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An Examination of *Crocodylus porosus* Nests in Two Northern Australian Freshwater Swamps, with an Analysis of Embryo Mortality

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Abstract

Crocodylus porosus nesting was examined in a perennial freshwater swamp (Melacca Swamp) adjacent to a tidal river, and in perennial floodplain river channels where floating mats of vegetation overlie fresh water (Finniss R. and Reynolds R.). Time of nesting was quantified. Vegetation at nest sites was identified and ranked according to importance indices, which are used as a descriptive tool. Most nests are exposed during mid-morning and afternoon, but variously shaded during early morning and late afternoon. Nests in Melacca Swamp are more shaded, and have lower nest temperatures, than those in the Finniss–Reynolds region. Nest visibility from the air is influenced by species-specific plant regrowth on nests.

In Melacca Swamp the height at which clutches are deposited is related to swamp water level. Mean clutch depth, the distance between top and bottom eggs, was 22·6 ± 8·3 cm (SD); the distance between the top egg and water level at the time of laying was 34·7 ± 8·0 cm. Mean clutch size was 53·1 ± 9·4 eggs; formulae relating egg and hatchling dimensions are presented. A highly variable but significant increase in egg size accompanied increased clutch size, but no relationship was found between clutch or egg size and time of nesting. A high correlation between egg widths of four pairs of clutches laid at the same sites strongly suggested multiple nesting by some females. Nest temperatures, embryo development rates and total incubation times were highly variable, both within and between nests. Of the 2712 eggs examined, 31·6% (856) produced live, apparently normal hatchlings. Flooding was the major cause of mortality, accounting for 36·3% of Melacca eggs and 40·6% of Finniss–Reynolds eggs. Other causes of egg failure included: infertility (M 9·4%, F–R 5·0%), high-temperature incubation (2·0%, 0·4%), low-temperature incubation (6·3%, 3·2%), mechanical damage to eggs by adult crocodiles (0·6%, 2·4%) and undetermined development failures (9·8%, 18·0%). No instance of dehydration of eggs within a nest, or predation on eggs, was recorded. A model for simulating Melacca nest flooding predicted a 33·2% loss of eggs in 1980–81 (estimated real loss was 36·3%), and indicated possible losses of 0–54·9% between 1960 and 1980 if the same numbers of nests had been made; mean loss was 26·3%. Three double-yolked eggs (0·1% of eggs examined) were recorded. Developmental anomalies and possible causes (incubation temperature–genetic), have been tabulated.

In attempting to analyse the siting of *C. porosus* nests and explain variation in nesting vegetation, nest site locations, nest mounds and embryo mortality rates, insights were gained by examining nest site selection from the point of view of the female's well-being rather than that of the nest. Resulting criteria considered important in nest site selection are listed and discussed. If the numbers of nests in freshwater swamps are an index of the total population size in such areas, there are clearly many more *C. porosus* in such swamps than have hitherto been estimated. Nest surveying may be the only practical method of estimating the total population. Regardless of high mortality rates, an egg-collection strategy may not prove a practical method of incorporating sustained-yield harvesting into an overall *C. porosus* management program.

Introduction

Estuarine crocodiles, *Crocodylus porosus*, deposit their eggs in a mound nest constructed of vegetation with varying proportions of mud and/or soil (Kopstein 1929; Deraniyagala

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1939; Webb 1977; Webb *et al.* 1977; Whitaker and Whitaker 1978*a*; Lang 1980; Magnusson 1980*a*; Whitaker 1980; Graham 1981). In Australia, the nest sites and nesting materials reflect, in part, the wide variety of wetland habitats the species occupies, both in fresh and saline waters (Magnusson 1980*a*; Magnusson *et al.* 1978*b*, 1980). In all areas nesting appears to be mainly a wet-season activity and total or partial flooding of nests is common; a major cause of embryo mortality is drowning (Webb *et al.* 1977; Magnusson 1980*a*, 1982; Magnusson *et al.* 1978*b*, 1980).

To a large extent, local topography determines whether or not an area is flood-prone, and within one river system some traditional nest sites consistently flood. *C. porosus* nesting in the Liverpool–Tomkinson River system, on the north coast of Arnhem Land, affords a good example (Webb *et al.* 1977; Magnusson 1980*a*, 1982). Crocodiles either nest at floodplain level on the banks of the main stream and its tributaries, or occasionally on the banks of floodplain billabongs, or they nest in small areas of spring-fed freshwater swamp that are elevated above the general floodplain level and drain into the downstream tidal areas. Nests in the higher areas rarely flood, whereas those on the banks usually flood. During 1974–76, for example, 12 of 14 nests in the elevated areas produced hatchlings, whereas none of 38 floodplain nests did so (Magnusson *et al.* 1980).

When it is considered that nesting at floodplain level is common outside the Liverpool–Tomkinson River system (Magnusson *et al.* 1978*b*, 1980), egg collection compensated for by a return to the wild of artificially raised young (Blake 1974; Blake and Loveridge 1975) appears a potential strategy through which sustained-yield harvesting could be achieved, while annual recruitment is enhanced.

However, when the recent published literature on *C. porosus* nesting in northern Australia (see, e.g., Webb 1977; Webb *et al.* 1977; Magnusson *et al.* 1978*a*, 1978*b*, 1980; Magnusson 1979*a*, 1979*b*, 1979*c*, 1980*a*, 1980*b*, 1981, 1982; Messel *et al.* 1979*a*; Lang 1980; Magnusson and Taylor 1980, 1981) is examined from the point of view of formulating any such management scheme, it becomes apparent that although a considerable database is available, information of direct application to management is lacking, insufficiently quantified, or the subject of conflicting interpretations and opinions (Magnusson 1979*b*, 1980*a*). Furthermore, much of the original data on nesting and nest success come from the tidal parts of the Liverpool–Tomkinson system, where all nests are 'bank' nests, built on solid substrates, and where the only nests in less flood-prone areas are in a reasonably homogeneous form of freshwater swamp.

The present study examines nesting in two exclusively freshwater areas, one a floodplain in which floating mats of vegetation extend over permanent water, and the other a somewhat elevated freshwater swamp (containing a variety of vegetation communities), connected by a small creek to a meandering, tidal floodplain river. Particular importance is attached to the extent and probable causes of embryo mortality, as these were considered to have a high management priority, yet are poorly quantified in the literature. General data on nesting were collected during the study and these are presented and discussed within the context of existing information.

Methods

Study Areas

(i) *Melacca Creek Swamp*

Melacca Creek is a relatively short (*c.* 16 km), permanent freshwater creek which flows into the downstream, mangrove-lined tidal section of the Adelaide River. From its headwaters (12° 23′S., 131° 12′E.) (Fig. 1) to approximately 2 km downstream, Melacca Creek flows within a relatively narrow (300 m) band of dense rainforest, itself somewhat enclosed within a border of tall dense *Melaleuca* forest. Between 2 and 5 km downstream the creek expands into a shallow (1–3 m deep) swamp dominated by large, discrete beds of *Thoracostachyum sumatranum*, a tall (2–4 m) sedge, which is often present as a dense understorey beneath *Melaleuca*, but also occurs as exposed beds without a canopy.

When present as an understorey, *T. sumatranum* is usually associated with the fern *Stenochlaena palustris*, and a number of other plants (particularly the vines *Flagellaria indica*, *Cayratria trifolia* and *Mucuna* sp., the fern *Cyclosorus interruptus*, and the sedge *Machaerina rubiginosa*).

Between *T. sumatranum* beds are isolated stands of other sedges and rushes, e.g. *Hymenochaeta grossa*, *Eleocharis* sp., and *Typha* sp., and these become more dominant downstream of approximately 5 km, where *T. sumatranum* is restricted to the main creek line. At the transition between the freshwater swamp vegetation and saline mangroves, *Typha* sp. and *Flagellaria indica* are dominant.

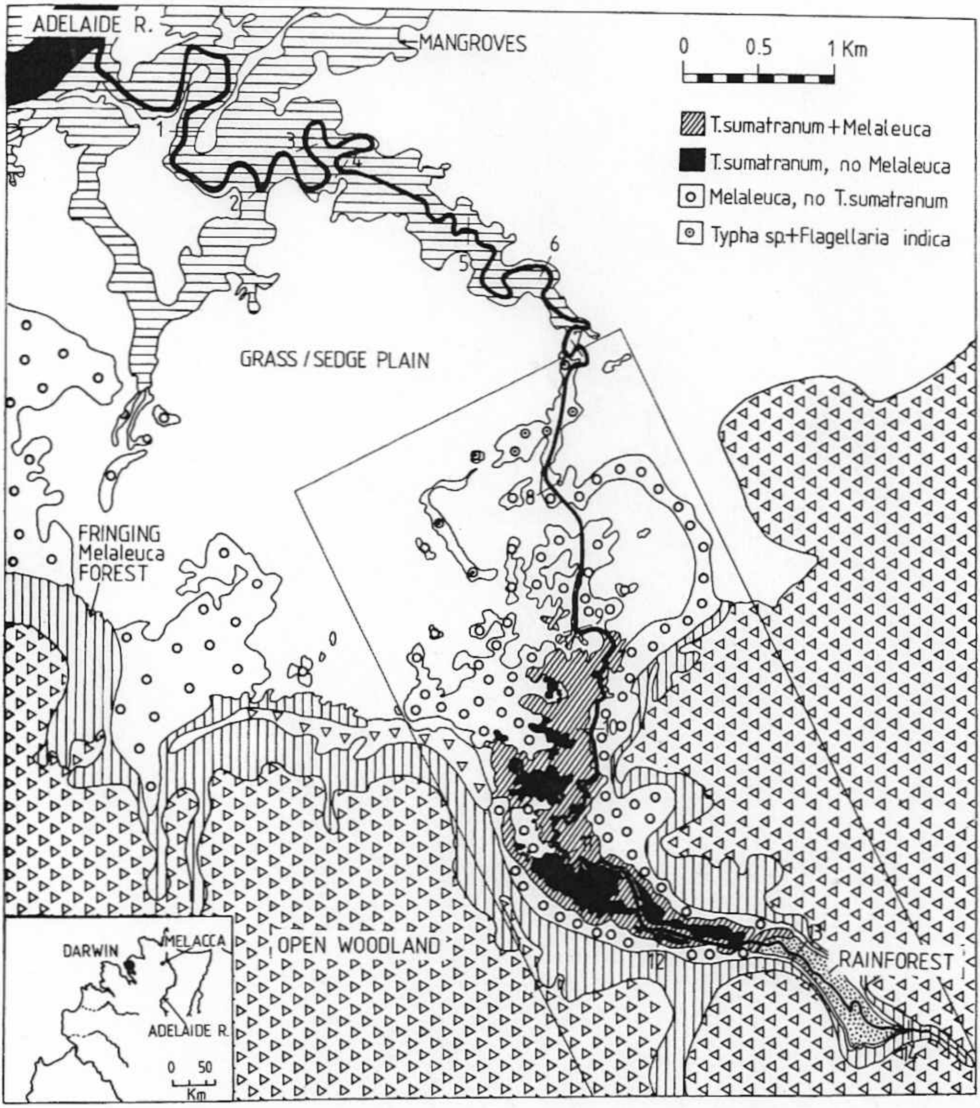


Fig. 1. Major habitats in Melacca Creek swamp from its headwaters to the Adelaide River. All nests were located within the area marked, which also transects the limit of tidal influence. Numbers are creek kilometres from the mouth. Nests were located in the *Flagellaria–Typha* in 1979–80 and 1981–82, but not during 1980–81.

Although small in area, Melacca Creek Swamp was known to contain a reasonably large number of *C. porosus* nests annually (unpublished preliminary surveys), and was our main study area.

(ii) *The Finniss–Reynolds River area*

The headwaters of both river systems consist of perennial and intermittent freshwater springs in a sandstone escarpment. Between these springs and the upstream limit of tidal influence (Fig. 2) are extensive floodplains containing a network of old riverbed channels and billabongs, which together constitute each river system. During the dry season, both rivers are composed of discrete bodies of water, but during the wet season these link through a number of channels, and with excessive rain are continuous, with sheets of water across the floodplains.

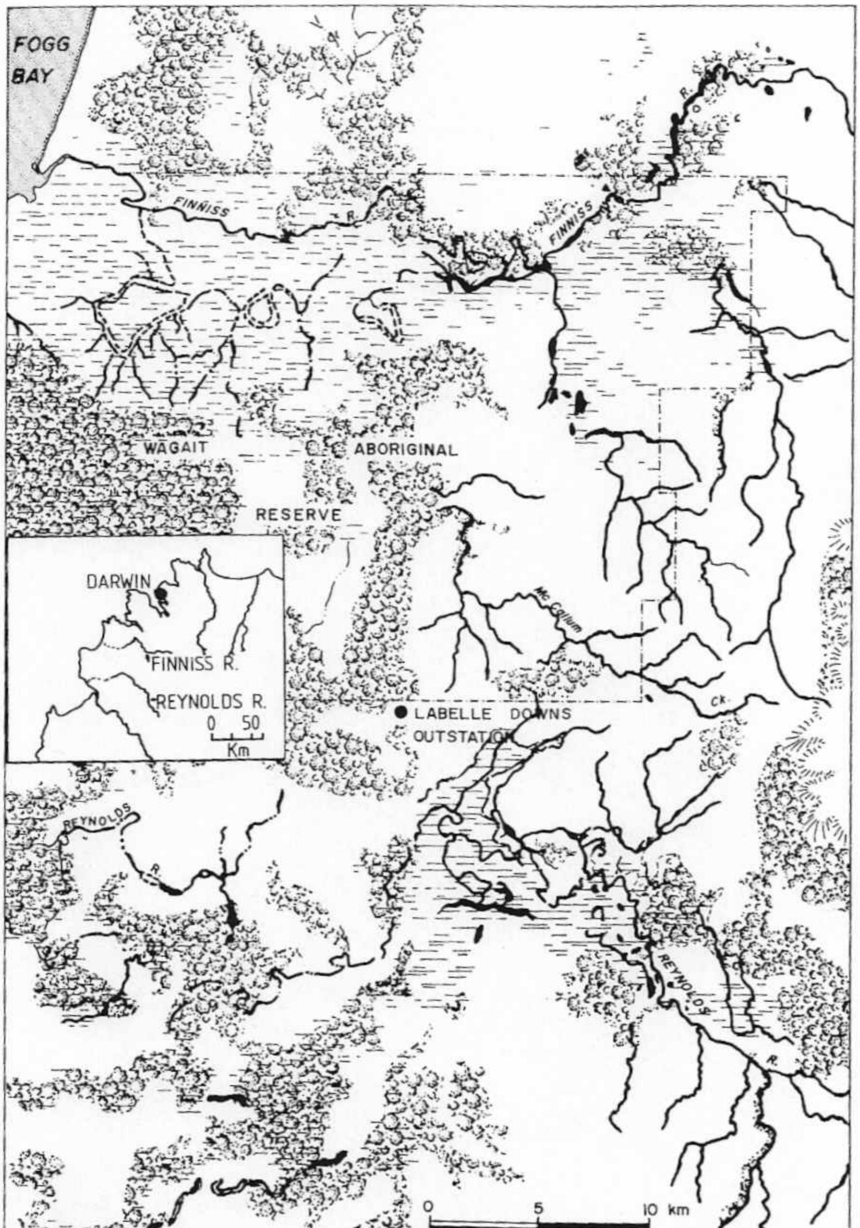


Fig. 2. The Finniss and Reynolds River study area. Horizontal shading indicates floodplains, and dense shading woodland. Horizontal shading in woodland is mostly *Melaleuca* swamp.

