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Dry-season Distribution and Ecology of *Carettochelys insculpta* (Chelonia : Carettochelydidae) in Kakadu National Park, Northern Australia

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Abstract

Carettochelys insculpta is widely distributed (though not necessarily abundant) in Kakadu National Park during the dry season, occupying permanent billabongs from the black-soil plains to the base of the escarpment. High population densities were found in the upper reaches of the South Alligator drainage (33·8 turtles ha^{-1}; 227·4 kg ha^{-1}) and are interpreted as dry-season concentrations of turtles that would occupy a much wider range in the wet season. *C. insculpta* nest in clean, fine sand adjacent to water from mid July to early November. About 15 hard-shelled spherical eggs were laid in a shallow chamber (maximum depth 18–21 cm) between 1·0 and 3·7 m from water, with the height above water ranging from 0·4 to 0·7 m. The nests suffered heavy predation from varanid lizards. The turtles are general omnivores that draw upon a wide variety of food, including algae, aquatic macrophytes, fruits, seeds and leaves of riparian vegetation, aquatic macroinvertebrates, and carrion. Its catholic tastes provide great scope for opportunism, and its diet varies greatly in accordance with the foods available from locality to locality. The ecological basis for the restricted global distribution of *C. insculpta* is unclear since the species appears to have very broad habitat requirements.

Introduction

As the sole surviving member of its family, the pig-nosed turtle or warradjan, *Carettochelys insculpta*, occupies an unusual position among living chelonians, representing all that remains of a lineage dating back some 40 million years (Chen *et al.* 1980). The species is very distinct morphologically, being perhaps the most suited of all freshwater turtles to an aquatic existence. It is large (the carapace length may exceed 55 cm), its nostrils open at the end of a prominent fleshy proboscis, its limbs are clawed and paddle-shaped like the flippers of sea turtles, and it lacks the epidermal scutes that overlie the shells of most turtle species (Cogger 1975; Pritchard 1979*a*). *Carettochelys* is Australia's only freshwater cryptodire (its vertebral column flexes vertically when the head is withdrawn).

Carettochelys was first described before the turn of the century from a New Guinean specimen (Ramsay 1886), but is presence in northern Australia was not widely known until recently (Cogger 1970; Peters 1970). At first, there was doubt whether the Australian population in the Daly River was self-sustaining or was merely a nonbreeding outlier of the New Guinea population. However, in 1972 a further specimen showing evidence of recent breeding was collected in the South Alligator drainage (Yellow Waters billabong, Schodde *et al.* 1972), and the species is now known to nest regularly at both localities (Legler 1982; Webb *et al.* 1986; Georges 1987). Evidence of breeding in Australia dates back to 1918,

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when eggs from the East Alligator River were lodged with the Victorian Museum (Georges *et al.* 1989), and the presence of Aboriginal rock paintings of *Carettochelys* (Dupe 1980), some dating back more than 7000 years (G. Chaloupka, personal communication), suggest that the species is a long-term resident of northern Australia. It is now known to occur in the Daly (Cogger 1970; Cann 1972; Webb *et al.* 1986; Georges 1987), Victoria (Cogger 1975), South Alligator (Schodde *et al.* 1972; Legler 1980, 1982; Press 1986) and East Alligator drainages (Georges *et al.* 1989). Anecdotal reports suggest that the species may also occur in the Darwin, Adelaide, McKinlay and Roper Rivers of the Northern Territory (Cann 1972; J. Bywater, personal communication; K. Day, personal communication) and the Wenlock River on the west coast of Cape York (K. Day, personal communication). It apparently does not occur in the Liverpool or Blyth Rivers on the north coast of Arnhem Land (Webb *et al.* 1986).

Restricted to the rivers of southern New Guinea and northern Australia, *Carettochelys* has generally been considered to be one of the rarest living chelonians (Groombridge 1982), but it is not known whether this reputation reflects its remote distribution or its low population densities (Pritchard 1979*a*). In fact, there is little published data relevant to the population status and management of *Carettochelys* (Georges 1988). In this paper, we describe the dry-season distribution, abundance and ecology of the species in the South Alligator drainage of Kakadu National Park. The Alligator Rivers drainage is one of two in Australia in which *Carettochelys* is known to be sufficiently abundant for detailed study (the other is the Daly River) and the only one in which the species and its habitat are afforded some measure of protection.

Study Area

Kakadu National Park covers approximately 19 600 km^2 between latitudes 12°00′ and 14°00′ and longitudes 131°50′ and 133°00′ (Fig. 1). It is bounded to the north by Van Diemen Gulf and to the east by Arnhem Land. The park encompasses almost all of the catchment of the South Alligator River and its major tributaries (Nourlangie and Jim Jim Creeks), most of the catchments of the West Alligator and Wildman Rivers, and the lower reaches of the East Alligator River.

The park has a monsoonal climate with a hot, humid wet season, usually between December and March, and a cooler dry season between May and September. The mean annual rainfall at Oenpelli (1910–1984) is 1388 mm, but typically little or no rain falls in the months of May to August. The onset of the wet-season rains, and associated flooding, may vary considerably from year to year (Taylor and Tulloch 1985).

The headwaters of the South Alligator River and its major tributaries rise in the Arnhem Land plateau to the east and flow across the lowlands in shallow valleys to discharge through an extensive floodplain into Van Diemen Gulf. In the wet season, the drainage is characterised by high flows and extensive flooding (Story *et al.* 1969, 1976). In the dry season, surface flow declines and eventually stops, except in the lower tidal sections of the main channel and in upstream sections fed by springs or seepage. Many waterbodies persist until the next wet season as rock pools above and immediately below the escarpment and as discrete waterholes, billabongs and swamps in the lowlands and floodplains.

