excavation, number of empty shells and unhatched eggs, stage of development of unhatched eggs and the presence of possible predators. Hatchlings were caught, weighed and measured as soon after hatching as possible. One caudal scute was branded so that all the hatchlings from each nest had the same identifying mark.

RESULTS

In June 1974, large hatchlings in the downstream regions of the Liverpool River indicated that at least two nests had been constructed either in late November or early December; there were heavy November rains. However, of the 16 nests found soon after construction in the 1973/74 season, 12 were made in January, (corresponding with the onset of daily rains and generally overcast conditions) and 1 in February.

Three nests (T12, 13, 14) located by aerial survey on 9 April 1974, were constructed between 12 and 29 March 1974 (based on embryo size), again following heavy rainfall. These were constructed progressively upstream, i.e. T12 the first constructed, 53.9 km upstream: T13 the second, 59.7 km and T14 the third, 65.1 km upstream. This followed a progressive fall in flood levels, related to rainfall and tidal cycles; flood levels were maintained longer in the upper reaches of the river.

During the 1974/75 season heavy rains again occurred in November. Five nests found were constructed in either late November or Decem-

Fig. 2. A *C. porosus* nest on the Tomkinson River (T14) constructed from *Ischaemum australe* var. *villosum* and mud. Three nest wallows are present.

ber. Hatchlings caught in the lower reaches of the Liverpool River (14 km to 20 km upstream) in April 1975 indicated 1 or 2 additional nests had also been constructed at this time. Eight nests were made in January 1975 when rainfall was regular but not intense; 5 in February and 1 in March, when rain was consistent and heavy. It was not always possible to estimate construction time.

River water salinity usually decreases as distance upstream increases. In the Tomkinson and Liverpool rivers, water salinity in the mouth was < 1.0‰ during the wet season. During the dry season, brackish water (> 5.0‰) was 100 km upstream in the Tomkinson R. and 70 km upstream in the Liverpool R. Of a total of 56 nests, 10 were in downstream sections of the rivers (less than 30 km upstream) all in freshwater swamps back from the river's edge. Forty-five upstream nests were on the river bank, and 1 on the bank of a riverside lagoon.

Riverside nests were not found in the mangrove forests. Most were on concave banks where the river comes close to or abuts the adjacent floodplain, or on the floodplain behind the mangroves. These nests were either in the floodplain grass or in the shrub layer bordering the floodplain. The lack of nests in mangroves may be because mangroves usually colonise convex or deposition banks which are marginally lower than concave banks and more subject to flooding. In addition, mangrove forests lack the grasses or herbs from which nests are typically constructed.

Floodplain nests were usually constructed principally of the grass *Ischaemum australe* var. *villosum* (Fig. 2). Other grasses and sedges (equally or more common in these areas) suitable for nesting material, however they are rarely used.

In areas lacking *I. australe* var. *villosum*, nests were constructed of a variety of materials. On the Goomadeer River nests were principally earth, vines and leaf litter. In a Tomkinson River swamp, Numbulgari Creek, 1 nest in the Liverpool River, and a nest without eggs in the Tomkinson R., ferns, earth, vines and leaf litter were used. Nests in the Liverpool R. swamps were constructed mainly from sedges and root matter.

Nests were close to permanent water, although it is difficult to obtain a realistic measure due to water level fluctuations. The distance between

the nest and the normal high tide mark, usually the river edge of the mangroves, was measured.

Water was present within 1 m of the nests in swamps, though this was not necessarily permanent, nor deep. The average distance of riverside nests from permanent water was 7.9 ± 0.4 m (range 0.3 to 300 m). Nests less than 2 m from permanent water had a track to them consisting of a smooth slope or slide into the water; those further back had well worn tracks leading to them. Tracks to nests never traversed distances greater than 3 m devoid of shrub cover.