The permanent billabongs and channels are frequently adjoined by freshwater swamps dominated by *Melaleuca* sp., and during the wet season the floodplains are covered by grasses such as *Hymenachne acutigluma*, wild rice *Oryza meridionalis*, swamp millet *Isachne globosa*, and para grass *Brachiara mutica*.

In the permanent channels and billabongs, floating mats of vegetation extend from the banks, over the water, for up to 100 m. These mats are usually anchored in culs-de-sac or concavities in the shoreline (out of the main stream flow) and contain quite complex vegetation communities, typically in discrete zones (Fig. 3) (Hill and Webb 1982). Cane grass *Phragmites karka* and bulrush *Typha orientalis* with an understorey of the fern *Cyclosorus interruptus* usually dominate the most landward communities and are on the more stable parts of the mat (1 m deep peat; will support the weight of a man without sinking). Further out a number of sedges, e.g. *Hymenochaeta grossa*, and grasses, e.g. *Echinochloa praestans* and *H. acutigluma*, occur, but the limit of the *C. interruptus* is usually also the limit of the stable mat. The outer extremities of mats are unstable (composed of a looser network of plant stems and roots with little peat) and may contain a variety of grasses, floating herbs, especially *Pistia stratiotes*, and inundation-tolerant scramblers, e.g. *Ipomoea aquatica*. Throughout the mat vegetation is a rich diversity of other grasses, herbs, sedges and climber–scramblers.

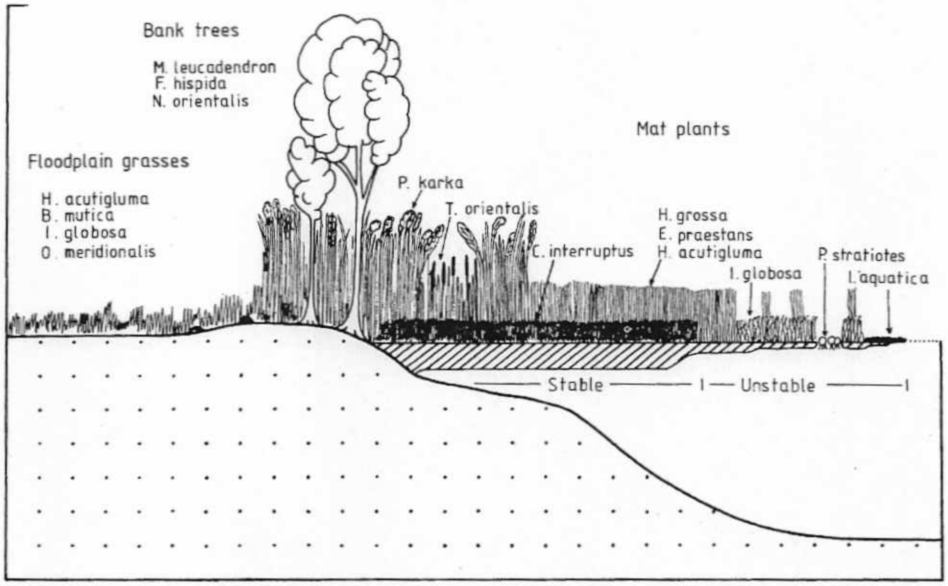


Fig. 3. A generalized cross-section through a Finniss–Reynolds floating mat, showing the dominant vegetation types.

All *C. porosus* nests located in the Finniss–Reynolds were constructed on floating mats, although bank nesting did occur in the past (Petherick, personal communication). The Finniss–Reynolds wetlands are now utilized by introduced cattle, wild pigs *Sus scrofa* and water buffalo *Bubalus bubalis*. The activities of the last, in particular, have resulted in bank vegetation being denuded (see Calder 1981, on *Hymenachne acutigluma*) and the bank anchorage of floating mats being severed to the extent that many have floated away in wet-season floods (Letts *et al.* 1979; Petherick, personal communication). Analysis of aerial photographs of a large segment of the Finniss River (Hill and Webb 1982) indicated that more than 80% of mats recognizable in 1964 had disappeared by 1978.

Due to the much greater area of the Finniss–Reynolds and the difficulty in sighting older nests (due to regrowth, see later), our results from this area are more generalized than those from Melacca Swamp, where most nests present were located.

General

The study was initiated in November 1980 and terminated in November 1981. Nests were located mainly from a helicopter and visited as soon after being located as was logistically possible. Of 59 nests with eggs located (19 had no eggs), 73% were visited within 2 days, 83% within 6 days, and 17% between 27 and 39 days after location.

In order to assess which, if any, plant species could be considered as more important than others in nest site selection, and to determine the degree to which plants used in nest construction represented a random selection of those in the sites chosen, importance indices were derived for the plant species at sites, and in the nests. The species present at each site were recorded (this often entailed the assumption that the vegetation on the periphery of the site was the same as that originally standing on the site), and each was assigned an approximate percentage of the total volume of standing plant material, at the understorey level, that it accounted for. The same procedure was applied to the vegetation actually used in the nest. The first importance method used (dominance importance index) concentrated only on the most dominant plant at each site (and nest), and simply assessed the proportion of sites (and nests) dominated by different species. The second method (ranking importance index) was modified from stomach contents studies (see Pollard 1973; Webb *et al.* 1982), and incorporated elements of percentage composition, the number of species at sites and the frequency of occurrence of species at different sites.

Plant species at each site were ranked according to their approximate percentage composition (highest = 1) at that site, and then a score for each species was calculated by subtracting that rank from the maximum number of species found at any site plus 1; scores for each species at all sites were totalled, the importance of a particular species being indicated by the percentage of the grand total score it accounted for. The same procedure was carried out with nest vegetation.

On the basis of the height and position of vegetation surrounding a nest site, and in particular the degree of canopy cover, an estimate was made of the extent to which nests were exposed to the sun during different periods of the day. The technique used was to delimit a vertical axis and 45° and 135° axes in the approximate direction of the sun's travel, and estimate the percentage of each 45° segment in which the nest would be exposed to the sun. By applying times to these angles (e.g. 0600–0900 ≡ 0°–45°) it was possible to approximate nest exposure. In reality, solar radiation varies throughout the day and is highest in mid-afternoon and lowest early in the morning (radiometric data collected in Cape York by Lang; personal communication).

After noting obvious signs of nest age in the field (e.g. fresh green nest material, old browned nest material, regrowth on nests) the vertical height between the top of the mound and the water was measured. A thermometer was then used to record the temperature within, below and above the clutch, along with that of the outside air and water ($\pm 0 \cdot 2$°C). The distance between the top egg and water was then measured, and in Melacca Swamp all heights were standardized to a water height measured on the edge of the swamp at each visit.

The top egg of each clutch was removed and opened, and if the embryo was alive the nest was recovered and the remaining eggs left to incubate. If it was dead, a second egg was taken, and where it was considered that all embryos were dead the complete clutch was taken. In these cases eggs were divided into three or four vertical layers for the purpose of approximately distinguishing between the upper and lower eggs. The upper surface of individual eggs was marked in order to facilitate finding dead embryos (Ferguson 1982, 1983).

Live and dead embryos were aged approximately, on the basis of their size and developmental stage, with a compensation for nest temperature (Webb *et al.* 1983*b*). This allowed the approximate time of laying and hatching to be predicted for live embryos, and age at death to be predicted for dead ones. Nests containing live embryos were revisited as close to 1 week before the predicted hatching date as was practicable. After the height and species composition of vegetation regrowth on the nest were noted, the complete clutch was retrieved and returned to the laboratory; the height of the bottom egg above water level (and sometimes the top egg again) was measured.

Ten eggs from each clutch were measured and weighed, and after the removal of eggs in which development had obviously ceased (i.e. those with opaque bands when the others were uniformly opaque; Ferguson 1980*a*, 1982; Webb *et al.* 1983*b*), the remainder were placed in controlled-temperature cabinets set at 30°C. At hatching, live hatchlings were measured and marked and notes taken on any obvious abnormalities. All eggs which failed to hatch were opened and an attempt made to locate and age all dead embryos (Webb *et al.* 1983*b*). If embryos could not be found, the presence of an opaque band on the inner surface of the shell was taken as an indication that an embryo had been present, although it may have died within the first few days after laying (Ferguson 1982).

In most nests, the presence of at least one live embryo allowed the approximate date at which embryos had died to be determined; however, when all embryos were dead, information from prior visits and the extent of flood-induced mortality in nearby nests were often used as guides to when the nest had been laid or when the embryos had died.

Assigning causes of embryo mortality was simplified and somewhat subjective, because detailed information on each nest throughout incubation was unavailable, and very few data on causes of embryo mortality exist. On the basis of the pattern of dead embryos within nests and observations made on site, the following categories were recognized.

Flood-induced mortality. Apparently normal embryos dead at the same stage (age) or staggered from the bottom of the clutch upward in discrete stages (indicating multiple floods), often with direct observations of the nest being submerged at the time of visit, or having recently been submerged, or knowledge that the water level at the site had been well above clutch level. Eggs were often greatly swollen and extensively cracked.

Physical damage. Badly crushed eggs within clutches, presumed to result from the activities of the parent(s) either during egg-laying or when subsequently crawling and/or lying on the nest.

Temperature-induced mortality. Embryos from warm nests (33–34°C or over) or cool nests (26–28°C or less) which if at all successful had a high proportion of abnormal hatchlings. Abnormalities typically included spinal deformities, curling of the tail, misalignment of jaws, and an apparent failure to absorb yolk once enclosed within the body (these could often be discerned in dead embryos).

Infertile or early embryonic death. Eggs with no sign of an enlarged embryo or an opaque band on the inside of the shell were assumed to have been infertile or failed to develop to 1 day old. On the few occasions where the majority of the eggs in a clutch were so classified, the position of these eggs relative to ones showing development was used as an indication of whether or not the nest had flooded at the time eggs were laid.

Dehydration. Air spaces in the egg where the shell membranes have parted from the shell and contracted around the egg contents and embryo. Eggs exposed to the sun often dehydrated, but the cause of death in such cases was assumed to be overheating. This category refers to embryos from intact nests with insufficient moisture.

Developmental failures. In many instances obvious reasons for mortality were not apparent, and this category was used as a catch-all to include those individuals which were dead at different ages, but distributed randomly through nests, or in a pattern unexplained by the above criteria. Ferguson (1982, 1983) lists a number of reasons why such deaths can occur, including misorientation: eggs vertically aligned in nests do not develop. In a few cases it was considered that abnormal embryos were the result of genetic anomalies, and these were included in this category.

In assigning embryos to the above categories, an attempt was made to isolate the cause of death when it appeared a number of factors had been operating. For example, although a complete clutch may have flooded at 50 days, the size and position of embryos may have indicated a 10% loss due to developmental failures before that flood.

Unless otherwise stated, variation around mean values is expressed as ± one standard deviation.

Results

Time of Nesting

C. porosus nests were constructed throughout the wet season with the earliest on approximately 5 November 1980 and the latest on 18 May 1981. In Melacca Swamp, there was little regrowth on nests (they are discernible 1–2 years later), and most 1980–81 nests were believed to be located.* The approximate monthly breakdown of new nests found is as follows:

	N	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Melacca Swamp	18	3	2	6	3	3	1	0
Finniss–Reynolds	41	0	4	9	16	6	4	2

* Surveys in 1981–82 have indicated two nests, which may have been missed during the 1980–81 study. They were most probably made in May–June, and have not been included in any analyses.

At Melacca Swamp, the distribution is thought to reflect the general pattern of nesting in the area. In the Finniss–Reynolds area, surveys were not begun until February, and regrowth (see later) made it impossible to ascertain the degree to which the observed time of laying reflects the overall trend in the population; more November–January nests may have existed. Contingency table analysis indicated the monthly frequencies between the two areas were not significantly different ($0{\cdot}01 > P > 0{\cdot}05$), even when partitioned into November–January, and February–May ($P > 0{\cdot}05$).

Nest Site Selection and Nest Constituents

In the Finniss–Reynolds all nests with eggs ($n = 41$) were on floating mats of vegetation, and crocodile access to nests was usually (95%) by an opening through the mat (there were often additional trails across the mat). These openings were expanded by continued crocodile activity at nest sites, and in most cases nests became detached from the mats and surrounded by water. In Melacca, all nests ($n = 18$) were in permanently inundated sedge beds, and shallow water surrounded each nest; distinct deeper areas (wallows: Webb *et al.* 1977) were present beside nests. Close proximity to permanent fresh water was thus a common feature of all nest sites in both study areas.