Pul Pul billabong in the upper reaches of the South Alligator River (132°35′E.,13°34′S.) was chosen for extensive study because the water was clear, free of salt-water crocodiles, and within one of two regions known to Aborigines as a good place for *Carettochelys*. At the time of sampling, it was approximately 400 m long and 20 m wide with a modal depth of 1·2 m and a maximum depth of 3·0 m. The substratum was sand and gravel covered with a thin layer of fine silt and litter. Fallen trees and branches, undercut banks, exposed tree roots, and local accumulations of litter provided a diverse range of underwater cover for turtles. The banks of the billabong were covered in a dense broadleafed forest, including the important turtle food *Ficus racemosa*. The many small sandbanks adjacent to the water were more than adequate in number and size for nesting. Water flows through Pul Pul billabong in all months of the year. *Carettochelys* shares the billabong with the northern snapping turtle (*Elseya dentata*), the saw-shelled snapping turtle (*Elseya latisternum*) and the northern yellow-faced turtle (*Emydura* sp.).

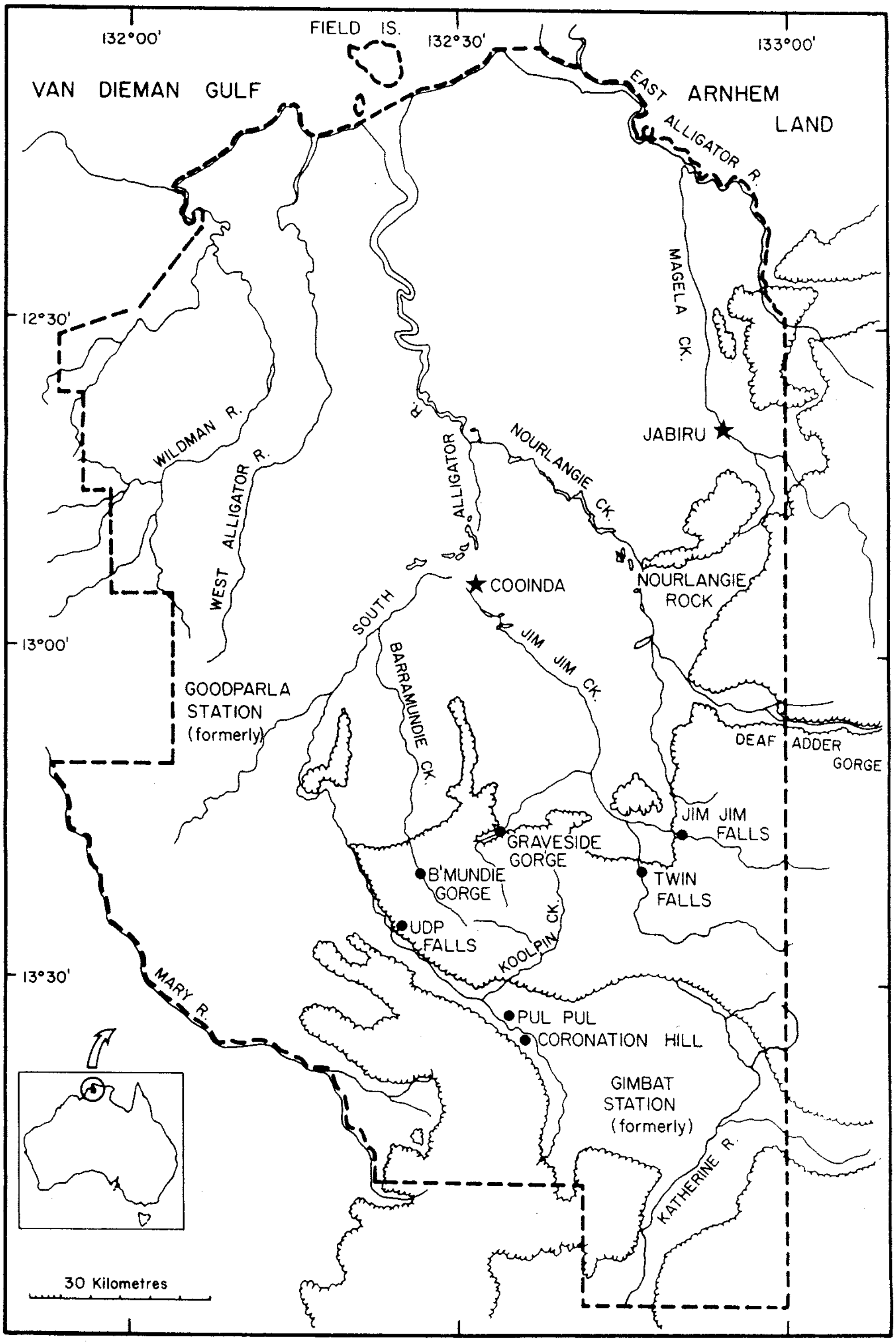

Fig. 1. Map of Kakadu National Park showing the current boundary (dashed line) and the placenames used in this paper. The Arhnem Land escarpment is shown as an irregular line.

