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Freshwater turtles of the TransFly region of Papua New Guinea – notes on diversity, distribution, reproduction, harvest and trade

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Abstract. The Chelidae is a family of side-necked turtles restricted in distribution to South America and Australasia. While their biology in Australia is reasonably well known, species in New Guinea are very poorly known despite high diversity, especially in the southern lowlands. In this paper, we report on the diversity, distribution, habitat and reproductive biology of the freshwater turtles of the TransFly region of the Western Province of Papua New Guinea, with special emphasis on reproduction of *Emydura subglobosa*, *Elseya branderhorsti* and *Elseya novaeguineae*. Seven species were captured, with reliable records of an eighth. A key to the freshwater turtles of the TransFly region is provided. Harvest methods, consumption, and trade in turtles by the TransFly communities are documented. There is mounting pressure to take advantage of revenue opportunities afforded by the Asian turtle trade, but this is impeded by lack of transport infrastructure. There is also insufficient demographic information on any New Guinean turtle species to make a reasoned judgment on the level of harvest that would be sustainable. Nor is there sufficient information on captive rearing for most species, and where it is available it is not accessible by local villagers. These knowledge gaps need to be addressed and factored into a management plan that is implemented before local communities can capitalise on the commercial opportunities provided by the turtle fauna without risking collapse of the resource and the implications for their concurrent subsistence economy that would follow.

Introduction

The Chelidae is a group of side-necked turtles restricted in distribution to South America and Australasia, not known from outside this range even as fossils (Pritchard 1979). With the exception of the pig-nosed turtle, *Carettochelys insculpta*, all freshwater turtles from Australia belong to the Chelidae, comprising 21 species in 6 genera (Georges and Thomson, in press). Regions of particular value for turtle biodiversity and endemism are the Mary–Burnett–Fitzroy region of coastal central Queensland (7 species, 3 endemics), the south-west corner of Western Australia (2 species, both endemic), and the rivers draining the Arnhem Land Plateau, including the Daly and Roper Rivers and adjacent drainages of the Northern Territory (10 species, 2 endemics). The Australian fauna has been reasonably well studied, in terms of their systematics (Goode 1967; Legler and Cann 1980; Cann and Legler 1994; Georges and Adams 1996; Thomson *et al*. 2000; Georges *et al*. 2002; McCord and Thomson 2002; Thomson *et al*. 2006), physiology (Kennett and Christian 1994; Booth 2002; Gordos *et al*. 2004; Georges *et al*. 2005), zoogeography (Georges and Thomson, in press) and ecology (Kennett and Georges 1990; Doody *et al*. 2004; Armstrong and Booth 2005; Spencer and Thompson 2005).

Chelid turtles also dominate the fauna of the island of New Guinea to the north, with the southern lowlands home to the highest diversity of turtles in the Australasian region. In total, 10 species are found there – *Elseya branderhorsti*, *E. novaeguineae*, *Emydura subglobosa*, *Chelodina novaeguineae*, *C. parkeri*, *C. pritchardi*, *C. reimanni*, *C. rugosa* (formerly *C. siebenrocki*), *Carettochelys insculpta* and *Pelochelys bibroni*. Seven of these are endemic to the region. In contrast to the Australian fauna, very little indeed is known of the life history and ecology of the New Guinean taxa. Much of what is known of their life history is found in the original descriptions (Rhodin and Mittermeier 1976; Rhodin 1994), the personal communications reported therein, and a few other papers (Georges and Rose 1993; Rhodin 1993; Rhodin *et al*. 1993; Rhodin and Genorupa 2000).

In this paper, we report on the diversity, distribution, habitat and reproductive biology of the freshwater turtles of the TransFly region of the Western Province of Papua New Guinea. The TransFly region comprises extensive lowland swamps, savannah woodland and monsoon forest between the lowland reaches of the Fly River and the border between Papua New Guinea and Indonesia. It is sparsely populated by Melanesians who rely upon a subsistence economy built around small-plot agriculture, hunting and fishing. Freshwater turtles are an important source of protein and are regularly harvested. We also report on harvest methods and trade in freshwater turtles and turtle products.