Table 1. Potential nest sites, sites actually used for nesting by *C. porosus* and areas of different habitats in Melacca Swamp

Habitats are not used in proportion to their abundance. (χ^2 on habitats 1, 2, 3 and 2, 3; $P < 0{\cdot}05$)

Habitat	Area (ha)	Nests located	Expected distributions 1,2,3	2,3	Potential nest sites spaced at: 200 m	100 m	50 m
1. *Melaleuca* without *T. sumatranum*	189	0	11·86	–	60	241	963
2. *Melaleuca* with *T. sumatranum*	69	17	4·32	12·67	22	89	355
3. *T. sumatranum* without a canopy	29	1	2·93	5·33	9	37	148

The indices of importance (Appendices 1 and 2) indicate reasonably major differences in the taxonomy of nest and nest site vegetation between the two areas, which reflects the distribution of the dominant plants. For example *T. sumatranum* is abundant at Melacca but absent in the Finniss–Reynolds, and conversely, *P. karka*, *T. orientalis* and *C. interruptus* are abundant in the Finniss–Reynolds but are scarce at Melacca.

In Melacca (Appendix 1) *T. sumatranum* was the dominant plant at 94% of nest sites, the single exception being a nest constructed on the base of a *Melaleuca* adjacent to a *T. sumatranum* bed, but within a stand of tall (2 m) *M. rubiginosa*. The ranking method (Appendix 1), clearly isolated *T. sumatranum* as the most important nest site plant, but indicated the paperbark *Melaleuca leucadendron* and fern *S. palustris* as also being important: 94% of nests were built beneath a *Melaleuca* canopy, at the base of a live *Melaleuca* tree or over dead fallen ones; and within *T. sumatranum* beds *S. palustris* is a common understorey plant. Comparison of nest vegetation with that at the site indicated similar species rankings, with a slight increase in *T. sumatranum* and reduction in *Melaleuca* (bark and leaves) and *S. palustris*; when present, *Melaleuca* trunks cannot readily be incorporated into the nests.

Analysis of aerial photographs indicated that within the Melacca study area (Fig. 1) there were 189 ha of inundated *Melaleuca* swamp without *T. sumatranum* as an understorey, 69 ha of *Melaleuca* swamp with *T. sumatranum* as an understorey and 29 ha of exposed *T. sumatranum* beds without a canopy. Depending on the amount of habitat needed for a nesting female these can be regarded as potential nest areas, and in Table 1 numbers of potential nest areas have been calculated for conditions where nests are 50, 100 and 200 m apart, assuming that a circle of that diameter constitutes a nest area, with the nest site within that area (the closest nests we believed to be from different females were about 30 m apart). χ^2 analysis indicated that the three habitats were not being used in proportion to their abundance ($P<0{\cdot}001$). When '*Melaleuca* lacking *T. sumatranum*' was removed from the analysis, '*T. sumatranum* beneath a *Melaleuca* canopy' was still used significantly more than 'exposed *T. sumatranum* beds' ($0{\cdot}05>P>0{\cdot}025$) indicating a preference for this habitat. The single 1980–81 nest in exposed beds, and some older nests still visible in this habitat, were constructed at the base of small isolated *Melaleuca* trees. The absence of trees may be what limits nesting in the exposed beds (Appendix 1).

At the Finniss–Reynolds (Appendix 2), cane grass *P. karka* was the most dominant plant at nest sites, next to which was bulrush *T. orientalis*, the sedge *E. praestans*, the fern *C. interruptus*, and the grass *I. globosa*. Compared to Melacca Swamp, there were many more dominant species, indicating the greater diversity of plants available. The ranking index showed *C. interruptus* as the most important plant, because, as well as being dominant at some nest sites, it was a common understorey plant at sites dominated by the taller vegetation (*P. karka, T. orientalis, E. praestans, S. grossus, I. globosa*) and was a major constituent of the stable mats on which most nests were located (Fig. 3). As in Melacca Swamp, utilization of plants for nest construction was a somewhat random selection of those available at the nest site chosen (with the addition of peat from the mat substrate). Regardless of which dominant species was at a particular nest site, others were usually in the immediate vicinity. If a strong preference did exist for a particular species, that preference could usually have been exercised by a minor change in the position of the site chosen.

If crocodiles select nest sites on the basis of the growth form rather than species composition of the vegetation present, the taller, denser stands of all species could be lumped, making them much more important than other understorey plants, regardless of which importance index was used.

In both Melacca and the Finniss–Reynolds, certain aspects of nest site vegetation seemed common:

(1) The dominant species at a nest site formed an understorey at least 1–1·5 m tall.
(2) The dominant species was sufficiently dense for a mound 50 cm high to be constructed from vegetation well within a circle 10 m in diameter.
(3) At a height of 0·8–1 m from the substrate, the surrounding vegetation was sufficiently dense for investigators to be usually unable to see more than 10 m to one side, and often on all sides.
(4) Due to vegetation surrounding the site, or taller vegetation nearby, the nest site was largely protected from prevailing winds.
(5) Nest sites were usually situated so that the nest received direct sunlight each day (see later).
(6) The dominant plants, although robust enough to be seldom flattened by wind, could be readily broken and lent themselves to being utilized by nesting *C. porosus*.
(7) If the site was in permanent water, the vegetation at water level was sufficiently dense, and/or the water sufficiently shallow, for a platform to at least water level to be made by flattening the vegetation present. If trees were present in such areas their bases appeared to be a preferred nest foundation.

Nest Exposure

At Melacca, the canopy and tall understorey (mainly *T. sumatranum*) restricted early morning and late afternoon exposure to usually less than 50%, and even during late morning and early afternoon (when solar radiation is greatest) nests tended to be partly shaded (Fig. 4); only 39% of nests had 100% exposure during the mid-morning and 17% of nests had 100% exposure in mid-afternoon. The Finniss–Reynolds nests tended to be more exposed at all times, 56% of nests having 100% exposure during the mid-morning and 63% having 100%

exposure during mid-afternoon. After applying approximate hours to each segment it was clear that the average Melacca nest received less exposure (6·7 h per day) than the average Finniss–Reynolds nest (8·0 h per day).

Nest Visibility and Regrowth on Nests

During incubation, the vegetation from which nests had been constructed often regrew. Such regrowth obscured the visibility of older nests from the air, and may well have influenced nest temperatures. The extent of regrowth depended in part on the plant species, and may relate to their method of reproduction, and to whether or not plants were uprooted when being incorporated into the nest; observations made during the present study are summarized in Table 2. Regrowth was negligible in Melacca; however, in the Finniss–Reynolds many of the understorey vines, and the fern *C. interruptus*, grew back rapidly, often making it difficult to relocate nests. Where adults used a nest as a basking site, regrowth appeared to be retarded; conversely, it was accelerated at abandoned nest sites. Nest visibility was also influenced by the height of vegetation surrounding a nest. In cane grass *P. karka*, for example, the plants tended to lean inward with time, reducing the extent of the nest area cleared as seen from above.

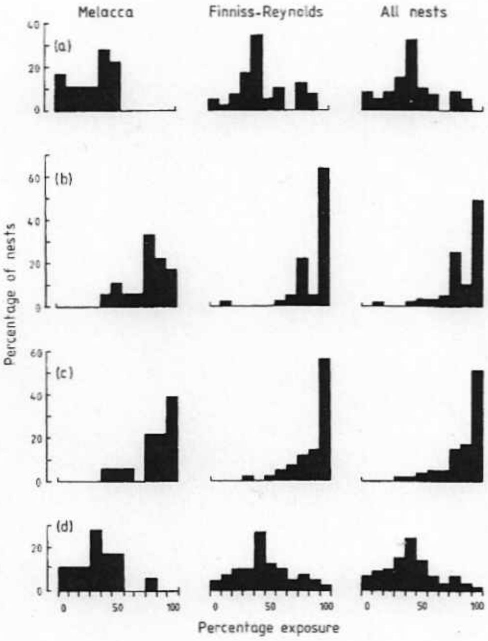


Fig. 4. The estimated percentage exposure of nests at different times of day (see text). Solar radiation is highest in mid-afternoon and lowest in the early morning.
(*a*) Late afternoon.
(*b*) Mid-afternoon.
(*c*) Mid-morning.
(*d*) Early morning.

Height of Eggs above Water

During the 1980–81 wet season, daily rainfall and water heights varied considerably (Fig. 5). However, at the time of nest construction in the Finniss–Reynolds, clutches had a reasonably constant height above water because they were built on floating mats (essentially mound height less depth to the top egg; 53 cm less 19 cm; Webb *et al.* 1977).

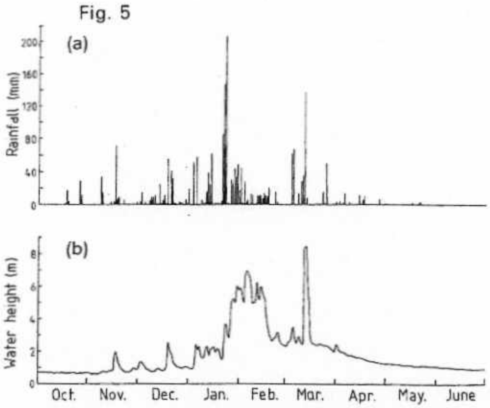
At Melacca, nests were not on floating mats, and although no continuous water height recorder was available, spot measurements at each visit correlated reasonably well with both mean rainfall for the 10 days preceding a measurement ($r^2 = 0{\cdot}74$; $P < 0{\cdot}05$) and with the Finniss River water heights (Fig. 5; $r^2 = 0{\cdot}83$; $P < 0{\cdot}05$). In Fig. 6, water heights predicted from the Finniss River data (by a regression formula) have been included, but the positions of the highest and lowest egg of each clutch are plotted relative to the real spot water heights measured at Melacca. Where the height of the lowest egg above water was not measured, mean clutch depth (22·6 ± 8·3 cm; $n = 12$) was used to set the lower level, and up to 10 cm was added to clutches from nests which appeared to have settled before being measured. Clutch height appears to have increased with the rise in water level (as described for *A. mississippiensis*; Kushlan and Kushlan 1979), and may have been maintained at an elevated level after the prolonged period of rain and high water in January. By taking the mean of the predicted water heights for the 5 days spanning a laying date it was possible to estimate the approximate mean height of the top egg above water at the time of laying for nests laid up until March (34·7 ± 8·0 cm; $n = 13$).

Table 2. Summary of observations on the extent of regrowth of the major vegetation used for nest construction by *C. porosus*

Species	Overall regrowth assessment	Notes
Sedges		
Thorocostachyum sumatranum	Very sparse	Virtually no regrowth during the incubation period, or in the first year after construction
Machaerina rubiginosa	None	In the single nest examined, no regrowth; the nest was distinct 1 year later
Typha orientalis	Very sparse	Only very light regrowth within the incubation period, although associated understorey ferns and vines do grow
Hymenochaeta grossa	None	No regrowth recorded during 3 months
Grasses		
Phragmites karka	Dense	Within 2 months, some plants up to 1 m; after 3 months, up to 1·5 m. In addition the 'leaning in' of surrounding vegetation can mask nest sites within 1 month
Echinochloa praestans	Medium to dense	After 2 months regrowth up to 0·4 m; may be up to 1·6 m by 3–3·5 months
Isachne globosa	Very sparse	At one site plants 0·05 m high present after 3 months
Hymenachne acutigluma	Medium to dense	At 2 nest sites, 0·1–0·9 m after 3 months
Ferns		
Cyclosorus interruptus	Dense	Regrowth on almost all nests where present. Usually 0·1 m after 1 month, 0·2–0·4 m by 2 months; may be up to 0·8 m by 3 months
Stenochlaena palustris	None	No regrowth recorded during 3 months
Herb		
Ludwigia sp.	Medium to dense	Regrowth common, up to 0·4 m after 2 months, and 0·7 m after 3 months
Climber–scramblers		
Flagellaria indica	Medium to dense	1 m high at one nest after 2 months
Merremia gemella	Dense	Runners commonly spread out over nests, usually <0·2 m but may be very dense
Commelina sp.	Medium to dense	Vines often spread out over nests; up to 0·4 m by 2 months and up to 0·8 m by 3 months

Clutch, Egg and Hatchling Sizes

Of the 51 complete clutches examined, mean clutch size was 53·1 ± 9·4 eggs (range 16–71) and the mean egg dimensions of individual clutch means were: egg length, 79·7 ± 4·9 mm ($n = 53$; range 65·7–87·7 mm); egg width, 49·5 ± 2·7 mm ($n = 53$; range 42·2–53·9 mm); egg weight, 113·4 ± 18·8 g ($n = 51$; range 65·4–137·2 g). The relationships



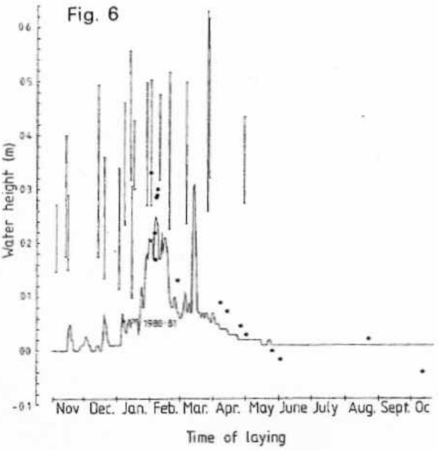


Fig. 5. Daily rainfall measured in Darwin (*a*), and Finniss River water heights (*b*), during the 1980–8 *C. porosus* nesting season.

Fig. 6. Standardized clutch levels for nests laid at different times in Melacca. Dots indicate water heigh measured; continuous line, the generalized flood height pattern predicted from Finniss River wat heights by regression analysis (see text). The vertical lines indicate the distance between top and botto eggs of each clutch.