Materials and Methods

The distribution of *Carettochelys* in Kakadu was determined from direct sightings of adults and nests, by collating information in published and unpublished accounts (Schodde *et al.* 1972; Legler 1980, 1982; Press 1986; Georges *et al.* 1989), and by collating and verifying anecdotal reports from reliable sources. Observations on adults were generally incidental to activities involved in locating nests, with the exception of an intensive marking and recapture study undertaken in Pul Pul billabong.

Aerial photographs of all billabongs in the Magela, Nourlangie, Jim Jim and South Alligator drainages within the park were examined carefully with a zoom-transferscope. Locations of major sandbars considered suitable for nesting (Legler 1982; Webb *et al.* 1986) were mapped, and representative examples were later verified on the ground. Waterbodies available to *Carettochelys* were classified as follows (Fig. 3).

Zone 0: Marine.

Zone 1: Estuarine (subject to tidal and saline influence). There were no suitable nesting banks.

Zone 2: Lowland billabongs in black-soil plains (e.g. Yellow Waters just north of Cooinda and Jabiluka on Magela Creek). These billabongs contained no suitable nesting areas.

Zone 3: Upland billabongs.

A: Lower reaches in paperbark forest adjacent to black-soil plains (e.g. Alligator billabong at the junction of the South Alligator River with the floodplain). Typically, two or three potential nesting banks were located adjacent to creek inflows on the upland side.

B: Middle reaches with large, deep, stable billabongs (e.g. Jim Jim south-east of Cooinda and Binji Waters on Nourlangie Creek). Sandbanks accumulated at the inflows and outflows of the main channel and adjacent to creek inflows.

C: Middle to upper reaches with small, shifting billabongs having sandy bottoms and shallow pools (e.g. Sandy billabong on Jim Jim Creek). Sand was very abundant both above and below the waterline, forming suitable nesting banks on bends, at the inflows and outflows of the main channel, and behind debris.

D: Upper reaches with small, shallow pools and creek channels not visible on 1 : 100 000 topographic maps or aerial photographs (e.g. Barramundie Creek, headwaters of the South Alligator River). Large sandbars formed at the inflows of the main channel and behind debris. Eroded banks also provided sufficient falling sand for nesting.

Zone 4: Plunge pools (e.g. Jim Jim Falls). Sandbanks formed where sand accumulated in eddies during the wet season to be exposed during the dry season.

Zone 5: Washpools above the escarpment. There was sufficient sand for nesting, but it was not abundant.

Within zones 2 and 3, the billabongs can be further classified as to whether they were permanent or ephemeral and whether they were in the main channel or a side-channel or side creek.

Billabongs within zones 2, 3 and 4 were selected on the basis of availability, with due respect for the wishes of the Aboriginal community, and accessibility. At each billabong, all nesting banks were systematically searched for nests using probes made from 3 mm spring steel rod (after Blake 1974), and for nesting tracks or the remains of nests destroyed by predators. For each nest, the distance from water, height above water and slope at the surface were recorded. Intact nests were uncovered and the depth to the first egg, maximum depth and core temperature were recorded. The eggs were then removed and numbered, while maintaining their original orientation at all times. The maximum and minimum diameters of each egg were measured with calipers (±0·1 mm), and the eggs were weighed on a field electronic balance (±0·1 g). One egg per nest was opened and its embryo preserved for later age determination using a relationship between head width and age at 30°C (Webb *et al.* 1986). The remaining eggs were returned to the laboratory and incubated at 30°C until hatching. The hatchlings were measured and weighed, then released.

Carettochelys specimens were captured in Pul Pul billabong by divers with the aid of mask and fins. During the day, the turtles could be found buried in the litter covering the riverbed or hidden beneath submerged logs and branches or in submerged cavities in undercut banks. When approached cautiously, they remained motionless for long enough to allow the diver to grasp the carapace at its anterior and posterior ends. The turtle was then manoeuvred to the surface. It the turtle escaped, the speed that it achieved made pursuit virtually impossible.

Turtles were marked with numbered plastic cattle eartags (Allflex medium female flange, small male button) attached to the shell through a 9·5 mm hole drilled in the lateral margins of the carapace. Maximum curved carapace length, head width (tympanum to tympanum) and body weight were measured. Turtles with carapace lengths greater than 35 cm could be reliably sexed by inserting a small finger, with the palm of the hand facing ventrally, into the cloaca. The grooved penis was immediately evident in males. In all cases, the males so identified could be distinguished from females of the same size by their tails, which were much larger than those of the females. Males with fully enlarged tails were considered to be mature. Turtles with carapace lengths less than 35 cm could not be sexed reliably, nor was an index to maturity available.

Population size was estimated, using the Peterson method as modified by Bailey (1951, 1952), from data collected during an initial capture and marking session on 26 September 1987, and an intensive recapture session one week later. The turtles were sampled again on 28 May, 15 June and 16 July 1988, and data from recaptures were used to estimate annual growth rates.

Stomach contents were removed by stomach flushing. A 12 V submersible pump supplied a steady flow of water that was passed into the stomach through a flexible plastic tube (after Legler 1977). The water passed back up the oesophagus carrying items of food. Water flow was adjusted for turtles of different sizes by using tubes with different diameters. All turtles were flushed as soon as possible, and never more than 2 h after capture. The animals were released following flushing. Three guts supplied by Aboriginal people were also examined.

The stomach contents were preserved in 70% ethanol and were later examined under a stereo microscope. Percentage composition by wet weight (excess moisture removed) and percentage occurrence (Windel and Bowen 1978) were used to evaluate the relative importance of different foods. The occurrence method involved counting the number of turtles that had eaten one or more items of a particular food and expressing each count as a percentage of the number of turtles examined.