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Materials and methods

Our approach was to work within the World Wide Fund for Nature network and the Suki/Aramba Wildlife Management Committee to give advance warning of our visit and to request that villagers retain turtles for our examination before they were killed and consumed. We visited the villages and associated camps of Suki (08°02.97′S, 141°43.50′E), Pukaduka (07°57.71′S, 141°46.07′E), Gukabi (08°13.42′S, 141°59.36′E), Serki (08°14.69′S, 141°45.99′E), and Keru (East, 08°32′S, 141°45.5′E) in the Fly River catchment; Keru (West, 08°26.68′S, 141°47.62′E), Daraia (08°37.00′S, 141°44.08′E), Morehead (08°42.95′S, 141°38.49′E), Mibini (08°50.42′S, 141°38.14′E), Tonda (08°55.80′S, 141°33.64′E) and Roku (08°42.12′S, 141°35.92′E) in the Morehead River catchment; and Wando (08°53.42′S, 141°15.53′E), Weam (08°37.10′S, 141°08.09′E) and Wereave (08°31.25′S, 141°06.33′E) in the Bensbach River catchment (Fig. 1). As standard procedure, villagers were asked for the name of their language group and the names they gave to turtles. Part of the questioning was to determine (a) whether any of the names were generic (for any turtle); (b) whether any two names referred to a single species of turtle, perhaps because of joint use of names from a neighbouring language group; and (c) whether different names were given to different morphotypes (juvenile versus adult) of the same species. Once a set of names was obtained, we matched these against species, by seeking to establish the presence of diagnostic features (without leading – ‘how many claws on the front feet’ rather than ‘does it have four claws on the front feet’) or with the aid of photographs in field guides (Cogger 2000; Iskandar 2000). The names were confirmed when live specimens came to hand. By this procedure, we could identify which species were regularly harvested in the local area, regardless of which species were passed to us for examination. A total of 257 turtles was provided by villagers, and a further 16 were caught by us in funnel traps (after Legler 1960) baited with deer meat. Villagers were paid 2 kina for each turtle from which tissue was taken, and a further 3 kina for allowing examination of gonads to ascertain reproductive status.

Turtles presented for examination were identified with the aid of field guides (Cogger 2000; Iskandar 2000). Sex of adults was determined using external dimorphic characters, particularly the tail, which is much longer in mature males. Each turtle was measured (maximum carapace length, midline plastron length) with vernier calipers (±0.1 mm) and a small sliver of tissue was taken from the clawless digit of a rear foot and preserved in 75% ethanol for DNA analysis. The method and location of capture was requested and recorded.

When a specimen of *Emydura subglobosa*, *Elseya branderhorsti* or *Elseya novaeguineae* was to be killed for immediate consumption, we requested permission to examine its gonads to determine reproductive status (mature, immature) and reproductive condition. Oviducal eggs were counted when present, and egg length and width was measured with vernier calipers (±0.1 mm). Egg mass was estimated using a relationship between linear egg measurements and egg mass developed for Australian turtles:

$$\text{Weight} = \text{Length} \times \text{Width}^2 \times 6.1468 \times 10^{-4} - 0.12$$

(units in grams and millimetres; R^2 = 0.99) using the data of Judge (2001). Also counted were preovulatory follicles, additional developing follicles and fresh corpora lutea on the ovary. Special attention was paid to determining whether there were two or more sets of corpora lutea present, as an indication of multiple clutching (Georges 1983). Males were examined to determine whether the testes were enlarged, pink and vascularised (as an indication of spermatogenesis or spermiogenesis) or if they were small, compact, yellow and lacking vasularisation (indicating quiescence) (Georges 1983). Epididymides were examined to see whether they were straight and translucent (an indication of immaturity), coiled and translucent (an indication of pending maturity), or coiled and white (an indication of maturity).

Details of harvest for trade was gained opportunistically. We recorded the species, the component of the turtle that was traded (live animal, meat, plastron), the buyer, and the amount received for the purchase. This work was undertaken under animal ethics approval CEAE 03/11 (15 August 2005).