Nests were built in open grassplain with no shade or protection, beneath small shrubs with only little protection from the sun or wind, beneath dense shrubs and in forests and swamps where they were almost continually shaded and protected from wind, or on one side of a forest where they were completely shaded during some part of the day and either protected or exposed to prevailing winds. Seventy-nine % of nests were built on a rich, black, floodplain soil. One was located on sandy soil in the upper reaches of the river and the remainder were in swamps. A considerable part of most nests was soil, the vegetation being mixed with wet mud during construction. The adult sometimes packed mud onto the nest after the eggs had been laid. Nests in swamps were on a peat-like tangle of roots and debris which formed the swamp floor. This substrate is spongy and the nests were built against, or close to, large trees (usually Melaleuca sp.), the roots of which provided a stable foundation.

Nesting sites were on flat country, and the nests were only slightly elliptical (see below), aspect per se being virtually the same for all nests. In more undulating topography, aspect could be an important variable.

Nest construction was unrecorded. Tracks around the nest indicate that at least the feet and tail are used to scrape up vegetation. Vegetation and soil from an area of 9 to 66 m² (mean of 26 nests with eggs = 46.7 ± 1.2 m²) was raked together and formed into a mound, usually situated centrally within the area cleared.

The largest nest found was 80 cm high, with base dimensions of 250 cm (longest axis) and 225 cm (shortest axis). Mean dimensions of all nests with eggs were: height 52.6 ± 0.6 cm (N = 27; range = 33 to 80 cm), longest axis of base 174.7 ± 1.0 cm (N = 27; range = 130 to 250 cm) and shortest axis of base 157.2 ± 1.0 cm (N = 27; range = 120 to 225 cm). On completion, the nest often had a distinct tail groove

across the top and, with the exception of one nest, the tail groove was indicative of nests with eggs.

Within the nest clearing 76% of nests examined had 1–4 wallows; depressions containing mud and water (mean 1.4; N = 34). Wallows were either shallow, and resulted from mud being scraped up onto the nest, or up to 2 m deep, appearing to have been excavated specifically for lying in (Fig. 2); tracks indicated the adult lies in both types. At some nest sites the wallow provided the closest deep water. Mean wallow depth was 68 ± 1.5 cm (N = 23; range = 4 to 200 cm), mean length was 284 ± 2.5 cm (N = 23; range = 130 to 520 cm) and mean width was 154 ± 1.5 cm (N = 25; range = 50 to 300 cm). Wallows at 8 nests formed a moat around the nest.

Egg laying probably takes place soon after the completion of the nest. Two nests were found with no eggs but contained eggs on a subsequent visit; 16 days elapsed between visits. Eggs are deposited in a cavity within the central area of the nest mound. No egg layering was apparent. Presumably, on completion of egg laying, the opening to the nest cavity is covered over and packed down. The egg cavity is usually deep, with a mean distance of 19.0 ± 0.6 cm (N = 21; range = 8 to 28 cm) between the top of the nest and the top of the eggs. At G1 and L14 eggs were so near the surface on one side that they could be seen. At L14 the adult later covered the eggs by adding 8 cm of vegetation.

Crocodylus porosus eggs are hard-shelled and white. Many contained an opaque ring around the middle of the long axis of the egg. Its significance was not determined. Egg number varied from 40 to 62 in 18 nests (mean = 50.3 ± 0.6). Within a particular nest, egg dimensions were remarkably constant, though there was considerable variation between nests. Mean length of eggs from 22 nests ranged from 7.18 ± 0.06 cm to 8.06 ± 0.06 cm. Maximum egg length was 8.95 cm and minimum 6.63 cm. Mean egg width ranged from 4.66 ± 0.05 cm to 5.36 ± 0.04 cm. The maximum egg width was 5.64 cm and minimum 4.23 cm. Mean egg weight ranged between 91.2 ± 0.4 gm to 132.4 ± 0.3 gm, with the maximum weight being 143 gm and the minimum 75 gm.