Table 3. Constants for predicting hatchling and egg dimensions of *C. porosus* from each other, wit linear regressions

Dimensions in millimetres; weights in grams. SEE, standard error of estimate (Zar 1974)

To predict	From	Intercept	Slope	r^2	N	SI
Egg length	Egg breadth	22·9	1·16	0·48	68	3
	Egg weight	52·7	0·24	0·76	68	2
	Snout–vent length	19·9	0·44	0·49	72	3
	Head length	14·8	1·53	0·45	56	3
	Body weight	55·6	0·34	0·71	64	2
Egg breadth	Egg length	15·9	0·42	0·48	68	1
	Egg weight	31·7	0·15	0·84	64	1
	Snout–vent length	7·2	0·30	0·63	69	1
	Head length	10·1	0·93	0·59	52	1
	Body weight	33·5	0·22	0·79	61	
Egg weight	Egg length	−139·9	3·17	0·76	68	
	Egg breadth	−156·2	5·50	0·84	64	
	Snout–vent length	−140·6	1·85	0·68	68	
	Head length	−139·8	5·97	0·59	56	1
	Body weight	25·0	1·25	0·79	56	
Snout–vent length	Egg length	47·2	1·14	0·49	72	
	Egg breadth	36·2	2·07	0·63	69	
	Egg weight	95·9	0·37	0·68	68	
	Head length	6·3	3·10	0·83	56	
	Body weight	99·6	0·53	0·68	65	
Head length	Egg length	19·2	0·30	0·45	56	
	Egg breadth	11·4	0·63	0·59	52	
	Egg weight	31·6	0·10	0·59	56	
	Snout–vent length	5·8	0·27	0·83	56	
	Body weight	32·3	0·14	0·55	56	
Body weight	Egg length	−97·1	2·12	0·71	64	
	Egg breadth	−105·5	3·61	0·79	61	
	Egg weight	−0·5	0·64	0·79	56	
	Snout–vent length	−103·4	1·27	0·68	65	
	Head length	−89·7	3·82	0·55	56	

between egg dimensions and hatchling dimensions are given in Table 3; mean hatchling size was 138 mm SVL, 43 mm HL and 71 g body weight (predicted from mean egg weight). The formula for predicting egg weight (W, in grams) from egg length and egg breadth (L and B, in millimetres) is: $W = -196 \cdot 4 + 3 \cdot 58B + 1 \cdot 68L \pm 2 \cdot 8$ ($r^2 = 0 \cdot 97$; $n = 64$).

Among the nests examined from the two areas, clutch sizes (Melacca, $50 \cdot 9 \pm 6 \cdot 1$; $n = 18$; Finniss–Reynolds, $54 \cdot 2 \pm 10 \cdot 6$; $n = 35$) and egg mean weights (Melacca $113 \cdot 5 \pm 11 \cdot 8$; $n = 16$; Finniss–Reynolds, $113 \cdot 3 \pm 21 \cdot 4$; $n = 35$) were not significantly different, although the Finniss–Reynolds clutches were more variable than those from Melacca (F test, $P < 0 \cdot 05$). There was a significant but highly variable ($r^2 = 0 \cdot 12$) tendency for egg weight to increase with increasing clutch size (C), as reported for *A. mississippiensis* (Deitz and Hines 1980) (Fig. 7; $W = 76 \cdot 81 + 0 \cdot 68C \pm 17 \cdot 5$). No significant relationship existed between clutch size (or egg size) and time of nesting (Fig. 8), as occurs with *Caiman crocodilus* (Staton and Dixon 1977), *A. mississippiensis* (Ferguson 1983) and *C. johnstoni* (Webb *et al.* 1983*a*).

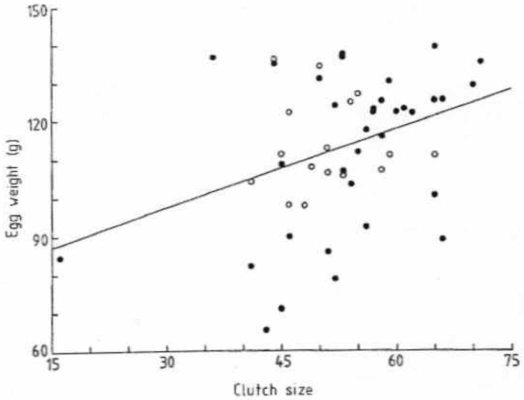


Fig. 7. The relationship between clutch size and mean egg weight for all nests with eggs examined.
○ Melacca nests.
● Finniss–Reynolds nests.

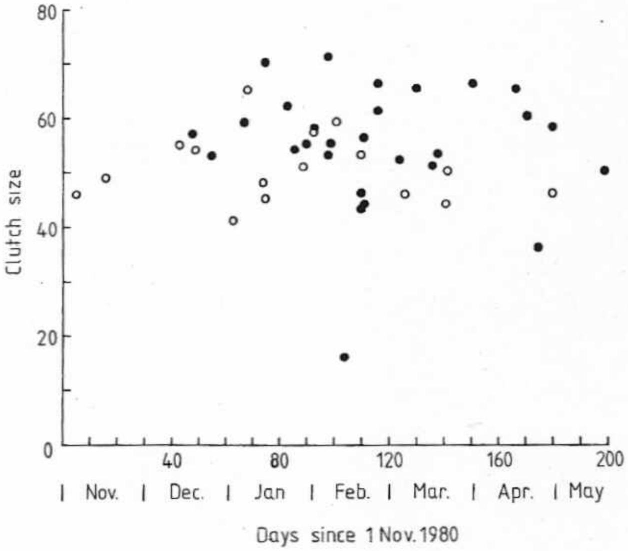


Fig. 8. The relationship between clutch size and time of laying for all nests with eggs examined.
○ Melacca nests.
● Finniss–Reynolds nests.

False Nests

As with *A. mississippiensis* (Joanen 1969; Deitz and Hines 1980) and *C. porosus* in the Liverpool–Tomkinson area (Webb *et al.* 1977), nests in which no eggs were deposited were located at both Melacca (2) and the Finniss–Reynolds (17). At one site there were four shallow heaps of nest material within 40 m of a completed nest with eggs; however, at other sites the nests were of normal appearance. There was less than 40 m between false nests and nests with eggs in 11 cases, and 90–500 m in eight others.

Nest Temperatures

In Fig. 9, nest temperatures measured in each study area are plotted against day of measurement, with symbols to indicate whether or not the nest had been flooded before the temperature was measured (temperatures from nests completely flooded at the time of measurement are not included). The overall mean temperature of unflooded nests was $31\cdot1 \pm 2\cdot6$°C ($n = 39$). Given the unmeasured variables which influence spot temperatures in mound nests (Magnusson 1979*c*), detailed analysis of such temperatures was considered unwarranted; however, some trends are apparent. The onset of cool weather (May in particular) is associated with a lowering of nest temperature, which in one heavily shaded nest reached 24°C (embryonic development ceased). Unflooded Melacca nests were generally cooler ($30\cdot3 \pm 1\cdot7$°C; $n = 12$; maximum $33\cdot0$°C) than unflooded Finniss–Reynolds nests ($31\cdot5 \pm 2\cdot9$°C; $n = 27$; maximum $35\cdot1$°C), and between 1 February and 2 May (before the cooling) this difference was significant (Melacca, $30\cdot5 \pm 1\cdot5$, $n = 11$; Finniss–Reynolds, $33\cdot0 \pm 1\cdot4$, $n = 18$; non-overlap of 2 SES). This result is consistent with the greater exposure of Finniss–Reynolds nests; however, it should also be noted that of the four highest nest temperatures recorded, three were from nests dominated by the fern *C. interruptus*—perhaps it generates more heat during decomposition.

The cool, partly flooded Melacca nests measured on 6–7 February 1981 reflect the generally low water temperatures found beneath the tall dense *T. sumatranum* beds.

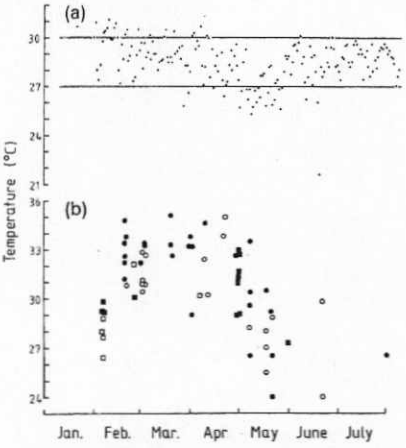


Fig. 9. (*a*) Mean daily air temperature (maximum + minimum/2) recorded in Darwin during the 1980–81 nesting season. (*b*) Spot nest temperatures recorded from unflooded nests in Melacca (■) and the Finniss–Reynolds (●); □ ○ temperatures recorded from nests known to have been flooded.

Incubation Times

Total incubation times in the field vary substantially, because not only do incubation temperatures (and other nest environment parameters likely to influence development rate) vary, but embryos may hatch and survive when the yolk has just been withdrawn into the body (minimum hatching stage) or they may remain in the egg unhatched until the umbilical scar has almost completely healed; some 10 days difference at 30°C (Webb *et al.* 1983*b*). The average stage at which they pip eggs (snout breaks through the egg shell), if left undisturbed, appears to be when the width of the yolk scar is 5–10% of SVL.

In the present study, definitive incubation times (day of laying to day of hatching) were not obtained. Generalized constants for temperature against development rate were used to estimate the ages of embryo when nests were first located (Webb *et al.* 1983*b*), because no specific constants for *C. porosus* were available. Tests indicated the constants were reasonable, and they predict the following approximate incubation times (to where yolk scar width is about 6% SVL): 27°C, 136 days; 28°C, 111 days; 29°C 94 days; 30°C, 85 days; 31°C, 81 days; 32°C, 77 days; 33°C, 73 days, and 34°C, 69 days. Given the disproportionate slowing of development rate with lower temperatures, a field nest at 30°C ± 1°C may have a slightly longer development time than one incubated at a constant 30°C. The incubation time of the average Melacca nest (30·3 ± 1·7°C) is probably 80–95 days, whereas that of the average Finniss–Reynolds nest (31·5 ± 2·9°C) is probably shorter, 75–90 days. Kar (1979) reported an incubation time of 66–70 days for one *C. porosus* nest (27–34°C; it contained a number of abnormal embryos). One Finniss–Reynolds nest, first located when embryos were 31 days old (33·4°C), was hatching when revisited 40 days later (33·8°C), indicating a total incubation time of about 71 days at 33–34°C. The influence of the general May cooling on nest temperatures and development rates has been tabulated elsewhere (Webb *et al.* 1983*b*; table 2).

Table 4. Fate of *C. porosus* eggs laid in different months

Values are percentages unless otherwise stated

	Eggs laid in:							
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Total
				Melacca				
No. of nests	3	2	6	3	3	1	–	18
No. of eggs	151	109	301	170	140	46	–	917
Successful	4·6	24·8	39·2	57·1	50·0	15·2	–	35·6
Infertile	7·3	0·9	14·3	13·5	0·7	15·2	–	9·4
Flooding	75·5	71·6	36·5	18·2	0	0	–	36·3
Temperature								
High	0	0	0	0	12·9	0	–	2·0
Low	0	0	1·3	0	26·4	37·0	–	6·3
Development failures	12·6	2·7	7·6	10·0	10·0	30·4	–	9·8
Physical damage	0	0	1·0	1·2	0	2·2	–	0·6
				Finniss–Reynolds				
No. of nests	–	2	7	13	5	4	2	33
No. of eggs	–	110	406	678	287	219	95	1795
Successful	–	50·0	28·3	31·3	35·2	6·4	29·5	29·2
Infertile	–	6·4	2·5	6·0	3·1	9·1	2·1	5·0
Flooding	–	0	53·0	41·3	27·2	50·2	47·4	40·6
Temperature								
High	–	0	0	1·0	0	0	0	0·4
Low	–	0	0	0	19·9	0	0	3·2
Development failures	–	41·8	13·0	14·0	14·3	32·9	16·8	18·0
Physical damage	–	1·8	0·2	4·7	0·3	1·4	4·2	2·4
Unknown	–	0	3·0	1·8	0	0	0	0·6

Embryo Mortality

In both study areas, drowning after nest flooding was the major cause of embryo mortality, accounting for 36·3% of all Melacca eggs and 40·6% of Finniss–Reynolds eggs (Table 4).

At Melacca, November and December nests experienced high flood losses in late January, although increased nest height (Fig. 6) lessened the losses after that time. Of all eggs found 9·4% were infertile (no development of an opaque band), although this value was inflated by two nests with unusually high numbers of infertile eggs (31% of 58 eggs; 55% of 51 eggs). Embryos from one nest in Melacca appeared to have been overheated; however, eggs laid in March and April showed greatly retarded development in May–June, and the high loss of embryos was presumed to be related to this. Relatively few eggs (0·6%) were crushed during either egg-laying or development, and the high proportion of unexplained development failures among April-laid nests may reflect retarded development as described above.