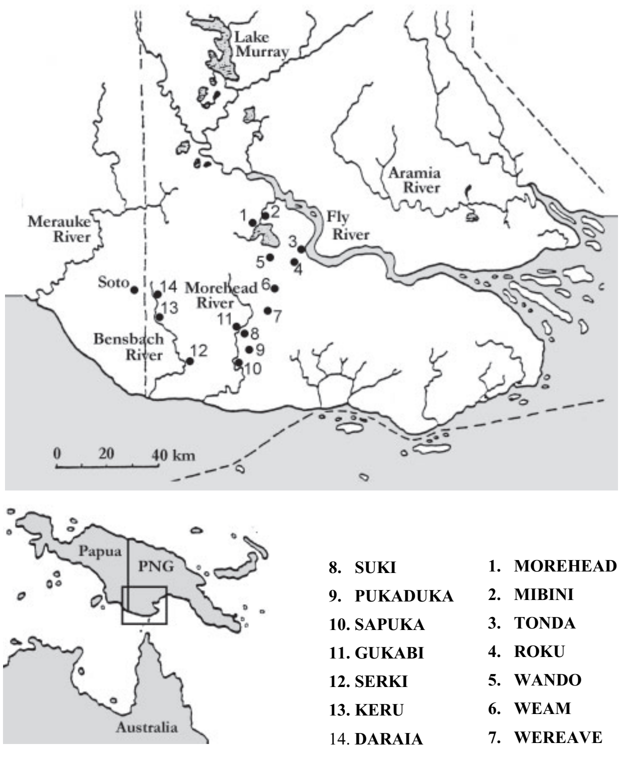

Fig. 1. The study area showing the locations of villages on the Fly, Morehead and Bensbach Rivers where turtles were obtained. More precise locations of collection are given in Table 1.

Results

Turtle diversity

We obtained seven species of freshwater turtle as part of our survey (Table 1, Fig. 2) and reliable reports of an eighth (*P. bibroni*). A possible ninth species could not be identified, and may be new. It resembled most closely *Emydura worrelli* from northern Australia. A dichotomous key to the species of the TransFly region was constructed to resolve difficulties with identification, particularly with *E. branderhorsti* and *E. novaeguineae* as animals of the same size are superficially similar.

Key to the species of TransFly region

1 (a) Forelimbs each with five (5) claws 2
(b) Less than five (5) claws on the front feet 4

2 (a) Cervical scute absent; prominent alveolar ridge on the triturating surface of the upper jaw, corresponding groove on the triturating surface of the lower jaw; pupil indistinct, as iris without a distinct lighter ring bordering the pupil . . . . *Elseya branderhorsti*
(b) Cervical scute present (except rarely); triturating surface simple, without alveolar ridge; iris distinct from pupil . . . 3

3 (a) A horny casque (head shield) on the dorsal surface of the head; a prominent dark spot on each of the costal and vertebral scutes; plastron white, cream or yellow; prominent rounded tubercles of low relief in the temporal region . . . . *Elseya novaeguineae*
(b) Dorsal surface of head covered in skin; carapace clear of regularly arranged spots or, if present, lighter in colour than the surrounding scute; plastron and parts of the ventral surfaces of limbs and tail suffused with red; no prominent rounded tubercles in the temporal region; prominent yellow or cream stripe behind the eye extending to the tympanum; iris with leading and trailing black spots . . . . *Emydura subglobosa*

4 (a) Four (4) claws on the digits of both front and rear feet; shell with cornified scutes 5
(b) Less than four claws on the digits of front and rear feet; shell covered in skin, not cornified scutes; head withdrawn straight back into shell (Cryptodire), not withdrawn sideways 7

5 (a) Head not dorso-ventrally compressed – distance from tip of snout to leading edge of the orbit approximately equal to distance from trailing edge of orbit to tympanum; temporal region with small regular tubercles of low relief; emits pungent odour when distressed . . . . . *Chelodina novaeguineae*
(b) Head dorso-ventrally compressed – distance from tip of snout to leading edge of orbit less than half the distance from orbit to tympanum; temporal region with flat scales of irregular shape and size 6

6 (a) Light patch immediately behind and above the tympanum, running at an angle of ~45° to the horizontal . . . . *Chelodina parkeri*
(b) Not as above . . . . *Chelodina rugosa*

7 (a) Three claws on the front limbs; margin of shell flexible . . . . *Pelochelys bibroni*
(b) Two claws on front limbs; margin of shell rigid . . . . *Carettochelys insculpta*