Egg number did not correlate significantly (at the 5% level) with either egg size or nest size. Nesting adults were not caught and measured; a relationship may exist between female age or size and egg number or size.
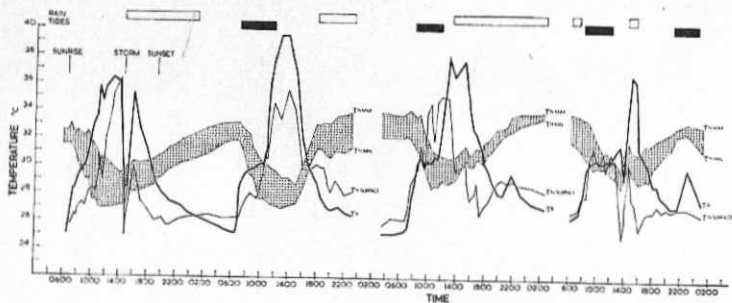
Fig. 3. Temperatures at nest L1 between 7 and 10 February 1974. Stippled region represents temperatures from within the nest. Thick line is substrate temperature (T^s) and thin line peripheral nest temperature (T^n surface). Open boxes represent rain and closed boxes tidal flooding of nest.

Egg damage of 2 types was noted; dents and longitudinal cracks. Dents, frequently surrounded by a mosaic of small cracks, were possibly caused by one egg being packed down on top of another. Longitudinal cracks may have been caused by the female packing down the nest; at least some were noted to occur with osmotic swelling of the eggs, following marked increases in nest moisture over long periods. Dents and cracks allow fungal infection to enter the egg. In some cases live embryos were found in severely cracked eggs. The percentage of eggs with dents in 16 nests varied from 0 to 19.1% (mean = 7.9%).

Ten nests were found which never received eggs. Five of these resembled normal nests, and 5 were mere piles of vegetation 20 to 33 cm high. Wallows were present at 3 of the complete nests and 2 of the incomplete ones. Nests without eggs were either in the immediate vicinity of nests with eggs (3 m away) or up to 1.3 km away. Of the 30 nests with eggs, only 6 produced hatchlings. All others were inundated with water. Of the nests with eggs that hatched, only 1 had eggs lost to flooding; T13 lost approximately 65%.

Size of dead embryos within a nest indicated differential loss by flooding. In L5, the curled length of dead embryos was between 1 and 2 cm, indicating that they were killed at approximately the same time. In L2, embryos were between 1.5 and 5 cm long and in T13, 26 eggs at the bottom of the egg cavity contained dead embryos, while those above hatched.

Adult C. porosus, believed to be the females, (see discussion), frequently lay in the nest wal-

lows or basked within the area cleared; they were observed occasionally from aircraft. Tracks often indicated that the adult had left the nest at the approach of our boat. Deep wallows near a nest were probed with poles to see if adults were present, as according to local aborigines the females may submerge in deeper wallows, reappearing while the nest is being disturbed. We have not encountered any such crocodiles, though on 4 occasions an adult has surfaced in the river less than 5 m from the nest being examined.

It appeared that the adult C. porosus abandoned nests which were flooded for a few weeks, whereas with periodic flooding (e.g. tidal flooding) the adult returned to the nest, even though the eggs may have contained dead embryos. At nests from which the eggs had been removed, the adults continued to visit the nest.

It is not known whether C. porosus protect the nest against predators or not. At L2, fresh varanid tracks were found on top of the nest. At L16, three Varanus indicus were seen basking on the nest, fresh tracks indicating that the adult C. porosus had been present. At L17, a C. porosus attacked the orange float on our flood height indicator (teeth marks; tracks). At the same nest 2 weeks later, all eggs were found scattered around the nest, and a V. indicus sighted running from the area; fresh tracks indicated that the adult had been present only minutes before. More data are needed to clarify the role of adult C. porosus at the nest.