In the Finniss–Reynolds area a high proportion of embryos were drowned in all months. High January and March water levels (Fig. 5) may have enhanced losses, as some mats are partly anchored to the bottom and may flood during high water. Loss of nest buoyancy, however, was the major cause of flooding. As stated previously, crocodile activities at the nest site break the mat down around the nests. Isolated floating nests are too heavy for small amount of buoyant vegetation beneath them (buoyancy declines as the plants bene the nest rot), and they gradually sink. This sinking was greatly enhanced with the onse cool weather, as crocodiles appeared to spend longer periods lying on the nests baskir

Table 5. Predicted loss to flooding of *C. porosus* embryos at Melacca swamp, for eggs laid in different months

Values are percentages unless otherwise stated

Year	Percentage loss from eggs laid in: Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Total
1960–61	0·0	0·0	0·0	0·0	0·0	0·0	0·0
1961–62	47·0	45·0	34·2	0·0	0·0	0·0	24·3
1962–63	0·0	17·4	5·0	0·0	0·0	0·0	3·7
1963–64	0·0	54·1	47·8	22·9	7·1	0·0	27·5
1964–65	4·6	36·7	31·2	32·9	0·0	0·0	23·0
1965–66	81·5	95·4	78·4	21·2	0·0	0·0	54·4
1967–68	92·1	91·7	76·7	16·5	0·0	0·0	54·3
1968–69	95·4	95·4	76·4	14·7	0·0	0·0	54·9
1969–70	0·0	0·0	0·0	0·0	0·0	0·0	0·0
1972–73	80·1	79·8	67·1	0·0	0·0	0·0	44·
1973–74	65·6	28·4	3·7	0·0	0·0	0·0	15·
1974–75	7·3	81·7	77·1	40·6	0·0	0·0	43·
1976–77	10·6	33·9	43·9	30·6	1·4	0·0	26·
1977–78	38·4	27·5	14·0	0·0	0·0	0·0	14·
1978–79	2·0	15·6	8·6	8·8	0·0	0·0	6·
1979–80	45·0	54·1	25·9	0·0	0·0	0·0	22·
1980–81	53·6	61·5	49·8	2·9	1·4	0·0	33·
Eggs per year	151	109	301	170	140	46	91
Total egg loss	941	892	1926	325	14	0	409
Mean loss month^{-1}	36·7	48·1	37·6	11·2	0·6	0·0	26·

The unpredictable manner in which Finniss–Reynolds nests flood (nest sinking rat than nest flooding) made it difficult to partition mortality in some nests. The percentag Finniss–Reynolds eggs which were crushed (2·4%) was appreciably higher than at Mela (0·6%), and this may reflect a generally larger size of females in that area, or perhaps mechanical properties of the nest vegetation. Some nests were greatly flattened, individual eggs being cracked and pushed into adjacent eggs.

With the results from both areas lumped, 31·4% of eggs produced live, apparently no hatchlings. No embryo within a nest appeared to die from dehydration, although s exposed eggs had dehydrated or overheated. No instances of predation on eggs was recor which is consistent with low levels of egg predation in the Liverpool–Tomkinson swa (Webb *et al.* 1977; Magnusson 1982).

Annual Trends in Flood Mortality

In the Finniss–Reynolds study area, flood-induced mortality was probably enhanc the generally high January rainfall (Fig. 5); however, nest sinking may be an annual occurrence, independent of flood levels. If so, a 30% success rate may be typical of nests laid from December–January onward. At Melacca, the swamp water level largely determines the extent of nest flooding, and this could be expected to vary substantially each year; the data collected in 1980–81 may not be typical of previous years.

In order to investigate this question in more detail, an attempt was made to model the Melacca nesting situation, given the major assumption that the time of egg-laying in 1980–81 was typical of other years (data now being collected generally support this assumption). The following additional assumptions were made: (1) The conversion formula used for predicting Melacca water heights from Finniss River heights (Fig. 6) was adequate for predicting Melacca water heights in previous years. (2) The height of the top egg above water could be estimated by using the mean height (35 cm) above the mean water level (over the 5 days spanning the predicted laying date). (3) The level at which nests were made during floods would be maintained when flood waters receded; that (2) above only applied to increasing water levels. This assumption is based on few data (Fig. 6); however, it makes little difference to the final results. (4) That mean clutch depth was 22·6 cm, and that the eggs were evenly distributed from the top to the bottom of a clutch. (5) That clutch size of nests laid on different dates was the same as in 1980–81. (6) That more than 24 h inundation was required for a lethal flood. Although embryos are probably killed in 9–13 h (Joanen *et al.* 1978; Magnusson 1982) the water height data available were maximum daily readings; two consecutive high levels was considered more indicative of a prolonged flood. (7) That mean incubation time was 85 days.

Table 6. Predicted percentage of total number of *C. porosus* embryos lost to flooding in each month at Melacca Swamp

$N=917$ per year

Year	Dec.	Jan.	Feb.	Mar.	Total
1960–61	0·0	0·0	0·0	0·0	0·0
1961–62	0·0	0·0	24·3	0·0	24·3
1962–63	0·0	0·0	3·7	0·0	3·7
1963–64	0·0	0·0	0·0	27·5	27·5
1964–65	1·5	0·0	0·0	21·5	23·0
1965–66	9·8	8·8	35·8	0·0	54·4
1967–68	0·0	13·7	40·6	0·0	54·3
1968–69	0·0	0·0	54·9	0·0	54·9
1969–70	0·0	0·0	0·0	0·0	0·0
1972–73	0·0	44·7	0·0	0·0	44·7
1973–74	0·0	15·4	0·0	0·0	15·4
1974–75	0·0	1·2	42·5	0·0	43·7
1976–77	0·0	0·0	2·7	23·6	26·3
1977–78	0·0	14·2	0·0	0·0	14·2
1978–79	0·0	0·3	6·3	0·0	6·6
1979–80	0·0	7·1	15·3	0·0	22·4
1980–81	0·0	9·2	14·5	9·5	33·2
Mean loss	0·7	6·7	14·2	4·8	26·3

Predicted Melacca water heights were plotted for each year (to 1960) that Finniss water height data existed, and clutch levels were inserted relative to those water heights (Fig. 10). The proportion of each clutch lost to flooding during incubation was subsequently estimated and summed (Tables 5, 6). It was immediately apparent that if the assumptions were correct, the years in which flood mortality would be greatest were those in which water levels first increased slowly and then rose rapidly in a step-like fashion (Fig. 10). This parallels the increased egg losses for *A. mississippiensis* following exceptionally high discharges of stored water (Kushlan and Kushlan 1979). For *C. porosus* egg losses were highest in January and

February (Table 6); i.e. eggs laid in November, December and January (Table 5). Mean annual loss of eggs to flooding was 26·3%, indicating that mortality in the 1980–81 year (estimated loss, 33·2%; real loss, 36·3%) was probably heavier than average, but well within the common range of flood losses.

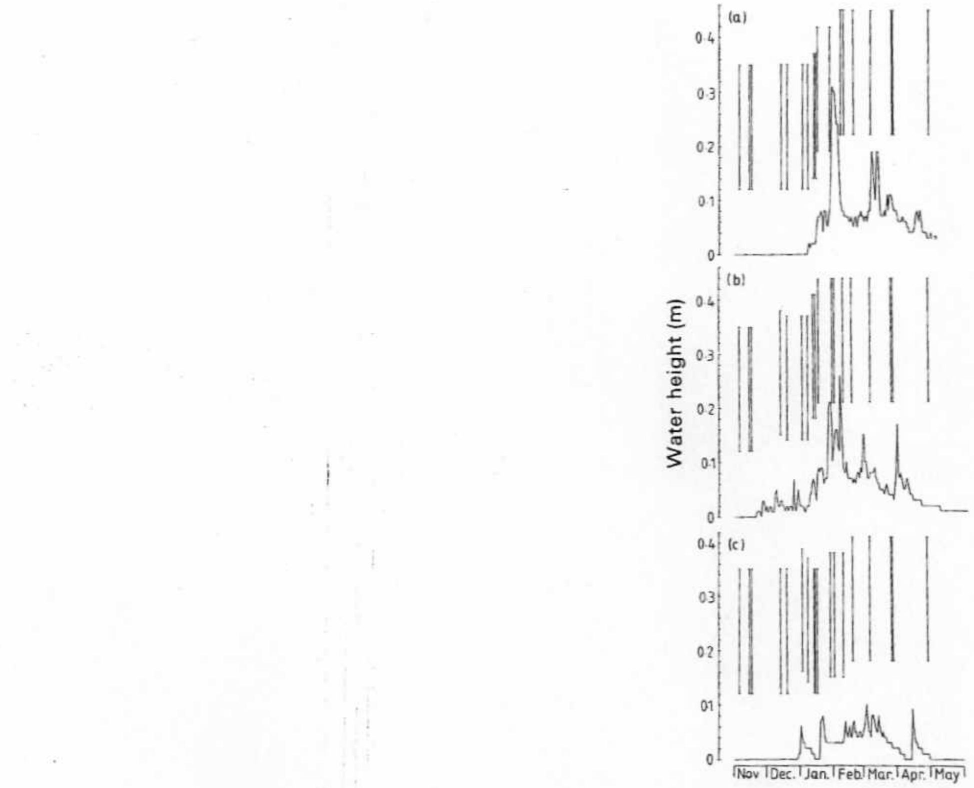


Fig. 10. The predicted relationship between clutch level and water level in three years with different patterns of flooding (see Tables 5, 6).

Multiple Nesting at the One Site

In both Melacca and the Finniss–Reynolds, some nests were located adjacent to other which had already been made and where, in some cases, eggs had hatched (Table 7). At on site the attendant crocodile was distinctively coloured and was in attendance when both firs and second nests were located. Between the members of a pair of nests, clutch size varie appreciably, but egg sizes were similar. The correlation between mean egg lengths ($r^2 = 0 \cdot 7$ $P = 0 \cdot 13$) was not significant, but mean egg widths were significantly correlated ($r^2 = 0 \cdot 9$ $P = 0 \cdot 012$), suggesting a non-random association between the first and second clutches. I egg widths are a reflection of oviduct diameter, the finding is consistent with multiple nestin by at least some females.

Embryo Abnormalities and Anomalies

Three double-yolked eggs were recorded (0·1% of all eggs examined) and although tw were from flooded nests and contained dead embryos, one hatched with two live b premature and stunted *C. porosus* (one appreciably larger than the other). In one nest whic had hatched before being retrieved, a single live hatchling remained within an egg; th individual had the tail missing from immediately behind the cloaca. Among the drown embryos from that nest, a further six were found with the same anomaly, suggesting that was genetically based. A *C. porosus* with an identical anomaly was found in another nest wi otherwise normal embryos. Two hatchlings with severe tail amputations, captured in the same stretch of the Cadell River (Webb and Messel 1977), may well have had a similar anomaly.

Table 7. Clutch and egg characteristics of *C. porosus* nests close together

All were found in the 1980–81 season. Egg weights and dimensions are means

	Nest 1	Nest 2	Nest 1	Nest 2
	Melacca Swamp			
Laying date	14 Nov.	22 Mar.	5 Nov.	16 Nov.
Clutch size	56	50	46	49
Egg length (mm)	80·1	85·5	80·1	77·4
Egg breadth (mm)	51·0	52·0	48·7	49·2
Egg weight (g)	—	134·2	—	107·8
Notes	20 m apart		4 m apart	
	Finniss–Reynolds			
Laying date	12 Feb.	18 Feb.	6 Jan.	18 May
Clutch size	16	46	59	50
Egg length (mm)	72·1	73·0	84·6	87·1
Egg breadth (mm)	45·2	45·5	57·3	51·2
Egg weight (g)	84·5	89·8	130·2	130·9
Notes	4 m apart; same female present		Nest 2 on top of nest 1	

Table 8. Summary of notes recorded on abnormal embryos of *C. porosus*, with an indication as to the probable cause of those abnormalities

N, number of instances that an abnormality was recorded

Abnormality	*N*	Notes
Kinked tail	19	Hot and cold nests: misalignment of caudal vertebrae to give laterally displaced tail section. Four also had kinked backs, one a distended abdomen and one a shortened lower jaw
Twisted and/or kinked back	23	Hot and cold nests: lateral, dorsal or medial misalignment of thoracic and lumbar vertebrae. Four also had kinked tails, one a skewed lower jaw, one a protruding lower jaw, one a pronounced 'bump' on the cranial platform, one a twisted head and two had distended abdomens
Twisted head	7	Hot nests: misalignment of cervical vertebrae such that the head was twisted in the medial plain; one also had a dorsally kinked back, one its head directed posteriorly over the midline of the back, and one a distended abdomen
Shortened abdomen	2	Hot and cold nests: severely shortened abdomen presumably resulting from missing thoracic or lumbar vertebrae. One also had a distorted abdomen and one a very wide neck
Pronounced 'bump' on cranial platform	7	Hot nests: bones of the central part of the cranial platform formed into a pronounced dome. Two also had distended abdomens, one a skewed lower jaw, and one a kinked back
Distended abdomen	19	Hot and cold nests: an apparent failure to utilize the yolk once enclosed within the body. The majority had thin tails and SVLs were small for given sized eggs. Two also had twisted backs, one a twisted head, one a shortened abdomen, one a kinked tail, and two had cranial 'bumps'
Jaw abnormalities	8	Hot and cold nests: five had short lower jaws, one a skewed lower jaw with kinked back and a cranial 'bump', one an apparently short upper jaw and one a short lower jaw with kinked tail and twisted spine
No tail	8	Genetic: tail completely missing from just behind rear limbs. Seven from one nest and one from another nest

Throughout the study, descriptive notes were made on obvious morphological abnormalities, and these are summarized in Table 8. It was noticeable that many of the embryos with spinal abnormalities did not manage to pip eggs and may have died within them if not released by us. Even so, most died within 24 h of being hatched, and when mortalities were assessed (Table 4) they were assigned to either development failures or, more usually, temperature-induced mortality. Embryos with kinked tails and no other abnormality often survived and those with tails completely missing (see above) appeared as vigorous as normal hatchlings. Kar (1979) described *C. porosus* embryos with abnormalities in the neck and tail, and similar conditions have been reported in *C. novaeguineae* (Bustard 1971) and *A. mississippiensis* (Ferguson 1981, 1983).

Discussion

Time Relations

As in the Liverpool–Tomkinson area (Webb *et al.* 1977), the nesting of *C. porosus* in Melacca and the Finniss–Reynolds is primarily a wet season activity. The first nests coincide with the normal start of wet-season rains, there is a slight peak in January–February, when in most years there is heavy rain (*C. porosus* nesting in Papua New Guinea also peaks at high water: Graham 1981; Lang 1980), and the last nests are constructed in the first month of the dry season (May).