Questioning on specific names in a local language, followed by matching those names with species, is considered a robust, albeit indirect, method of ascertaining the number of species commonly encountered (Table 2). Where it was the most common species present, *E. branderhorsti* was acknowledged in several languages as the 'regular' turtle by use of the unqualified general word for turtle (fisor, chelba, nthelon or forr). The red coloration of *Emydura subglobosa* resulted in a name (Mani, Maro, Mane, Mare) drawn from the red bark of the red beech tree (*Dillenia alata*) or a name (Anki) drawn from the fruit of the walnut (*Endiandra sp.*) which, when eaten, turn the lips red. The name Kiya Eise used by the Suki people for *Pelochelys bibroni* is a reference to its soft shell margins, whereas its name Sokrere in Arammba (Serki people) means earthquake, a reference to the movement of the floating mats when *P. bibroni* passes underfoot. Budu Susa, used for *Carettochelys*, is a reference to the medial ridge of the posterior carapace (sharp back). The names for *Chelodina novaeguineae* are derived either from its terrestrial habits (m'bro – savannah, magi – land) or the pungent smell it emits when distressed (fasar – smell). Not surprisingly, the long neck of *Chelodina rugosa* and *Chelodina parkeri* is the basis of their common names (kakta, tanfer – long; kun, marr – neck). *C. parkeri* and *C. rugosa* were not distinguished, as they did not to occur in sympatry nor were both within the range of a single language group.

It is clear from the names used in the villages of the three drainages that we visited (Table 2) that turtle species richness was highest in the Fly drainage and lowest in the Bensbach drainage, which is consistent with the species number we recorded for each of these drainages.

Harvest and trade

Freshwater turtles and their eggs were regularly harvested for food by people of all villages we visited. All species are eaten with the exception of *C. novaeguineae*, whose pungent odour discourages many from consuming them. *C. insculpta* and *E. branderhorsti* are favoured by virtue of their large size. Typically, the plastron is removed as one piece to gain access to the meat and entrails. The gut is removed, cleared of contents and cut into small pieces. The gut, liver, heart and meat of the body, limbs, head and neck, the liver and heart are boiled, often with kaukau (yams, *Dioscoria* sp.). Turtles provide an important source of protein to complement agricultural produce, together with rusa deer (*Cervus timorensis russa*), introduced by the Dutch in 1928 (Bowe 1997), pig (*Sus scrofa/celebensis*), wallaby (*Macropus agilis*), cassowary (*Casuarius casuarius*), waterfowl and fish.

Turtles are captured in the rivers and streams on lines baited with deer meat, wallaby meat, fish or cashew nut, or in set gill-nets, particularly *C. insculpta*, *E. branderhorsti* and more rarely, *P. bibroni*. Fishing beneath fruiting riparian vegetation is common, with the falling fruit attracting the turtles in. These turtles are also caught during the nesting season by digging pit traps in favoured nesting areas, into which the turtles fall when leaving the water to nest or when returning to water after nesting. If the eggs are laid, they are located and harvested. In the Suki swamps, nesting areas for *E. branderhorsti* are very limited, and the pit traps are constructed to provide an approach from water with attributes suitable for nesting (cleared of vegetation, upward slope, clay soil) to attract nesting turtles. In the Bensbach River, these turtles are collected primarily in the nesting season by patrolling nesting areas at night. *E. subglobosa* and *C. parkeri* are also captured on baited lines and in gill-nets, but are caught more commonly by hand either when nesting or in shallow water. Several people form a line across a pool and move systematically across collecting the turtles as they collide with legs or arms. *C. rugosa* was caught by probing the mud around the base of *Melaleuca* sp. roots and fallen logs with a steel-bladed arrow or a long bush knife. The aestivating turtle was then dug from the mud. A similar technique was used in the tidal reaches of Tonda Creek, where the turtles had moved from the drying swamps to seek refuge in undercut banks exposed at low tide. *E. branderhorsti* was caught by probing small pools in between the root masses of *Pandanus aquaticus* exposed by the falling tide. *C. novae-*

Table 1. Specimens of freshwater turtle examined from the Fly, Morehead and Bensbach Rivers
There is also a reliable report of *Pelochelys bibroni* in the Fly River, Sapuka