Means are presented with standard errors throughout this paper.

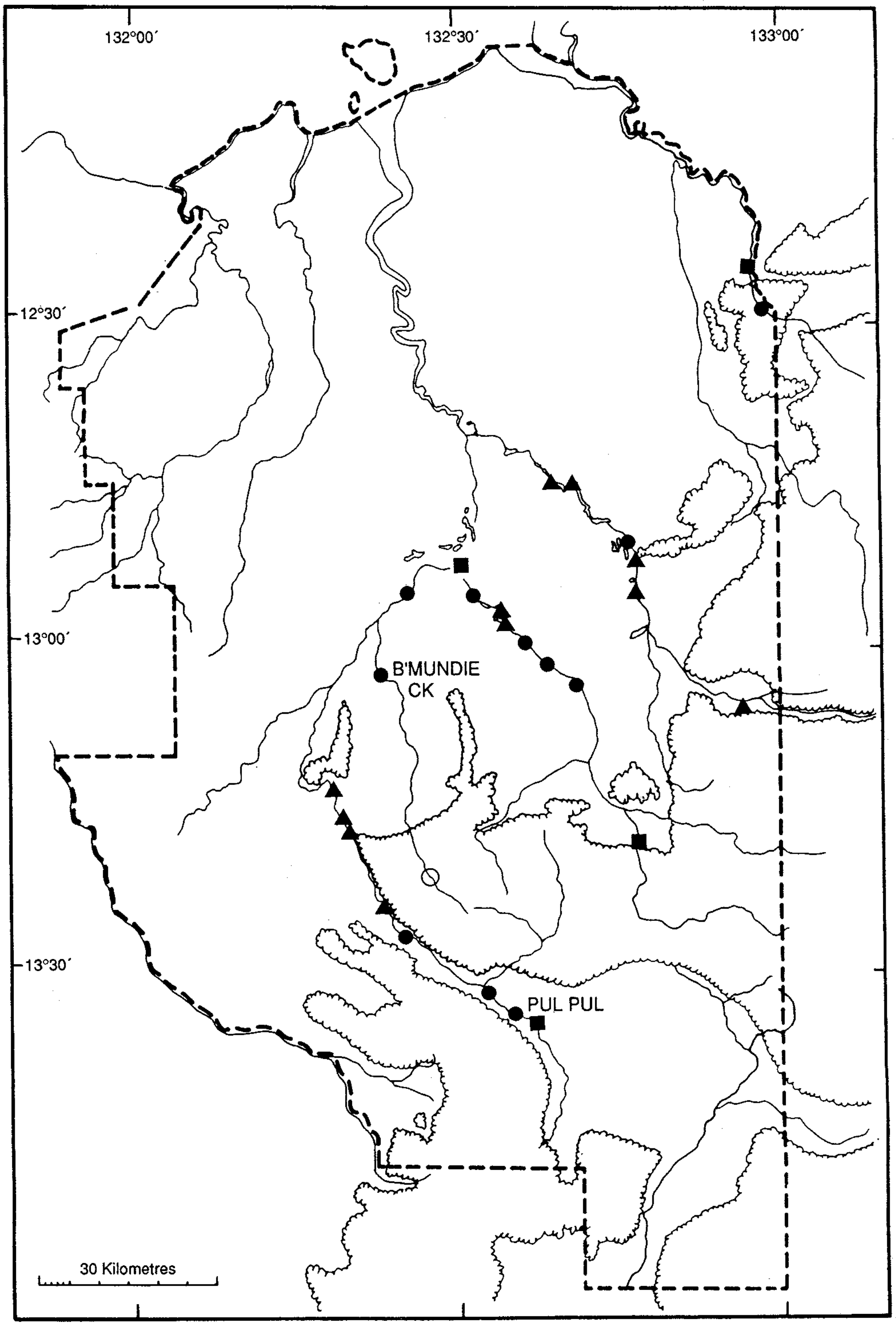

Fig. 2. Map of the known dry-season distribution of *Carettochelys insculpta* in Kakadu National Park. The map is based on data collected in the present study (●), on published accounts (■) and on anecdotal reports from reliable sources (▲). The open symbol (○) shows where *Carettochelys* is known not to occur.

Results

Distribution

During the dry season, *Carettochelys* occupies billabongs throughout the South Alligator drainage below the escarpment (Fig. 2). It occurs in the lowland billabongs of the black-soil plains (Zone 2) such as Yellow Waters (Schodde *et al.* 1972) and in the large, deep, stable upland billabongs of the middle reaches of the drainage (Zone 3B) such as in Jim Jim Creek, Nourlangie Creek and the South Alligator River. *Carettochelys* must contend with high densities of salt-water crocodiles in these billabongs. The turtles are also found further upstream in the shallower and clearer waters of Zones 3C and 3D, where they are regularly hunted by Aboriginal people in the dry season, and there are reports of them from plunge pools in Deaf Adder Gorge (T. Press, personal communication) and at Twin Falls (Legler 1982). They also occur in the East Alligator within the park (Georges *et al.* 1989; Ian Morris, personal communication; Fig. 2) and are reported to be common in Mekan Valley of the East Alligator drainage.