If nesting can be considered as a process extending from mating until the end of parental investment (dispersal of creches), it becomes clear that some portion of the adult female population is involved in the nesting process throughout the year: mating precedes egg-laying by at least 4–8 weeks (Lang 1980); incubation during cooler months may take nearly 4 months; females may remain with creches for 2 months (Webb *et al.* 1977); and some females may nest more than once during any one season. It would not be surprising that most females select nest sites within a range of normal activity (Webb *et al.* 1977) (rather than travelling long distances between feeding and nesting grounds: Magnusson 1980*a*), as they would be spending the majority of the year at the nest site.

The extent to which the nests per month in Melacca (p. 577) reflect trends in other areas remains to be clarified. Regrowth on Finniss–Reynolds nests (Table 2) could readily explain the lack of early nests found there (surveys were not commenced until February), but nesting there may be later. The situation for floodplain bank nests (Webb *et al.* 1977) may be different. Wet-season growth of vegetation may be required in order to achieve a suitable nest site (whereas in permanently wet swamps it is always present), and prospective floodplain nest sites beside rivers and billabongs may be under water for appreciable portions of the wet season (Messel *et al.* 1979*a*).

Whether or not female *C. porosus* will become gravid if nest sites are unavailable is unknown, as is the fate of the eggs if they do. *A. mississippiensis* do not appear to be able to retard egg development successfully, but they can resorb fully developed eggs and may void eggs into the water (Ferguson 1983). Long-distance movements away from traditional nest sites if egg-laying is imminent is possible, but would seem unlikely. In captivity *C. johnstoni* and *C. porosus* may void eggs into the water if nesting material is not supplied (Dunn 1977; unpublished observations), and presumably they too can resorb eggs. In the Liverpool–Tomkinson area few if any riverside nests are constructed during periods of heavy flooding (Webb *et al.* 1977), and perhaps the annual complement of nests in such areas is much more variable than in areas like Melacca and the Finniss–Reynolds. It should perhaps be noted that some nest construction in the Liverpool–Tomkinson area appears to follow falling flood levels (Webb *et al.* 1977), suggesting that *C. porosus* may be able to exert more control on the time of egg-laying than appears the case in *A. mississippiensis* (Ferguson 1983).

Nests, Nest Sites and Suitable Nesting Vegetation

When information in the literature on *C. porosus* nests, nest sites and nesting habitat (Deraniyagala 1939; Webb 1977; Webb *et al.* 1977; Magnusson *et al.* 1978*b*, 1980 Magnusson 1979*c*, 1980*a*; Graham 1981) is combined with data presented in the presen study, it becomes apparent that when *C. porosus* occupy wetlands containing a variety o vegetation communities, nests are usually non-randomly distributed among those com munities. Nesting tends to be restricted to specific (often easily recognizable) communities or habitats, which can be lumped as 'suitable' for nesting.

Some suitable vegetation communities are dominated by one species of plant, others by groups of plant species of similar form, and others by a suite of plant species of both similar and dissimilar forms (Deraniyagala 1939; Webb 1977; Webb *et al.* 1977; Magnusson *et al.* 1978*b*, 1980; Magnusson 1980*a*; Graham 1981). The nest mounds within any one community may be similar in composition, size and general appearance (e.g. Melacca nests), or show appreciable variation (e.g. Finniss–Reynolds nests), largely determined by the variety and abundance of plants in that community. In areas where wetland communities are particularly diverse, variation among nest mounds can be extreme, e.g. 'mud' nests, grass nests and swamp vegetation nests in the Liverpool–Tomkinson system (Webb 1977; Webb *et al.* 1977; Magnusson 1979*c*, 1980*a*).

The type of suitable nesting vegetation *C. porosus* select is a determinant of the environment in which the embryos will develop. The height and density of vegetation surrounding nests influence exposure to both wind and sun, and it is likely that the heat of decomposition varies among plant species (although the variation may be slight: Magnusson 1979*c*); all influence nest temperature, embryonic development rates and probably the sex ratio of hatchlings (Bull 1980; Ferguson and Joanen 1982, 1983). Some suitable nesting communities are associated with low-lying flood-prone areas, and when nest sites are selected in these communities there is indirect selection for nest moisture and mortality levels. In communities where appreciable amounts of mud are incorporated into nests, gas exchange between the inside and outside of the nest is reduced (Lutz and Dunbar-Cooper 1982), which may influence both development and mortality rates.

Variation in location of nest site has often been assumed to be explained by the characteristics of site vegetation, yet our understanding of why *C. porosus* nesting is so variable is rudimentary. Why do *C. porosus* nest where they do? What characteristics of vegetation communities (or habitats) distinguish those suitable for nest site selection from those unsuitable?

Graham (1981) has recently discussed aspects of this question as it relates to surveys of *C. porosus* and *C. novaeguineae* nests in Papua New Guinea, but the only attempt to analyse parameters in a manner which could have led to the quantification of the significant features of nest sites appears to be that of Magnusson (1980*a*). Unfortunately he did not pursue this question specifically, and the information cannot be extracted from his discriminant analysis coefficients. Caution needs to be exercised in the use of Magnusson's (1980*a*) formulae, as the variables require a somewhat subjective assessment as to which broad habitat category a vegetation type should be classified in, and some variables are highly negatively correlated (percentage cover of mangroves/percentage cover of freshwater swamp); suitable nesting vegetation is usually classified as such (largely as a result of the habitat category assigned), but so too are many areas known to be unsuitable, e.g. short mangroves (Magnusson 1980*a*).

Important insights into why females nest where they do may come from consideration of the requirements of the female, as distinct from those of the eggs. Criteria used in nest site selection have no doubt evolved as a compromise between the well-being of females and eggs, but a number of published and unpublished observations suggest that when conflicts of interest arise, the welfare of the female is favoured at the expense of the eggs, as could be expected.

In captivity, female *C. porosus* construct nests from a wide variety of materials which appear to have little association with those available in suitable vegetation communities in the wild, for example lawn clippings, dry bale hay, sand, dead *Pandanus* leaves (Yangprapakorn *et al.* 1971; unpublished observations). It would thus seem unlikely that sites are selected primarily on the basis of the suitability of the vegetation for nest construction. Similarly, sites do not seem to be selected on the basis of the thermal or moisture properties associated with nests built of particular materials, as in the wild and in captivity eggs may be deposited in nests which are dry and/or so hot that most if not all embryos die once they stabilize to nest temperature (unpublished observations; this study with regard to high temperatures in wild nests).

Nest sites often appear to be selected on the basis of criteria only tenuously associated with nest construction *per se*, as evidenced by the following examples. In the tidal section of the Adelaide River, as in the Liverpool–Tomkinson system (Webb *et al.* 1977; Magnusson 1980*a*), nests on the floodplain are often restricted to areas containing tall, broad-leafed grasses. On the Adelaide River, most broad-leafed grasses have been lost due to grazing (Messel *et al.* 1979*c*; unpublished data) and of 122 km of open floodplain bank surveyed by helicopter, remnant stands remained on only 19 km. Of seven nests located in that area, all have been within those stands, indicating a significant association between nests and broad-leafed grasses in that area (cessation of nesting following eradication of broad-leafed grasses in similar floodplains was reported from the Liverpool–Tomkinson system: Webb *et al.* 1977). *Eleocharis* sp. (a reasonably short, cylindrical-stemmed sedge), on the other hand, is a common plant which grows in large homogeneous stands in both the Liverpool–Tomkinson and Adelaide River systems, but no *C. porosus* nests have been located in these stands; it would appear that in this form it is unsuitable for nest site selection. Yet two nest sites in the Adelaide River system, in an area where broad-leafed grasses and *Eleocharis* grow adjacent to each other, were located among broad-leafed grasses, but the nests themselves were constructed solely from *Eleocharis*. The broad-leafed grasses appear to have been involved in site selection, but not in nest construction.

In Melacca, *T. sumatranum* is associated with nest site selection, and as most sites are constructed in reasonably homogeneous stands of *T. sumatranum* it is also the principal material incorporated into nests. However, one nest site was on the edge of a *T. sumatranum* bed, but the nest itself was constructed of *M. rubiginosa*, a tall narrow-stemmed sedge which, when in homogeneous stands, appears to be unsuitable for nest sites.

By examination of the common features of nest sites (rather than of nest mounds) from the point of view of advantages to the female, criteria that may be important in site selection become apparent.

(i) *Access to permanent water*

As emphasized by Graham (1981), most nest sites are within 20 m of deep permanen water which affords a refuge for the female. When nests are constructed on the banks o rivers and billabongs, the wallows (Webb *et al.* 1977) beside nests are usually shallow, and i females are disturbed they usually leave the site completely and submerge in deeper water. I shallow swamps such as Melacca, wallows are greatly deepened (>2 m), and if disturbed a nests females often use them as refuges. On most occasions when a female has surfaced in swamp wallow while we have been at a nest, she has left the wallow in haste, and travelle through shallow channels to a nearby, deeper refuge. Defence of nests against humans ha been reported rarely in the wild (Deraniyagala 1939), although it is common in captivit (Lang's and our own unpublished observations), and may be commonly directed again small egg predators (Magnusson 1982).

Since completing the present study we have encountered three wild *C. porosus* femal (all in Melacca Swamp) which exhibited the same nest defence behaviours as described Deraniyagala (1939), Joanen (1969), Deitz and Hines (1980) and Kushlan and Kushl (1980); it may be a behaviour exhibited more commonly as 'post-protection' females (whi have not been hunted) reach maturity (Deitz and Hines 1980). Even in *A. mississippiens* however, only a small proportion of wild females opt for defence against large potent predators (humans) rather than retreat (Joanen 1969; Deitz and Hines 1980; Kushlan a Kushlan 1980).

C. porosus nest sites located 100 m or more from permanent deep water are rare, and the time of nest construction such sites are usually on the flood-extended periphery of de water. When waters recede, and the wallows dry, these nests are usually abandoned. Whether or not deep-water refuges are also feeding sites is unknown. Females at nests examined by Deraniyagala (1939) had empty stomachs, and one caught at a Melacca nest (1979–80) was obviously emaciated (the nest was just hatching). In contrast, females sighted near nests in the Liverpool–Tomkinson system (Webb *et al.* 1977) and many sighted in this study, appeared in good condition.

(ii) *Access to permanent water which does not become excessively saline*

In the downstream sections of tidal rivers there are few records of *C. porosus* selecting nest sites adjacent to permanent deep water unless there are nearby, permanent freshwater seepages, in which case nests are sited within them (Webb *et al.* 1977). As pointed out by Magnusson (1980*a*), this appears to be utilization of the only suitable nesting vegetation available (nests are not constructed in the saline mangroves), and could be unrelated to salinity. However, salinity and not just suitable vegetation may play a direct or indirect role in nest site selection, and on the basis of information available at present we do not discount it. Messel *et al.* (1979*a*) have concluded that *C. porosus* generally avoid waters which exceed 54‰ salinity.

In the downstream saline areas of the Liverpool–Tomkinson system, the broad-leafed grasses used for nesting in upstream, less saline areas occur where the land adjacent to the water is slightly elevated. Although such areas are not abundant, the vegetation associated with the freshwater seepages is not the *only* suitable vegetation in downstream saline areas (it is, however, the most abundant: Magnusson 1980*a*), yet nesting is almost exclusively restricted to it.

In addition, isolated patches of freshwater swamp are often small in area, and may be well back from the river's edge; their location in the dry season, but not the wet season (when there are numerous temporary freshwater channels) is indicated by freshwater input into an otherwise saline stream. As stated previously (Webb *et al.* 1977) adult female *C. porosus* in downstream saline areas do not appear to be randomly distributed, but rather to maintain territories in association with low-salinity water during the dry season.

Whether or not low-salinity water is physiologically important to adult females is unknown. *C. porosus* have salt glands (Taplin and Grigg 1981), and juveniles are quite capable of withstanding high salinities (Grigg *et al.* 1980); however, the peak of salinities in the field usually coincides with the peak of internal egg development, and a need for access to freshwater for only a small portion of the year (during shell deposition?) could tend to restrict female territories to areas where there is low-salinity water. In the Liverpool–Tomkinson area (Webb 1977; Magnusson 1982) nests in freshwater swamps are made earlier than those in saline areas lacking nearby fresh water. It is perhaps of interest to note that one nest we did locate in what appeared a very saline area lacking fresh water (creek D of the Adelaide River: maps in Messel *et al.* 1979*c*) had only four eggs in 1979–80; a much larger clutch (the eggs were not counted) was at the same site in 1980–81, and developed successfully.

(iii) *A secluded refuge site*

Within the constraints of access to water, and perhaps salinity, nest sites can perhaps be interpreted as secluded (largely terrestrial) refuges for the females. Sites tend to be surrounded by tall (>1 m) vegetation, which restricts vision on all sides, or on river banks does so particularly on the land side. Such seclusion may reduce predation on the females and eggs, and may isolate nesting females from each other. Female *C. porosus* appear to be more intolerant of conspecifics than most other crocodilians which have been studied (Lang 1980, personal communication), and where nest sites were located close together in this study (<30 m), they appeared to result from multiple nesting by the same female rather than two females tolerating each other.

(iv) *Avoidance of deep and/or flowing water*

Although nest sites may become completely inundated, at the time of selection they contain an area where a female can lie (and later the nest can be constructed) that is either emergent, or in very shallow water (10 cm). This emergent area may be the base of a live tree, the trunk of a fallen tree, or a centrally situated part of the substrate on a floodplain riverside or a floating mat. Two nest sites have been located in reasonably deep water (1–2 m) where the only emergent site was a robust, isolated clump of *F. indica*, on which the female was just able to fit the nest. In permanently inundated areas females appear to avoid sites where the water is flowing, although selected sites may later be in flowing water if heavy rains occur.