Waterbody	Location	Coordinates		*C. insculpta*	*C. novae-guineae*	*C. parkeri*	*C. rugosa*	*E. brander-horsti*	*E. novae-guineae*	*E. subglo-bosa*	*Emydura* sp.
Fly River											
Gigwa Swamp	Suki village	08°04.00′S	141°51.00′E							1	
Suki Ck	Dibgwagi	08°04.00′S	141°51.00′E			1					
Suki Ck	Guaga Sagwari	08°07.57′S	141°46.00′E	1				1			
Suki Ck	Riti Village	08°04.00′S	141°51.00′E							4	
Suki Ck	Gwibaku	08°04.00′S	141°51.00′E					1			
Suki Ck	Pamena, Pukaduka	08°07.88′S	141°50.00′E	7				1			
Sapuka Region	Sapuka village	08°09.94′S	142°00.03′E	1	1	2					
Burei Ck	Gukabi camp	08°13.42′S	141°59.36′E					4		22	2
Kouma Lagoon	Gukabi camp	08°17.65′S	141°54.60′E					1		5	
Serki Swamp	Serki village	08°14.69′S	141°45.99′E							13	
Serki Swamp	Serki village	08°14.69′S	141°45.99′E			1					
Serki Region	Serki village	08°14.69′S	141°45.99′E			3		1		17	
Kubriki Swamp	Serki village	08°14.69′S	141°45.99′E							1	
Bisereia Swamp	Serki village	08°18.21′S	141°59.00′E							6	
Jikwa Swamp	Serki village	08°18.21′S	141°59.00′E			2				48	1
Kikmatu Swamp	Serki village	08°19.00′S	141°53.04′E			3				1	
Taua Taua Ck	Fosarrdebensam	08°17.43′S	141°52.59′E							1	
Dufideben	Keru village	08°33.78′S	141°42.63′E			10				11	
Morehead River											
Aruba Ck	Keru village	08°26.68′S	141°47.62′E					1	10	2	
Kasar	Keru village	08°33.78′S	141°42.63′E					2			
Kerowanje Ck	Daraia village	08°37.00′S	141°44.08′E					1			
Morehead R.	Roku village	08°42.12′S	141°35.92′E				1	3		3	
Morehead R.	Morehead	08°42.78′S	141°38.37′E					2			
Cikire Swamp	Mibini village	08°50.42′S	141°38.14′E				2				
Morehead R.	Tonda camp	08°55.80′S	141°33.64′E					6			
Tonda Ck	Tonda camp	08°55.80′S	141°33.64′E				9	7		2	
Tonda/Roku Region	Tonda camp	08°55.80′S	141°33.64′E					29			
Bensbach River											
Bensbach R.	Weam village	08°37.10′S	141°08.09′E					1			
Nambilo Swamp, Yambrevber Ck	Weam village	08°44.52′S	141°24.93′E							1	
Mbale Swamp	Wando camp	08°53.42′S	141°15.53′E				1	2			
Wando Region	Wando village	08°53.42′S	141°15.53′E							3	
Bensbach R.	Wando village	08°53.42′S	141°15.53′E					1			

guineae and *C. parkeri* are also caught opportunistically when encountered migrating over land.

All turtles collected during our visit were consumed locally. Some were traded between villagers or at informal markets, but there was no evidence of trade in live animals with the more substantial markets of Daru to the south or Sota to the west. Plastra were retained for trade. All were of value for trade with Indonesia through the border town of Sota, but the clean white plastra of juvenile *E. branderhorsti* yielded the greatest return. The plastra are prized as an ingredient in traditional Chinese medicine, based on centuries of traditional custom (Jenkins 1995). In Sota, plastra fetch ~10 kina per kilogram. Plastra are retained and traded for this market from as far away as Suki, using established trade avenues for deer antlers, but there was no evidence that this opportunity for trade increased harvest rate except at the Papua New Guinea border communities of Wereave and Weam. Here, nesting *E. branderhorsti* were heavily harvested during the breeding seasons of 2004 (300 turtles) and 2005 (60 turtles) for their plastra, though the meat was also