The nest cavity containing the eggs was always moist, even in nests with outer layers of mud, baked hard in the sun. During routine
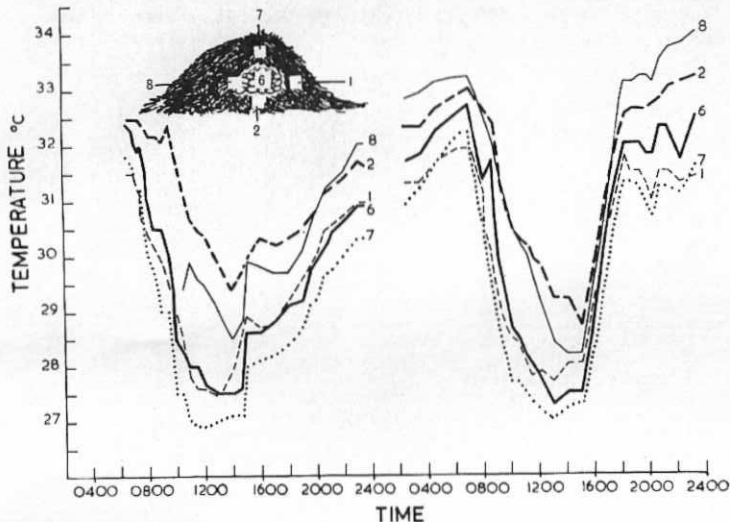
Fig. 4. Nest temperatures of T1 on 7 and 8 February 1974. Numbers refer to sites of temperature measurement as shown in the insert.

nest checks, mean nest temperature of fully exposed nests was 30.7 ± 0.3 C (N = 28) and of flooded nests 32.9 ± 0.7 (N = 17). When flooded, nest temperatures were significantly correlated with water temperatures (.0025 < P < .005). This was not the case when exposed (not significant at the 5% level).

Two distinct patterns of thermal fluctuation occurred in the 2 nests in which temperature was monitored continuously (Figs. 3, 5). Data from 4 days of temperature monitoring at L1 are presented in Fig. 3. During the night, internal nest temperatures increased while peripheral nest temperatures and substrate temperatures decreased. Following sunrise the opposite occurred; internal nest temperatures decreased while external temperatures increased. This pattern characterised 21 days' recordings. Tidal flooding tended to equalise all temperatures, and storms during the day resulted in a rise in internal nest temperatures (Fig. 3).

In Fig. 4 the internal nest temperatures of L1 are plotted separately for the first 2 of the days included in Fig. 3. Probes 8 and 2 were deepest in the nest, the warmest part at all times. Probes 7 and 1 were the most superficial (of the internal probes) and probe 6 was intermediate. Fig. 4 clearly indicates that the heat of the nest comes from within, probably heat of fermentation. The daily rise and fall of internal nest temperature and the rise associated with rain, appear to result from changes in the rate of heat loss from the nest to the exterior. It is thought that condensation of atmospheric moisture at night (or during rain) would decrease aeration (by reducing peripheral air spaces), and thus reduce heat loss to the exterior. During the day, the drying of the nest periphery would have the opposite effect. Mean temperature among the eggs in L1 was 31.4 ± 0.05 C (N = 374); mean hourly temperature varied between 33.4 C (0500 hr.) and 30.0 C (1300 hr.).

Nest T14 was the last nest built in the 1973/74 season and the period over which nest temperatures were recorded (20 May 1974 to 18 June 1974) extended into the windy, cool, beginning of the dry season, when air temperatures at night dropped as low as 11 C and there was no rain. Unlike L1 (loosely constructed of
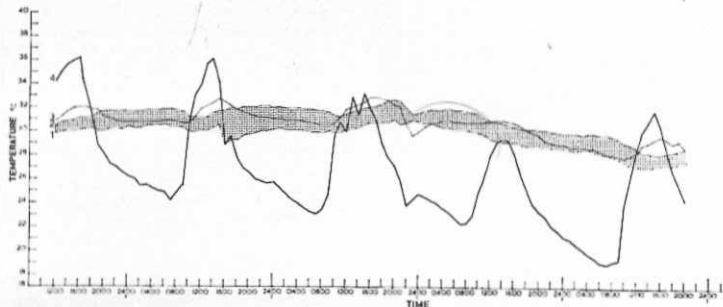
Fig. 5. Temperatures from T14 between 21 and 26 May 1974. Thermister positions were 1) center of eggs, 2) top of eggs, 3) between top of eggs and top of nest, 4) substrate outside nest. Region between 1) and 2) is stippled.

grass), T14 was tightly compacted with mud and grass. Mean nest temperature among the eggs was 27.3 ± 0.5 C (N = 687), much lower than in L1. Diurnal variation in nest temperature was minimal, hourly means were between 26.7 C (1100 hr.) and 27.5 C (2200 to 0200 hr.). The sequence of heat uptake was ambient temperature, top of nest, top of eggs and middle of eggs (unlike L1) indicating that the heat of the nest was solar in origin. Internal nest temperatures progressively fell throughout the period of recording as did ambient temperature, demonstrating the dependence of nest temperature on ambient temperature.