(v) *Physical and mechanical aspects of nest site vegetation*

In some freshwater swamps and riverside nest sites, understorey vegetation is not abundant and selection of a site does not involve the females clearing or flattening vegetation; they construct nests mainly from the peat or mud of the substrate with whatever vines, plants and foliage are available. However, where nest sites are selected in taller stands of dense vegetation (e.g. *P. karka*, broad-leafed grasses, *T. orientalis*, *C. interruptus*, *T. sumatranum*), the dominant plants appear to have common mechanical and physical characteristics. They are sufficiently robust to withstand flattening by prevailing winds, yet they can be effectively flattened by a female crocodile crawling on them. The plant stems can be either snapped and broken by a female (e.g. *P. karka*, *T. orientalis*, *T. sumatranum*) or uprooted (e.g. broad-leafed grass), and most have reasonably dense foliage from the substrate up, rather than having thin stems and the bulk of foliage in a canopy.

(vi) *Microclimate*

The microclimate in most nest sites appears to be as suitable for the female as it is for the eggs, and when conditions become unacceptable for the female the eggs may be sacrificed in order that she achieve optimal conditions (e.g. the high incidence of nest sinking during cool weather in the Finniss–Reynolds).

Water for the females is available at or near most nest sites, and at mound level nest sites are usually shielded from prevailing winds and exposed to the sun for most of the day. In the Liverpool–Tomkinson a tendency for nests to be built on the west-north-west aspect (Magnusson 1979*c*), giving increased exposure to the afternoon sun (maximum radiation), was as advantageous to the female as it was to the eggs. In Melacca and the Finniss–Reynolds no strong preference for either morning or afternoon sun was apparent; however, nests were not constructed on the edge of tall, fringing vegetation, which would make a choice between morning and afternoon exposure necessary. In cool weather *C. porosus* maximize exposure to the sun by lying over the mound and elevating themselves, even though in some cases eggs may be cracked and broken, and a flattened, lowered mound (more susceptible to flooding) may result (especially with larger females).

Nesting Vegetation as an Indicator of Flood-induced Egg Mortality

Although vegetation communities suitable for nesting can be recognized and mapped from the air (Magnusson *et al.* 1978*b*, 1980), it is not clear how far mortality due to flooding can be inferred from the plant species present (Magnusson *et al.* 1978*b*, 1980). In tidal and non-tidal rivers, nests made on the banks are subject to high annual flood losses, irrespectiv of the vegetation dominating the nest site (Webb *et al.* 1977; Magnusson 1980*a*, 1982), and i would not be surprising if fewer than 10% of eggs produced hatchlings in most years. In th Liverpool–Tomkinson area Magnusson (1980*a*, 1982) reported that none of 38 bank nest produced hatchlings (1974–75; 1975–76), which was an exceptionally high mortality, eve for that area. In the previous year three bank nests produced hatchlings (Webb *et al.* 1977 and at least some nests hatched in the previous two years (unpublished data on hatchling and 1-year-olds), and have hatched since (Messel *et al.* 1979*a*).

The situation in permanent freshwater swamps is more complex. Where such swamps are located in the downstream sections of tidal rivers, e.g. Melacca and the freshwater swamps in the Liverpool–Tomkinson system (Webb *et al.* 1977; Magnusson 1980*a*, 1982), they are clearly elevated above the general floodplain level, as evidenced by the lack of saltwater intrusion. Such *elevated* freshwater swamps are presumably not subject to the general floodplain level of flooding, or the influence of spring tides, and as a generalization probably have low losses due to flooding (12 out of 14 nests produced hatchlings in the Liverpool–Tomkinson swamps (Magnusson 1980*a*) and 14 out of 18 in Melacca in 1980–81). These *elevated* swamps can be recognized from the air, as they are freshwater swamps behind and/or adjacent to saline mangroves.

Upstream in most major rivers there is a reduction in salinity, and the presence of a freshwater swamp adjacent a mainstream channel does not signify elevation, even though the same plant species found in elevated downstream swamps occur. In fact, many such swamps appear slightly lower than the floodplain and are lateral extensions of the main river channels, e.g. Andranangoo Creek on Melville I. (Messel *et al.* 1979*b*) and extensive swamps in the Mary and Finniss–Reynolds systems. Flooding in such swamps is presumably as severe, if not more so, than on grassy floodplains in the same area.

Flood-induced mortality in nests on floating mats may be partly correlated with the vegetation composing the mats, as some species (Fig. 3) are indicative of stable mats, which are less likely to be broken down by the activities of adults at the nest site. However, most nests are made on stable mats, and thus stable mats *per se* can probably be considered a uniform suitable nesting vegetation or habitat with a more or less uniform extent of flood-induced mortality; 22 out of 41 nests with eggs on floating mats produced hatchlings in this study. As pointed out by Graham (1981), many of the plant species colonizing mats also occur on solid substrates adjacent to those mats, so that any relationship between mortality and plant taxonomy *per se* could be expected to be highly variable.

Males and Females at the Nest Site

In the Liverpool–Tomkinson area (Webb *et al.* 1977; Magnusson 1982) and in Melacca (this study), males did not appear to utilize nest sites although females were often present. In the Finniss–Reynolds, the tracks of large crocodiles (4–5 m +, presumed to be males; see Webb *et al.* 1978) were obvious at a number of sites, and during the surveys three very large individuals were sighted at nests. During the period of legal hunting, Petherick (personal communication) definitively recorded both males and females at nest sites in the Finniss–Reynolds area.

Although this finding could indicate a paternal role of the male in the Finniss–Reynolds region, the nesting site may also simply be a basking site readily accessible by a well worn track beneath the mat; its use by males could be largely unrelated to nesting. In the Liverpool-Tomkinson, Melacca and the Finniss–Reynolds, some females appear to use nest sites as activity centres throughout the year (Webb *et al.* 1977, and present study), independently of whether active nests were present or not.

By collecting eggs before hatching we excluded data on nest excavation by adults; however, 11 nests were first visited after hatching (seven), visited at hatching (one), or hatched before revisits (three). In nine of these the nests appeared to have been excavated, and in two the hatchlings had made their own exit, as described by Magnusson (1980*b*).

Eggs, Clutches and the Internal Nest Environment

The egg and clutch parameters recorded in the present study were consistent with those reported previously (Webb *et al.* 1977), although the SDs reported previously are in error (they can be corrected by the conversion $n(\text{SD error})^2 = \text{SD correct}$*). Analysis of the parameters is somewhat confounded by the extent to which females may nest twice during any one season, although the tendency for egg size to increase with clutch size may well be a reflection of crocodiles tending to have larger eggs with increasing age and size, and for clutch

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* Corrected values can be obtained from G. Webb.

size to increase and then decrease as senescence is approached (Graham 1968, 1981; Ferguson 1981, 1983).

The lack of a correlation between clutch size (and egg size) and time of nesting is not surprising, as even in species with discrete and contracted nesting periods (*A. mississippiensis*, *C. johnstoni*) the correlation is slight; in *A. mississippiensis* it has been interpreted as the result of the larger, more dominant animals ovulating, mating and nesting first (Ferguson 1983; Ferguson and Joanen 1983).

The slight differences in clutch and egg sizes between Melacca (50·9 ± 6·1 eggs; mean size 113·5 ± 11·8 g) and the Finniss–Reynolds (54·2 ± 10·6 eggs; mean size 113·3 ± 21·4 g) were not significant; however, the differences in variance were. This finding may be confounded by multiple nesting, but it is also consistent with general observations indicating that the Finniss–Reynolds had more large female *C. porosus* than were obvious at Melacca; the variances of clutch size may reflect the size (age) range of females in both areas.

In general, *C. porosus* nest mounds appear more moist than those of *A. mississippiensis* (Chabreck 1975), as dehydration of eggs within the nests of the latter species is reasonably common (Ferguson 1980*b*, 1983; Ferguson and Joanen 1983), whereas with *C. porosus* it is rare.

It is difficult to generalize about *C. porosus* nest temperatures, as they show substantial variation between nests in different sites and when measured on different days. Heat of decomposition is a significant factor in nest temperature regulation (Webb *et al.* 1977; Magnusson 1979*c*), and, although spot temperatures from 12 nests did not indicate significant variation attributable to the materials used (Magnusson 1979*c*), a more detailed analysis would seem necessary before nest materials could be assumed to be equivalent in regard to the heat generated during decomposition. In the present study nests made of *C. interruptus* and the peat of stable mats gave the highest temperatures recorded.

Exposure to the sun was an obvious variable influencing nest temperatures in this study, and was probably the major reason why Melacca nests were cooler than Finniss–Reynolds nests. It was also apparent during the study that metabolic heat production was a significant source of heat, particularly during the later stages of development, as temperatures inside the clutch were often 1–2°C higher than those from its periphery. A similar increase due to metabolic heat production occurs in *A. mississippiensis* nests (Ferguson 1983).

A detailed study of *C. porosus* nest temperatures (and the nest environment *per se*) would seem a worthwhile area for future study. From the information available at present it would appear that in northern Australia exposure to the sun determines the nest temperature baseline, which fluctuates as ambient conditions change (particularly wind and minimum temperatures). During the early stages of incubation heat of decomposition is probably maximized because of the fresh vegetation, and decomposition would presumably be enhanced if females excreted into or onto nests when constructing them, as reported for *C. palustris* (Whitaker and Whitaker 1976, 1978*b*). During the later stages of incubation, metabolic heat would be maximized, and presumably this varies with the proportion of the clutch containing live embryos. It is unlikely that many wild nests maintain the same mean temperature throughout incubation (Webb *et al.* 1983*b*, table 2) and highly likely that in the field incubation times vary greatly (Magnusson 1979*b*; Webb *et al.* 1983*b*).

Possibility of Multiple Nesting by Individual Females in the One Season

Vaughan and Whitaker (1980) and Whitaker *et al.* (1980) have reported multiple nesting in *C. palustris*, and found egg size to be more consistent, between clutch pairs, than number of eggs. If oviduct width is the same, one would expect egg width to be more consistent than either egg length or weight, as found in this study.

The significant correlation between egg widths from nests at the same location is difficult to explain by any hypothesis other than multiple nesting by the same female. It is unlikely that females in the wild would tolerate other females at their nest sites (Lang 1980), and at one Finniss–Reynolds nest site the same female appeared to be present with both clutches. Given that at one site two clutches were deposited in the same mound, the large clutch (150 eggs) reported by Boake (1870) could represent two, or even more clutches.

The high number of multiple nests reported at some sites in Papua New Guinea (Graham 1981), the two river-bank nests 10 m apart reported by Magnusson (1980*a*), and those in swamps 'frequently separated by a lesser distance', may include cases of multiple nesting.

The minimum distance between nests of different females is obviously difficult to estimate from the data available and may be partly determined by whether or not females remain at nest sites. In elevated freshwater swamps adjacent to tidal rivers (e.g. Melacca and the Liverpool–Tomkinson swamps), some females appear to abandon their nest sites, so that if nest site defence is indeed a factor in nest site spacing, nests of these females could be expected to be closer together. Clarification of whether or not female *C. porosus* produce more than one clutch in a season and, if so, what proportion of breeding females do so, is an important area for future study.

Embryo Mortality

The assessment of mortality rates and causes was often based on subjective criteria and untested assumptions, but the results do demonstrate trends in both areas. Flooding was a major cause of mortality, and a substantial loss of eggs to inundation is probably a general feature of *C. porosus* nesting in most habitats.

The absolute mortality values derived by simulating previous years at Melacca are likewise viewed as an indication of trends, and little confidence can be attached to the absolute predicted values until additional data are available. The model indicates the extent of annual variation in flood-induced mortality which could be expected, with the 1980–81 mortalities being slightly more than would be expected in most years.

The Melacca results should only be extrapolated to other areas with caution, as some variables which appear important in Melacca may not be so in other areas. For example, a relationship between clutch height and water height existed in Melacca, as for *A. mississippiensis* in the Everglades (Kushlan and Kushlan 1979), yet this has obvious limits, even in Melacca, and may not exist in more level nesting areas subjected to higher water levels. The combined influence of high flood levels and high tides (Magnusson 1982) is an important variable in tidal areas, but not in Melacca.

That no egg predation occurred in the present study was particularly interesting, as most crocodilians, in most habitats, appear to lose a substantial number of eggs to one predator or another (Cott 1961, 1969; Joanen 1969; Pooley 1969; Attwell 1970; Blake and Loveridge 1975; Staton and Dixon 1977; Goodwin and Marion 1978; Choudhury and Bustard 1979; Crawshaw and Schaller 1980; Deitz and Hines 1980; Kushlan and Kushlan 1980; Magnusson 1982; Webb *et al.* 1983*a*).

Varanid lizards appear to be the only significant crocodile egg predator in the Northern Territory (Webb 1977; Webb *et al.* 1977, 1983*a*; Magnusson 1982), and perhaps the freshwater swamp habitat is not an ideal one for them. Magnusson (1982) reported that two of 14 (14%) *C. porosus* nests in the Liverpool–Tomkinson freshwater swamps were taken by varanids but, in contrast, all of 38 nests in river-bank situations were raided by varanids, although one of these appeared to have been taken before the embryos had been inundated and killed by flood waters (predators took the eggs 2–10 weeks after flooding).

When it is considered that attendent females deter varanids (Magnusson 1982), and that varanids appear to use olfactory cues to locate eggs (Webb *et al.* 1983*a*), anything causing a female to abandon a nest site (flooding; regular visits by investigators; setting up of recording apparatus at nests), or anything enhancing olfactory cues from a clutch (opening a nest; rotting eggs inside a nest), is likely to increase predation (Deitz and Hines 1980). It is unlikely that bank nests would all be taken by predators in the absence of floods. In fact, three bank nests in the Liverpool–Tomkinson area (Webb *et al.* 1977) and seven adjacent to the Adelaide River mainstream (unpublished observations), which did not flood, were not preyed upon, and hatched. Predation on *C. porosus* eggs in northern Australia may not be a major cause of mortality.