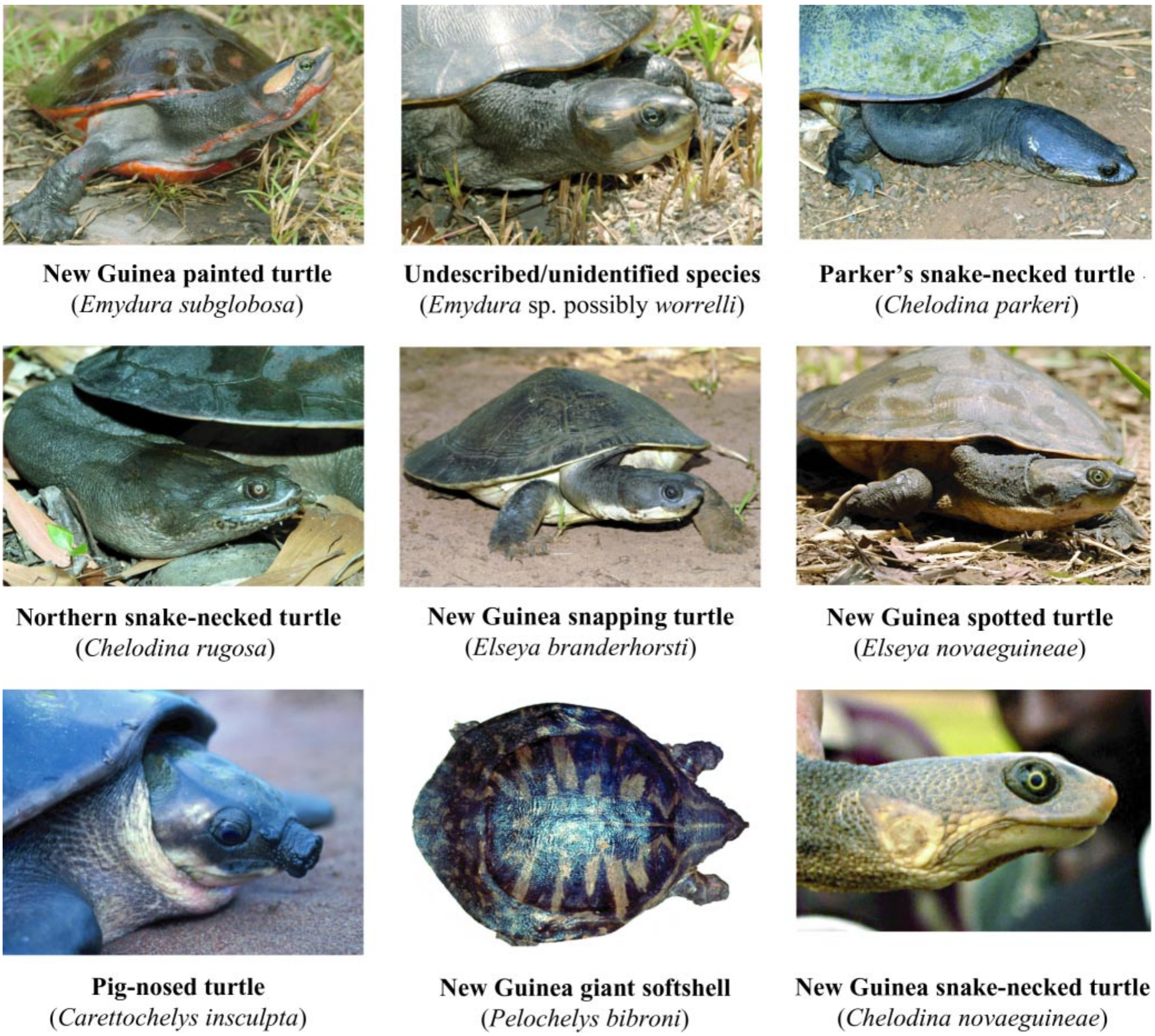

Fig. 2. Photographs of the nine species of freshwater turtle from the TransFly region. The prominent red colouration of *Emydura subglobosa* distinguishes it from the undescribed *Emydura* in which the red colouring is totally lacking. The white patch immediately above and behind the tympanum of *Chelodina parkeri* distinguishes it from *C. rugosa*. Note the absence of a cervical scute in *Elseya branderhorsti* that distinguishes it from *Elseya novaguineae*. The *Pelochelys bibroni* is from Lake Murray, the photograph taken and kindly provided by Anders Rhodin. The photograph of *Carettochelys insculpta* is a file shot taken on the Daly River, Queensland.

consumed locally (Wereave Wildlife Officer, Silas Yanai, personal communication).