Carettochelys is not found in Barramundie Gorge during the dry season. The water there is exceptionally clear and was thoroughly searched on three occasions. Nor do they appear to be common in the Magela system (Legler 1982; R. Jeffree, personal communcation; D. Walden, personal communication), the biota of which has been the subject of intensive study related to the Ranger uranium mine. *Carettochelys* does not occur above the escarpment, nor are there any reports of it from marine or estuarine areas of the park.

Nesting

Of the 12 nests located in Kakadu National Park, only one had not been destroyed by predators (probably *Varanus panoptes* or *V. gouldii*). The data from these nests are summarised in Table 1.

Table 1. Characteristics of *Carettochelys insculpta* nests, eggs and hatchlings from Kakadu National Park

These data are primarily from nests previously robbed of eggs by predators, as only one intact nest was located in the present study. The temperature is as measured at 1000 hours on 21 September 1987, and the carapace length is the straight-line maximum

	Mean ± SE	Range	*n*
Nests			
Distance from water (m)	2·16±0·28	1·1–3·7	8
Height above water (m)	0·59±0·04	0·4–0·7	8
Slope at sand surface (deg.)	17·5±2·0	11·3–26·6	8
Depth to top of uppermost egg (cm)	12·5	12–13	2
Depth to bottom of lowest egg (cm)	19·5	18–21	2
Temperature (°C)	29·1	–	1
Clutch size	15·0±1·0	14–16	2
Infertility (%)	0·0	–	1
Eggs			
Length (mm)	41·8±0·03	40·6–43·5	15
Width (mm)	40·6±0·01	39·6–41·4	15
Weight (g)	40·2±0·51	36·5–42·6	14
Hatchlings			
Weight (g)	24·7±0·84	22·0–28·0	6
Carapace length (mm)	56·1±0·91	52·4–58·6	6

Carettochelys nests in many permanent upland billabongs (Fig. 3). Nests were constructed in clean, fine sand adjacent to water (Table 1), and all sandbanks used for nesting were in direct contact with the water. With a depth to the top egg of 12–13 cm, the nests were very shallow. Temperatures at this depth are at a minimum at 1000 hours (Georges, unpublished data), so the measurement of 29·1°C (Table 1) suggests that the nests incubate at high temperatures.

The known nesting dates of *Carettochelys* in Kakadu National Park (Table 2) suggest a protracted nesting season, ranging from mid July to early November.

Population Size and Structure

The Petersen method yielded a population estimate of 27 ± 9 turtles for Pul Pul billabong.