Incubation times for T12, 13 and 14 were approximately 83, 80, and 88 to 98 days respectively. An egg from T12 hatched in the laboratory on 8 June 1974. Longitudinal cracks were noted in the shell less than 2 hrs before hatching. No sounds accompanied hatching. The juvenile remained attached to the egg shell for 10 min before breaking away. Body weight was 88 gm, snout-vent length 14.0 cm and total length 29.0 cm. The abdomen was noticeably distended and had a longitudinal fleshy strip on the midline. Nest T12 hatched between 4 and 9 June 1974. One egg with a dead embryo (fully formed) remained in the nest. The river-facing side of the nest had been excavated. Egg shells were mostly within 1 m of the nest though some were up to 3 m away. The hatchlings were grouped in shallow water among mangroves on the edge of the river. The hatchling call had been recorded, and it is a high pitched nasal "gn-arr." T13 also hatched between 4

and 9 June 1974. The baked hard exterior of the nest had been torn apart as in T12. Only 4 egg shells were found, all within 2 m of the nest. Fourteen hatchlings were located grouped in the mangroves and it is possible that the egg shells were among the mangroves, which were inundated with river water. In T13, 26 eggs contained embryos killed at an early stage by flooding and one egg contained a hatchling which was alive but very lethargic; it died within 2 hrs.

Both T12 and 13 were checked on 4 June 1974. Hatchling sounds were not heard. If the adult excavates the nest in response to hatchling vocalization within the nest, the maximum time they could have called prior to excavation was 3 to 4 days. Hatchling calls from T14 were heard and recorded on 17 June 1974. The juveniles did not call continuously, but only in response to a light tapping on the nest or the stamping of feet around the nest. Nest T14 was checked daily from 17 to 22 June by on-site or aerial observation. The adult was usually in the river immediately in front of the nest. Excavation occurred on the night of 21 June 1974, on the riverside of the nest. When examined on 22 June, some hatchlings were in the water, others exposed in the sun at the excavation site, and others still squeaking from within the nest. The same was noted on 28 June. The nest was re-excavated at least twice between the 22 and 28 June. On 22 June, the nest was surrounded by large numbers of birds, mainly *Nycticorax caledonicus* and *Egretta* sp. Two dead hatchlings were in the sun between

the nest and the water. Partially hatched eggs containing lethargic, inactive juveniles (as in T13) were noted. No direct predation was observed, though one dead hatchling contained a fresh wound; as similar congregations of birds had not been seen before, it is likely that they were responsible for some hatchling loss. By 4 July 1974 no live eggs were within the nest. The snouts of dead hatchlings protruded through holes in 2 egg shells. Nine hatchlings were known to have successfully reached water.

Samples of hatchlings were weighed and measured at various intervals after hatching. One week after hatching, hatchlings from T12, 13 and 14 respectively were: snout-vent length 14.9 ± 0.1, 14.0 ± 0.15 and 14.5 ± 0.15 cm; total length, 31.7 ± 0.15, 32.0 ± 0.2 and 31.0 ± 0.25 cm; body weight 92.7 ± 0.4, 94.9 ± 0.6 and 82.8 ± 0.6 gms (N = 29, 14 and 9 respectively). Mean daily growth rates of the same hatchlings over 69, 63 and 52 days (T12, 13 and 14 respectively) were: snout-vent length 0.6, 0.5, 0.5 mm; total length, 1.3, 1.3 and 1.0 mm; body weight 0.6, 0.5 and 0.7 gms.

Most hatchlings remained with the adult, grouped in a few square metres, for up to and possibly more than 2 months after hatching. The hatchling group was always within 50 m of the nest site: in the mangroves during high tide; on the mud bank during low tide in the day; and in shallow water on the edge of the mudbank during the night. When on the mud, the adult tracks were among the hatchlings. When approached by boat the hatchlings were often sighted diving into the water; on a few occasions the adult was sighted.