Implications for Management

(i) *The size of* C. porosus *populations in freshwater swamps*

The size of the *C. porosus* population in Australian freshwater swamps is difficult t estimate (Messel *et al.* 1981). Spotlight counts in heavily vegetated areas have limite application, and a methodology through which nest surveys (Chabreck 1966) could b undertaken has only recently been given serious consideration (Graham 1981).

In Melacca, 327 live hatchlings were produced in 1980–81, and juveniles can be seen night on the swamp edges (where there is less vegetation). Adults and juveniles are present year round in the swamp, and even though there may be interchange with the Adelaide Riv mainstream, the resident population could be expected to be in hundreds. As there are oth areas of freshwater swamp associated with the Adelaide River, the population outside t mainstream channels must represent a significant segment of the total population. T channel population was estimated as 456–591 in 1978 (Messel *et al.* 1979*c*).

In the Finniss–Reynolds, 3·1 nests were located for every nest located in Mela between February and May (p. 577). If this correction is used to estimate the number nests that would have been sighted in the Finniss–Reynolds (assuming that regrowth lessen the chances of finding early nests), some 56 nests could be expected. Independent a correction for nests located relative to the real number of nests, this indicates a popula in excess of that found in the Adelaide River system, where the total number of nests w appear to be less than 40 (18 have been found in Melacca and approximately 10 out Melacca), and well over that in the Liverpool–Tomkinson system (280–363 crocodil 1978; Messel *et al.* 1979*a*), where Magnusson (1980*a*) reported 38 nests, presumably loc in one year. [It should be noted that a considerable amount of nesting habitat in the Ade River system appears to have been destroyed (Messel *et al.* 1979*c*; unpublished dat

When it is considered that freshwater swamps are commonly associated with tidal r in Arnhem Land (Magnusson *et al.* 1978*b*), and may be well upstream of tidal influenc the Arafura swamp, Moyle and Daly Rivers; 600 km^2 in the Moyle area alone (Messel 1979*c*)], the total population of *C. porosus* in freshwater swamps in the Northern Ter can be expected to be more than 836 individuals (Messel *et al.* 1981); 856 live hatc resulted from the 2712 eggs we found in our two study areas, alone.

(ii) *An egg-collection management strategy*

From the results of the present study it is clear that mortality resulting fro inundation and suboptimal temperatures could be overcome if eggs were retrieved fr wild soon after laying and incubated under controlled conditions. Losses due to inf physical egg damage and developmental failures such as those associated with eggs be at the wrong angle (Ferguson 1982, 1983), would still occur, and could be expected to for some 20% of all eggs laid.

In areas such as the Finniss–Reynolds and Melacca, a return of crocodiles to the compensate for eggs collected, can be expressed in terms of hatchlings. The retur need to be about 30% and 40% of all eggs laid (i.e. approximately 38% and 50% of via available for collection) if the present recovery rate was to be maintained; this woul minimum value applicable *if* collecting extended throughout the nesting seas included a random sample of all nests), and if we could be satisfied that such 'r individuals would indeed eventually be incorporated into the breeding popula keeping hatchlings until they were older (larger), the return to the wild could be red without data on age- or size-specific mortality it is not possible to quantify the exte a reduction.

The hatchling compensation needed for floodplain nests on the banks of rivers would be less than that required in areas such as Melacca and the Finniss–Reynolds, and is probably less than 10% of all eggs laid (13% of viable eggs available for collection).

Given that nests laid earlier in the wet season suffer higher mortalities than those laid later (Magnusson 1982; this study), a variety of collection strategies and compensations (in terms of hatchlings) could be devised; however, a number of practical factors also need consideration. The extended laying period of *C. porosus* means that nest searches would need to be carried out regularly, and such searches might initially need to encompass vast tracts of wetland. As nesting is primarily in the wet season, vehicular access to potential nest sites is restricted, and a helicopter is probably the only practicable method of locating nests, in many areas. Even with a helicopter, eggs may need to be carried 100 m or more through dense, heavily vegetated swamps. As eggs would ideally be retrieved as soon after laying as was possible, most would need to be moved after the embryos had attached to the dorsal egg wall, and before they were large enough to withstand mechanical disturbance; as with turtles (Parmenter 1980), *A. mississippiensis* (Ferguson 1983) and *C. johnstoni* (Webb *et al.* 1983*a*), increased mortality could be expected.

Taking these points into consideration, an egg collection strategy of the type used with *C. niloticus* (Blake 1974; Blake and Loveridge 1975), and perhaps applicable to *C. johnstoni* (Webb *et al.* 1983*a*) may not have widespread application to *C. porosus* at present.

(iii) *Nest surveys as a method of monitoring* C. porosus *populations*

Spotlight counts may be suitable for monitoring short-term trends or gross density changes in areas of open water (Messel *et al.* 1981), but have limited application to an overall population assessment: they do not account for the proportion of the population in heavily vegetated areas away from mainstreams; do not distinguish between immature and mature animals, between males and females, and in some cases between *C. johnstoni* and *C. porosus*; and in the light of the limited data available on movement of larger *C. porosus* (Webb and Messel 1978) they are difficult to interpret.

Surveys based on nests (Chabreck 1966; Graham 1981), on the other hand, are intimately related to the breeding adult female population, are independent of whether or not an area is accessible by boat, and in Australia are species-specific. Devising a method for conducting and interpreting nest counts for *C. porosus* (Graham 1981) would seem a very worthwhile area for future research.

In concluding the discussion, we would like to emphasize that many of the facets of *C. porosus* nesting biology touched on in this study merit detailed examination which, if undertaken, may clarify the apparent trends we have discussed. There are many additional aspects of *C. porosus* and general crocodilian nesting and reproductive biology of which we are almost totally ignorant (e.g. parental movements, time relations between mating and laying), but which have direct bearing on both the biological significance of the nesting strategy employed, and the various management options which could be implemented. Establishment of a well controlled captive breeding population could greatly enhance the logistics of obtaining some of these data, because the factors discussed above as militating against an egg collection strategy of management, also apply to the logistics of obtaining data in the field. Interpretation of the results of this study, and previous ones on *C. porosus* nesting, continue to be greatly restricted by the lack of direct data on movements, territoriality and the social and mating systems of adult *C. porosus*. The results of basic studies of the type carried out on *A. mississippiensis* (Joanen and McNease 1970) could be expected to greatly alter or clarify current hypotheses regarding the temporal and spatial distribution of *C. porosus*, and have far-reaching ramifications for management.

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Appendix 1. Vegetation used in Melacca Nests, with Dominance and Ranking Indices of Importance

Species	Common name	Distinguishing features	Dominance (%)		Ranking (%)	
			Site	Nest	Site	Nest
Thoracostachyum sumatranum	Sedge	Permanent water; beds either open or under a *Melaleuca* canopy; long, saw-like edges; up to 4 m high	94	94	35	40
Melaleuca leucadendron	Tree (paperbark)	Moist habitat; widespread; leaves long, thin-textured, pendulous habit, papery bark up to 25 m high; may form dense forests			26	24
Stenochlaena palustris	Fern (climbing swamp fern)	Moist habitat; tangled thickets or climbs on trees; fronds leathery, pinnate and spiny tooth margins; perennial			20	16
Cyclosorus interruptus	Fern	Moist habitat; pinnae leathery lobed throughout, pale green erect fronds up to 1 m			6	6
Flagellaria indica	Vine–scrambler	Wet and dry habitat; rambling plant cane-like stems; sheathed leaves; ends of leaves form tendrils for climbing			3	5
Phragmites karka	Grass (cane grass or tropical reed)	Wet habitat; bamboo-like thickets–clones; plumelike flower at apex up to 4 m high			4	5
Cayratia trifolia	Vine–scrambler (wild grape)	Moist habitat; scrambler vine, tendrils with (edible) tubers; soft textured 3-toothed leaflets 5–7 cm long; dark globular berries; small green flowers			2	—
Machaerina rubiginosa	Sedge	Permanent water; perennial, up to 1·8 m	6	6	2	2
Glochidion sp.	Tree	Moist areas; densely foliaged tree with small capsular fruit; small to medium height			1	2
Mucuna sp.	Vine–scrambler	Moist areas; vigorous climber; trifoliate leaves; pods black with irritant, external hairs; large black seeds; greenish flowers			1	—

Appendix 2. Vegetation used in Finniss–Reynolds Nests, with Dominance and Ranking Indices of Importance

Species	Common name	Distinguishing features	Dominance (%)		Ranking (%)	
			Site	Nest	Site	Nest
Cyclosorus interruptus	Fern	See Appendix 1	10	10	22	27
Phragmites karka	Grass (cane grass or tropical reed)	See Appendix 1	46	44	15	19
Echinochloa praestans	Grass (pit pit)	Permanent billabongs; stems up to 4 m long; lies over or through the floating mat substrate; scabrid leaves; flowers above the mat surface; perennial	13	13	8	9
Hymenochaeta grossa	Sedge	Variety of habitats associated with permanent moisture; forms dense beds stiff hard triquetrous leaves up to 2 m	2		7	6
Isachne globosa	Grass (swamp millet)	Variety of flood plain habitats; small, short-leaved grass; can form dense clumps but not extensive	6	7	6	6
Merremia gemella	Climber–scrambler	Vigorous climber common on floodplain billabongs; heart-shaped, dark green leaves; yellow flowers			5	2
Polygonum sp.	Climber–scrambler	Vigorous climber; reddish stems between leaves; forms dense communities on billabong edges		1	5	5
Typha orientalis	Rush–sedge (bulrush or broadleaf cumbungi)	Permanent water; elongated, brown flowerhead; flowers during the dry season; grows to 3 m, in dense swards	13	11	5	6
Hymenachne acutigluma	Grass	Floodplain–dense mat grass; vigorous during the wet season; often in dense monospecific stands			2	1
Ludwigia octovalvis	Herb (willow primrose)	Widespread in wet habitats, may die off in seasonally dry areas; erect perennial; soft-stemmed; yellow flowers; up to 1·5 m			2	–
Eleocharis sp.	Rush–sedge (spikerush or goosegrass)	Wet habitat; leafless plant; green flowering stem; forms dense swards on floodplain	4	1	2	2
Commelina cyanea	Climber–scrambler (wandering Jew or scurvy weed)	Moist areas; vigorous, soft-stemmed creeping plant; ends of stems turn upwards; may form dense mat close to ground; blue flowers; perennial			2	–
Brachiaria mutica	Grass (para grass)	Floodplain habitat; introduced species for cattle; behaves similarly to *H. acutigluma*; may form dense mats; grows to 1 m high	4	4	2	2
Ludwigia sp.	Herb	Varying moist habitat; small annual; dies out in the dry in seasonally wet areas			2	1
Cayratia trifolia	Climber–scrambler	See Appendix 1			1	trace
Vigna affin. adenanthus	Climber–scrambler (pea vine)	Moist areas; vigorous, twining plant; leaves alternate, trifoliate; purple-bluish flower in dry season; perennial			1	2
Pandanus aquaticus	Shrub–tree (pandanus)	Moist habitat; large dense clumps; sword-like leaves; mature fruit (15–20 cm dia.) with numerous seeds; grows to 5 m			1	–
Unknown climber	Climber–scrambler				1	2
Melaleuca leucadendron	Tree (paperbark)	See Appendix 1			1	trace

Ipomoea aquatica	Climber–scrambler	Permanent water; widespread on floodplains; tropical, aquatic, soft-stemmed, floating, trailing plant; forms large tangled mass on water; white-purple flower			1	1
Oryza meridionalis	Grass (wild rice)	Forms dense communities in swamp areas; sheds seeds in dry season; annual			1	–
Coleus scutellarioides	Herb	Widespread in a variety of habitats; purple flower with aromatic foliage			1	–
Stenochlaena palustris	Fern (climbing swamp fern)	See Appendix 1	1	2	1	1
Machaerina rubiginosa	Sedge	See Appendix 1		2	1	1
Unknown vine	Climber–scrambler				1	–
Monochoria cyanea	Herb	Aquatic; often in shallow muddy areas; emergent, spade-like leaves; skyblue flowers			1	–
Luffa cylindrica	Climber–scrambler (loofah)	Widespread in permanent water and in monsoon forest areas; annual, climbing scabrid plant with tendrils; yellow petals; dry and fibrous fruit; may form dense curtain over tree canopies			1	1
Ludwigia ascendens	Herb	Floating, white-flowered, trailing plant; white float roots present on stems, leaf shape variable, depends on habitat			1	–
Ficus hispida	Tree (wild fig)	Watercourses–billabong edges; large branching tree; hairy leaves; figs borne in trunks of tree in large cluster			1	–
Pistia stratiotes	Herb (water lettuce)	Permanent shallow or deep water; free-floating, perennial plant; rosette of overlapping leaves above water, long feathery roots beneath; yellow flowers			trace	trace
Oryza australiensis	Grass (Australian rice)	Floodplain areas; sheds seed in dry season; grows 1–2 m high; perennial			trace	–
Polygonum attenuatum	Climber–scrambler	Vigorous climber; may form dense communities on floodplain areas			trace	–
Flagellaria indica	Climber–scrambler	See Appendix 1			trace	1
Unknown legume vine	Climber–scrambler				trace	–
Cyperus platystylis	Sedge	Always associated with wet habitats, particularly floating mats; grows to 0·4 m high			trace	trace
Colocasia esculenta	Herb (taro)	Wet, open areas; widespread across floodplain; large heart-shaped leaves; tuberous, edible root; greenish flower; 1 m high; perennial			trace	–
Nauclea orientalis	Tree (Leichhardt)	Swampy regions; large, symmetrical, deciduous tree; very large stipules and leaves; conspicuous flowers (white and yellow) in dense, spherical head			trace	–
Microsorium scolopendria	Fern	Moist habitat; long, creeping rhizome; erect, membranous, light green fronds, up to 60 cm long; deeply lobed			trace	–
Peat-like material	Decaying organic matter			4	*	5

* Not included at site as vegetation because it actually forms the mat substrate.