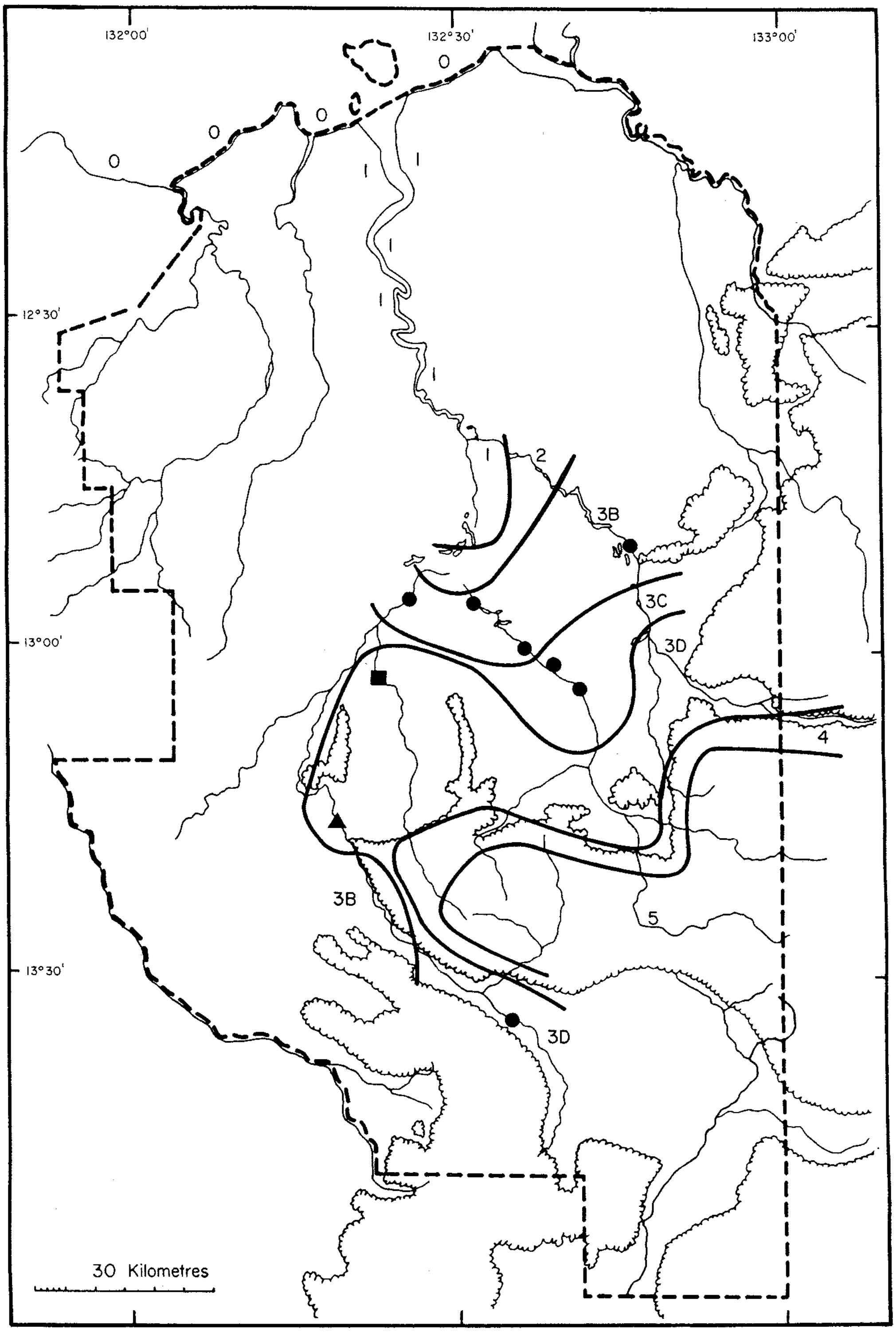

Fig. 3. Map of the known distribution of nesting areas for *Carettochelys insculpta* in Kakadu National Park. The map is based on data collected in the present study (●), on published accounts (■) and on anecdotal reports from reliable sources (▲). Numbered zones indicate waterbodies classified as in the text.

This represents $33 \cdot 8 \pm 11 \cdot 3$ turtles ha^{-1} or 67 turtles km^{-1} of channel. The corresponding estimate of biomass was $227 \cdot 4$ kg ha^{-1}. These estimates are considered accurate because the sampling intensity was high (21 of the estimated 27 turtles were caught and measured) and because the population was closed to immigration and emigration. Given the short duration of the study, the population was also closed to recruitment and mortality. In addition, marked and unmarked animals did not appear to respond differently to the approach of a cautious swimmer.

The size of the Pul Pul population is depicted in Fig. 4. Of the 32 turtles examined, 13 were mature males, 11 were mature females and 8 were juveniles. One of the juveniles

Table 2. Known nesting dates of *Carettochelys insculpta* in Kakadu National Park

Date	Evidence	Source
17.vii.86	Oviductal eggs	P. Wellings, pers. comm.
23.viii.86	Nest aged from embryo	Present study
25.viii.87	Nest aged from embryo	Present study
28.viii.81	Fresh nest	Legler 1982
6.ix.81	Fresh nest	Legler 1982
6.x.87	Fresh tracks and test digs	Present study
5.xi.71	Fresh corpora lutea on ovary	Schodde *et al.* 1972
6.xi.81	Fresh nest	Legler 1982

was a male (carapace length = 35·0 cm) on the verge of becoming sexually mature as the penis was clearly evident but the tail was not yet fully enlarged. The adult sex ratio of 13 : 11 was not significantly different from 1 : 1. The sex of *Carettochelys* is strongly influenced by the temperature prevailing during incubation (Webb *et al.* 1986), so sex ratios may vary considerably from locality to locality.

Five of the 12 turtles captured in Pul Pul billabong in 1988 had been among the 21 turtles captured in the same billabong the year before, indicating some site fidelity. Two of the five had lost their tags (the insertion hole expanded beyond the margin of the carapace), and the tag of a third specimen was on the verge of being shed. Marking with cattle eartags is therefore suitable only for short-term studies.

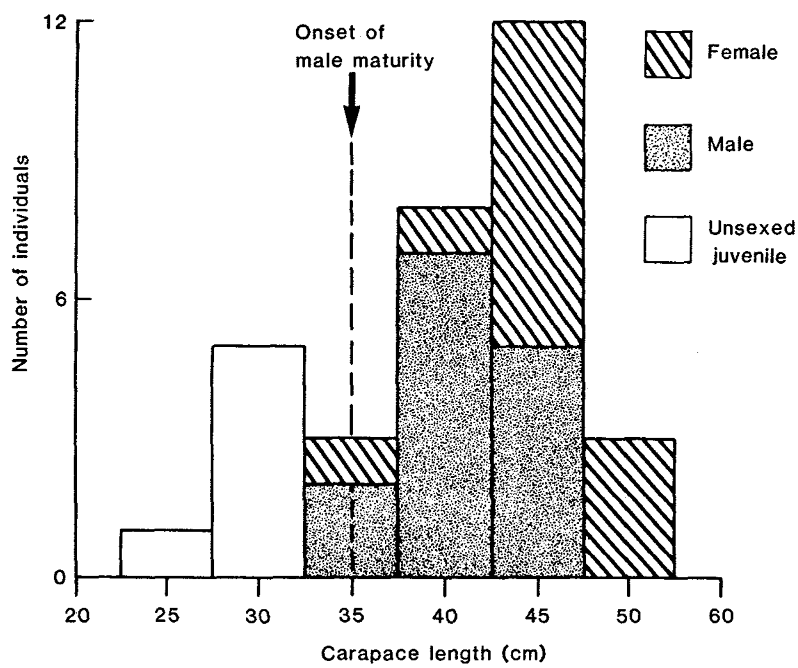

Fig. 4. Size distribution of 32 *Carettochelys insculpta* from Pul Pul billabong at the head-waters of the South Alligator River. The carapace length is the curved maximum.