The hatchlings of T12 were usually on the southern bank of the river, where the nest had been. Once, 20 days after hatching, the adult and hatchlings were on the northern bank of the river, requiring a 50 m swim across the river and regrouping.

When the juvenile from T12 hatched in the laboratory was returned to its nest site, it had not previously been exposed to the hatchling call. In response to the tape of the hatchling calls, it turned 180° from its direction of travel towards the river, and, calling itself, approached the tape recorder. The experiment was repeated, with the same result.

Hatchling groups were located at night by listening for the calls. It is not known whether the adult crocodile communicated vocally with the young.

Some hatchlings left the hatchling group

within the first few days, moving both upstream and downstream. A hatchling marked at T12 was found in the T13 hatchling group (5.6 km upstream) 55 days after hatching. A hatchling from T14 was located 0.8 km downstream of the hatchling group 5 days after hatching and another hatchling from T14 was found, 39 days after hatching, 5.6 km downstream in the T13 group.

Between 16 and 18 August 1974, 49 hatchlings from T12, 13 and 14 were caught after having been in the river for approximately 70, 68 and 54 days respectively. Forty one hatchlings were within 1 km of the nest site and 45 within 2 km of the nest site. Two individuals had moved 6.6 km upstream from their nest site joining another hatchling group. Two individuals were 3 km downstream from their nest site.

Observed predation on eggs and hatchlings was slight. A native rat, *Rattus colletti*, burrowed into L1 and ate 2 eggs. Three species of varanid (*Varanus indicus, V. gouldii* and *V. mertensi*) are large enough to take *C. porosus* eggs and occur in the area of the nests. Two *V. indicus* were shot at L4; one had been eating rotten eggs and the other crabs, which were in the open nest. One *V. gouldii* shot at G4 had not eaten any eggs. Eggs from L16 were found scattered around the nest and it is possible that a varanid was responsible (a *V. indicus* was sighted at the nest site). To date, no evidence of varanids being predators of live eggs is available.

In T14 an unidentified ant colony was established, and lethargic and dead hatchlings could possibly be attributed to ant bites. The bird congregation at T14 was most unusual and probably accounts for further losses.

A principal predator on *C. porosus* nests is the Australian aborigine, who eats the eggs. Two nests in the Liverpool/Tomkinson river system were robbed by aborigines in the 1973/74 season.

DISCUSSION

Worrell (1952), Kopstein (1929) and Neill (1971), noted that *C. porosus* nesting coincided with the annual wet season. In the 1973/74 season there were both early and late wet season nesting periods. In the 1974/75 season nesting occurred throughout the wet season. In Sri Lanka, *C. porosus* nests during the hottest and driest period of the year (July/August), with hatching commencing at the start of the wet season (Deraniyagala, 1939). This is markedly different from *C. porosus* in Australia.

The restriction of downstream nests to freshwater swamps suggests that water salinity during the dry season is a major factor in the determination of a nesting site; during the wet season the rivers are fresh. This could be explained in a number of ways: 1) The site is selected where freshwater will be available at the start of the dry season, when many nests hatch, or 2) Females may live in regions where freshwater is available throughout the year, and build their nest within these activity ranges. Both suggestions would account for all downstream nests being located in freshwater swamps and upstream nests on the river bank.

Nesting adults were not caught and sexed because it was thought likely that they would abandon the nest. The same sized tracks were always present at each nest and it is presumed that this indicates the same individual in attendance. These tracks, combined with occasional sightings, indicated crocodiles of between 2 and 3 m in length, which is consistent with the size of adult females caught by ourselves at other times of the year, and that reported by hunters. Large tracks, presumably of adult males, were present along the river banks, but not at nest sites.