Morphometry and Growth

Measurements of 32 turtles from Pul Pul billabong yielded the following statistics:

Carapace length:	Mean 40·3 ± 1·2 cm (range 24·3–52·3 cm)
Head width:	Mean 6·8 ± 0·2 cm (range 4·4–8·9 cm)
Weight:	Mean 7·4 ± 0·6 kg (range 1·7–16·0 kg)

Relationships for predicting body weight (WT) from carapace length (CL) and head width (HW), and for predicting carapace length from head width, are given below. The addition of data from 16 captive juvenile specimens from various localities ensured a range of sizes from hatchling to adult. Weight is in kilograms, linear measurements are in centimetres and r^2 is the coefficient of determination.

$$WT = 1{\cdot}63CL^{2{\cdot}88} \times 10^{-4} \quad r^2 = 0{\cdot}997,\ n = 48$$

$$WT = 9{\cdot}58HW^{3{\cdot}40} \times 10^{-3} \quad r^2 = 0{\cdot}997,\ n = 48$$

$$CL = 6{\cdot}24HW - 2{\cdot}75 \quad r^2 = 0{\cdot}99,\ n = 48$$

There was a suggestion that males were slightly heavier than females having the same length or the same head width, but the differences were not significant.

Males reach smaller maximum sizes than females (Fig. 4). The largest male observed in Pul Pul billabong had a carapace length of 45·4 cm and weighed 9·5 kg, whereas the largest female had a carapace length of 52·3 cm and weighed 16·0 kg. Females may grow larger still, as a skull obtained from Nourlangie Camp had a width of 9·25 cm, corresponding to a weight of 18·5 kg.

Of the five turtles caught in both 1987 and 1988, one grew 4 mm (female, CL = 48·5 cm), one grew 7 mm (male, CL = 40·7 cm), two failed to grow appreciably (female, CL = 42·6 cm; subadult male, CL = 35·0 cm), and one had lost its tag and could not be identified from other features.

Table 3. Items from the stomachs of 24 specimens of *Carettochelys insculpta* from Pul Pul billabong in Kakadu National Park

The items were removed by stomach flushing (Legler 1977). Recaptures were flushed again if caught some time after the previous flushing. Two specimens, not included, yielded no food items when flushed, their stomachs were presumed to be empty. Percentage occurrence gives the number of stomachs that contained one or more items of a particular food type, expressed as a percentage of the total number of stomachs examined. Percentage weight gives the wet weights of each food type expressed as a percentage of the total wet weight of food extracted. A plus sign indicates a contribution of less than 1%

Food type	Percentage occurrence	Percentage weight
Plant material	92·1	92·0
Division Chlorophyta		
Spirogyra sp.	8·3	34·6
Division Magnoliophyta		
Ficus racemosa		
Fruit	70·8	19·3
Leaves	62·5	38·1
Miscellaneous (mushrooms, etc.)	4·1	+
Animal material	42·3	8·0
Class Insecta		
O. Odonata (Corduliidae, Gomphidae)	8·3	+
Class Crustacea		
Palaemonidae (*Macrobrachium rosenbergii*)	8·3	1·5
Pisces	29·2	6·5
Black bream (*Hephaestus fuliginosus*)		
Barramundi (*Lates calcarifer*)		
Catfish (Ariidae, Plotosidae)		
Miscellaneous (Formicidae, Murid faecal pellet)	8·3	+
Raw totals	24 turtles	199·5 g

Diet

The stomachs of *Carettochelys* specimens in Pul Pul billabong were found to contain mainly fruits and leaves of the fig *Ficus racemosa*, algae, and fish possibly eaten as carrion (Table 3). A few stomachs contained small numbers of benthic macroinvertebrates and some miscellaneous material of terrestrial origin. Further downstream, a specimen was found to contain the remains of a flying fox *Pteropus alecto* together with the leaves and fruits of the bush apple *Syzygium* (probably *S. forte*). Another specimen, a male from Jim Jim Creek, had a gut packed with the fruits and leaves of *Pandanus aquaticus* interspersed with the hair, bones and flesh of a flying fox (*Pteropus* sp.). A third specimen from Nourlangie Creek had a stomach full of the water nymph *Najas tenuifolia* (Najadaceae).

Discussion

Data on the abundance of *Carettochelys* are scarce for most of its range in Kakadu National Park, and it cannot be concluded from this study that the species is abundant throughout the park. However, estimates of abundance and biomass for Pul Pul billabong are exceptionally high in comparison with estimates for other freshwater turtle species elsewhere (Iverson 1982; Congdon *et al.* 1986). Production within the Pul Pul billabong alone is almost certainly insufficient to maintain the observed population density, which probably represents a dry-season concentration of turtles that would occupy a much wider range in the wet season. The high abundances of *Carettochelys* reported by Legler (1982) for Barramundie Creek can be similarly explained. We believe that these two regions—the many billabongs along the upper reaches of the South Alligator River, including Pul Pul billabong, and the billabongs of Barramundie Creek—are important dry-season refuges for the species. Both regions are clearly recognised by Aboriginal people as places where one can fish in the dry season with a high expectation of catching *Carettochelys* (Georges and Kennett 1988).

Legler (1982) considered the Barramundie Creek locality to typify the preferred dry-season habitat of *Carettochelys*, and his description of it is similar to that of Pul Pul billabong in this study. In addition, both localities are fed by a continuous low flow throughout the dry season of most years. This continuous flow, which is also characteristic of the Daly River habitat, may be an important feature of the preferred habitat of the species. Schultze-Westrum (1963) observed that *Carettochelys* takes up water through its mouth with clearly visible gular movements (24 times a minute) and pushes it out again mainly through the nostrils. He also found that the lining of the pharyngeal space is covered with many cone-shaped papillae that, together with the finely branching blood vessels of the under-surface of the shell, may serve a respiratory function. Perhaps *Carettochelys* prefers flowing water because of its higher level of dissolved oxygen.

Carettochelys nests in many permanent upland billabongs, but the distribution map for nests (Fig. 3) is somewhat misleading because surveying for nests in areas heavily stocked with buffalo was made very difficult by the damage the buffalo did to potential nesting banks. Carr (personal communication in Pritchard 1979*b*) believed that *Carettochelys* may have become much more restricted in its Australian distribution since the introduction of water buffalo, whose activities he believed destroyed nesting banks. Sandbanks often provide easy access to water, and in some areas within the former Gimbat and Goodparla stations (Fig. 1) virtually every square inch of potential nesting area had recently been disturbed by hooves. Trampling by stock was a source of nest mortality at the Daly River (Georges, unpublished data), and even a misplaced human heel is sufficient to destroy many eggs in the shallow nests of *Carettochelys*. It is unlikely that many nests would survive in heavily stocked regions, and current moves to remove buffalo from Kakadu National Park are welcomed.

Observations on the nesting of *Carettochelys* in Kakadu National Park are broadly consistent with those from the Daly River (Webb *et al.* 1986; Table 2 of Georges and Kennett 1988) and New Guinea (Cogger 1975; Cann 1978; Pernetta and Burgin 1980). Although the turtles nest almost exclusively in fine sand, there has been one reliable report of *Carettochelys* nesting on mud banks in the freshwater reaches of rivers in Papua New Guinea (Cogger, personal communication regarding plate 59 in Cogger 1975). The female *Carettochelys* collected from Yellow Waters in Zone 2 and found to have fresh corpora lutea on its ovaries (Schodde *et al.* 1972) may have nested in the black-soil banks of the billabong since no sandbanks were available. In the dry season, however, all of this black soil is rock hard except for a few centimetres next to the water, so it is more plausible that the turtle nested in an adjacent upland billabong that may have had some connection to Yellow Waters during 1971. It is also unlikely that *Carettochelys* nests in the gelatinous tidal mud of the estuarine reaches of the South Alligator draingae. This mud, which is quite different from the silty loams of the freshwater reaches, would provide an anaerobic environment unsuited to the incubation of eggs. Furthermore, there have been no reports from estuarine reaches of the distinctive tracks left by *Carettochelys*, despite frequent surveys for crocodiles since 1980 in which mud slides are often noted (R. Jenkins, personal communication).

The nesting period in the continuous Daly River near Oolloo Crossing (131°15′E., 14°04′S.) ranged from 19 August to 8 October in 1986, and there is good evidence that some individuals lay two clutches of eggs per season (Georges, unpublished data). The nesting season in Kakadu is more protracted (Table 2), suggesting that individuals may lay up to three clutches per year. However, conditions in the discrete billabongs of Kakadu National Park during the dry season may vary considerably from locality to locality, providing an alternative explanation for the greater spread of nesting dates there.

Data on the diet of *Carettochelys* presented in this paper are consistent with observations published elsewhere. Legler (1982) found that *Carettochelys* from the Twin Falls area of Jim Jim Creek were eating *Eucalyptus* flowers, *Melaleuca* leaves and miscellaneous fruits and seeds, whereas in the South Alligator River they were eating predominantly figs. Mammalian vertebrae and mussel shells were found among the faeces. A specimen from Yellow Waters (Schodde *et al.* 1972) defaecated large quantities of *Pandanus* fruit, leaves (*Melaleuca* and Leguminosae), seeds, roots, pieces of aerenchymatous plant stem, and traces of animal material. The animal material included fragments of water snails (Thiaridae), water boatmen (Corixidae), water beetles (Dytiscidae: *Homoeodytes scutellaris*, Hydrophilidae: *Hydrophilus latipalpus*) and ants (*Iridomyrex* sp.). Clearly, *Carettochelys* is an omnivorous species with a tendency more towards herbivory than towards carnivory. The wide range of foods eaten provides great scope for opportunism, and the diet varies greatly with the foods available from locality to locality.

Is *Carettochelys* rare? Certainly, the results of this study show that it is widespread between the tidal reaches of the South Alligator River and the escarpment and that high densities may be present in the upper reaches during the dry season. However, the complexity of the biological concept of rarity is often obscured by the inadequacy of the English language to describe it, and several distinct forms of rarity are recognised (Rabinowitz *et al.* 1986). There can be little doubt that *Carettochelys* is both a geographic and a taxonomic relic species (*sensu* Simpson 1944) and that it is rare in the sense of being geographically restricted. Regardless of high densities in some areas within their range, locally abundant species with restricted ranges are possibly more vulnerable than scarce but widely distributed species.

The ecological basis for the restricted distribution of *Carettochelys* is unclear since the species appears to have very broad habitat requirements. The species inhabits rivers, grassy lagoons, swamps, lakes, waterholes and billabongs within its range (Groombridge 1982; Cogger 1975), and its presence in estuarine and mangrove areas of New Guinea (Liem and Haines 1977; Groombridge 1982) suggests a tolerance of saline conditions. The species nests on sandbanks adjacent to water in the middle reaches and mouths of rivers, on sandy shores of islands in river deltas, and on coastal beaches (Rhodin and Rhodin 1977; Groombridge 1982). With this range of habitats and a generalised diet, why is the species not more abundant and widespread in Australia and elsewhere? This study did not address the seasonal movements and wet-season requirements of *Carettochelys*, nor did it address the requirements of juveniles, and the answers may lie there. Such information is also needed before the possible impact of proposed or potential development within catchments (Groombridge 1982; Georges and Kennett 1988) can be assessed, and before the adequacy of existing reserves for protecting the species can be judged.

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