Arnhem Land aborigines normally kill the adult at the nest before taking the eggs and these crocodiles have been reported in discussions as invariably being females. We know of no evidence of male *C. porosus* participating in any aspect of nesting and assume the "adults" referred to throughout the paper were females. Alvarez del Toro (1969—from Campbell, 1973) has described male participation in nest excavation in *Caiman crocodilus* (*C. sclerops*). Worrell (1952) noted that *C. porosus* females in lagoons were usually permanent residents of those lagoons, and that wanderers were males. The following observations support this hypothesis: 1) All except one of the adults caught in the downstream reaches of the rivers have been males. Females caught in the rivers have been from well upstream. 2) Old nesting sites are frequently found during the dry season by following fresh tracks of adult female-sized crocodiles (none have been found by following tracks of *C. porosus* larger than 3.5 m). 3) If the adult at the nest is the female, she remains in the immediate vicinity of the nest (with the juveniles) for at least the first half of the dry season, i.e. until the end of August.

These observations suggest that females spend the dry season in regions suitable for nest construction in the wet. Thus their selection of a

freshwater site during the dry season may ultimately determine the location of the nest in the wet. Joanen and McNease (1970) found that female *Alligator mississippiensis* had a small home range, and that they nested within this region.

Worrell (1952) and Ogilby (1904) described *C. porosus* nesting materials in Australia as "leaf mould" and "grape-vines, grasses and other rubbish" respectively. Smith (1931) noted rushes, reeds and dead leaves as nest constituents in India and Burma. Neill (1971) pointed out that though dead material was sometimes used, tall green grass or herbaceous aquatic plants were most commonly used in the Philippines, Indonesia and Papua. Kopstein (1929) noted in Java that nests were constructed of "manheight" grass and small branches. In Sri Lanka there was an association between *C. porosus* and the plant *Lagenandra toxicaria*; *C. porosus* females built their nests from it and the eradication of the plant was closely followed by the the disappearance of *C. porosus* from a particular region (Deraniyagala, 1939).

In the Liverpool and Tomkinson rivers, *Ischaemum australe* var. *villosum* seems to parallel *L. toxicaria* in Sri Lanka. Aborigines showed us some areas where *C. porosus* had nested annually, but where no nests had been made since the introduced water buffalo (*Bubalis bubalis*) had so trampled the ground that *I. australe* var. *villosum* was no longer present. Nests of *C. porosus* in northern Australia were similar in form and dimensions to these of *C. porosus* in other parts of its range (Kopstein, 1929; Deraniyagala, 1939; Neill, 1971).

Wallows beside nests were not mentioned by Kopstein (1929). In Sri Lanka they are similar to those in northern Australia; some are shallow and seem to result from scraping material for nest construction, while others are deep and used as "guard wallows" (Deraniyagala, 1939). As in our study, Deraniyagala (1939) found wallows beside nests next to permanent water and nests a long distance from it. Deraniyagala (1939) shot two female *C. porosus* in their wallows. They had empty stomachs and appeared emaciated. We have no comparable data, though one adult (at T14), sighted a number of times, was not emaciated.

Egg numbers and sizes reported by Kopstein (1929), Deraniyagala (1939) and Worrell (1952) are consistent with our data. Between-nest variation was much greater than within-nest, and as noted by Kopstein (1929), the largest eggs did not necessarily come from the largest

clutches. Kopstein (1929) and Deraniyagala (1939) reported nest temperature to be 32 C, consistent with our routine checks of nests in the present study ($\bar{x} = 30.7 \pm 0.3$ C). The delayed hatching of T14 (hatched over a period of 10 days; up to 18 days longer incubation time) may have resulted from late deposition and low temperatures. Similar delays having been reported in *C. porosus* (Worrell, 1952) and in *Alligator mississippiensis* (McIlhenny, 1934).

Of particular interest were the marked temperature fluctuations in L1 compared to the relatively thermostable conditions in T14. Chabreck (1973) measured temperatures in *A. mississippiensis* nests (a similar mound nest) and showed that changes in nest temperature lagged behind changes in ambient temperature, as in T14, the tightly compacted nest. *C. porosus* nests are generally not as tightly compacted as those of most other crocodilians (Neill, 1971), and in this study were frequently loosely constructed initially, some being packed down later. It is probable that the two types of temperature fluctuation observed characterize nests of different construction.

The effect of flooding on *C. porosus* nests in northern Australia is catastrophic. In Java, Kopstein (1929) found flooded *C. porosus* nests, whereas in Sri Lanka the earlier nesting period removes this danger (Deraniyagala, 1939). Pooley (1969) demonstrated that flooding destroyed the eggs of *Crocodylus niloticus*. Chabreck (1973) found flooded nests of *A. mississippiensis*. No authors report losses of the magnitude found with *C. porosus* in northern Australia.

In contrast to the losses due to flooding, predation on *C. porosus* eggs was minimal. Cott (1961) and Pooley (1969) found varanid lizards to be major predators on *C. niloticus* eggs. We found varanids eating only eggs in which the embryos had already been killed by flooding. Predation on *C. porosus* hatchlings, once in the river, was found to be slight. In the Tomkinson River, 58 hatchlings were known to have successfully hatched. Forty-nine of these were recaught after 2 months and 3 additional ones were sighted but not caught. This represents a maximum mortality rate of 15.5% in the first 2 months. Cott (1961) and Pooley (1969) present a formidable list of predators on *C. niloticus* hatchlings, and an experimental release of juvenile *C. niloticus* by Pooley (1969) suggested a far higher mortality rate than was found for *C. porosus*. McIlhenny (1934) presented data on the growth of 32 hatchling *A.*

mississippiensis released into a wildlife refuge area. Of these, 25 were caught between 6 and 11 years later, demonstrating a high survival rate.

It is possible that the high survival rate of *C. porosus* and *A. mississippiensis* is a feature of depleted populations. The literature contains reports of cannibalism amongst *C. niloticus* (Pooley, 1969; Cott, 1961). In Australia, hunters have told us that adult *C. porosus* eat juveniles, sometimes from hatching groups. If cannibalism were a major source of juvenile mortality, hatchling survival would be higher in depleted populations than in well stocked populations.

That adult *C. porosus* remained near their nest and assisted hatching by excavating the nest, is not surprising. Greer (1970) has reported such behavior in a number of species. Our data suggest that nests were excavated in response to the call of hatchlings from within the nest. Adult *C. porosus* did not excavate nests from which hatchlings did not call. In some flooded nests, adults remained by the nests without excavating them, even though the hatching date was long past.

The hatchling call may function to maintain the hatchling group (Campbell, 1973) and to keep the adult near the hatchlings. Our data indicate that at least some adult *C. porosus* remain in the vicinity of the hatchlings for at least two months. Worrell (1952) observed hatchling dispersal within a few days. We have never found aggressive adult *C. porosus* at nest sites, though on a number of occasions, a crocodile surfaced and then submerged close to the nest while it was being investigated. Pooley (1969) and Deraniyagala (1939) report similar behaviour in *C. niloticus* and *C. porosus* respectively. Deraniyagala (1939) also found one female *C. porosus* which growled and hissed from its wallow when they approached it.

The building of nests without eggs is not understood. Some of these nests are small with no permanent wallow, whereas others are complete and in all respects resemble nests with eggs. Some may be found adjacent to nests with eggs, suggesting that they are some type of "test" nest. Others are not associated with nests containing eggs. The most likely explanations are: 1) They are made by adolescent *C. porosus*, i.e. "practice" nests. 2) They are false starts where conditions at the site were not suitable for completion or changes in weather stopped nest construction. 3) They were intended for eggs and abandoned because of human or other disturbance.

It is difficult to determine the effect of disturbance by the investigators visiting *C. porosus* nests. It is likely that undisturbed females tend to build annual nests around a particular wallow or track from the river. We have observed such sites with a new nest and 1 or more older nests. During the 1973/74 season, such a nest congregation (1 new and 2 old) was found on the Goomadeer River, and none at that site the next year. In the Liverpool and Tomkinson rivers, the 1974/75 nests were never built next to 1973/74 nests which had been studied, yet some nests located for the first time in 1974/75 had nests from both seasons. This suggests that disturbance by the investigators led to the selection of a new site, usually within a few hundred meters.

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