Live hatchlings of *E. branderhorsti* once fetched 25 kina per head in Sota, but a flooded market led to a drop in returns to 2.5 kina per head (Silas Yanai, personal communication). Captive breeding of *E. branderhorsti* is being explored in Morehead to capitalise on this opportunity for trade, but is yet to be successful in producing any hatchlings for sale. Harvested eggs were also sold locally, in groups or singly. One egg would typically fetch 10–20 toia, whereas a group of eggs would fetch 1–2 kina.

The income generated by the turtle trade provides important revenue for the purchase of rice, sugar, salt and fuel from Sota.

Habitat and distribution

The freshwater turtles we observed differed considerably in habitat preferences and distribution. *E. branderhorsti* and *C. insculpta* were primarily both river turtles, but we found them also in large permanent lakes and lagoons of the Suki/Aramba swamps (e.g. Kouma Lagoon and Lake Tininseapu/Xanxu). *C. insculpta* was most common in the Fly River system and associated tributaries and lagoons, and infrequently captured in the smaller Morehead and Bensbach drainages. *E. branderhorsti* was most abundant in tributaries of the Morehead River (e.g. Tonda Creek, 08°55.80′S, 141°33.64′E), where fallen logs and undercut banks provided adequate cover, though substantial populations occurred also in the main channel of the Bensbach River, near Wereave (08°31.25′S, 141°06.33′E). *E. subglobosa* was found throughout these river systems, but is most abundant in the freshwater swamps and seasonally inundated grasslands and wetlands. Lowest densities were in the open water associated with these swamps. *C. parkeri* and *C. rugosa* are superficially similar (indeed, they are not distinguished in local language), but *C. rugosa* is restricted to the seasonally ephemeral *Melaleuca* swamps of the southern coastal regions where it aestivates beneath the mud during the annual dry or retreats to adjacent streams. In contrast, *C. parkeri* was collected in the extensive swamps associated with the Fly River where it occupies habitat similar to that of *E. subglobosa*. These swamps and associated lagoons often contain water all year round, and are associated with permanent water lagoons. The habits of *C. novaeguineae* are poorly known, but this species spends extensive periods on land, aestivating in the dry season beneath leaf litter. The specimen we obtained was caught in terrestrial habitat.

Reproduction

Emydura subglobosa

Female *E. subglobosa* mature at a carapace length (CL) of 14–15 cm. The smallest mature female identified in the dissections had a CL of 15.33 cm and the largest immature female had a CL of 14.1 cm. Two mature males that were dissected had CL of 14.4 and 16.2 cm, whereas two of the immature males that were dissected had CL of 11.9 and 15.1 cm. The latter had translucent epididymides, but they were coiled, indicating that sexual maturity was imminent. Males therefore also mature in the range 14–15 cm CL. This range is consistent with data on the maturity of males based on the external characteristic of tail length. The maximum observed size for females of 24.6 cm CL was greater than that for males at 17.4 cm CL.

The species lays white, hard-shelled (calcareous), ellipsoid eggs typical of *Emydura* in general. In total, 26 (39.4%) of the 66 mature females palpated for eggs were gravid at the time of our sampling (2–18 September). Multiple clutching was almost universal among the specimens examined by dissection. Of the 11 gravid animals for which full data were available, 8 had corpora lutea on the ovary in two sets – one corresponding in number to the eggs in the oviducts and one set of smaller structures corresponding to a previously laid

Table 2. Names for freshwater turtles from the eight language groups we encountered during the study
Language groups were confirmed by reference to the Ethnologue (Gordon 2005) and other reports (Wurm and Hattori 1981; Ayres 1983). These names complement those published by Rhodin *et al*. (1980)

	Fly River		Fly/Morehead	Morehead River		Bensbach River		
	Suki (Suki, Puka-duka)	Arammba (Serki)	Neme (Keru)	Nama Wat (Daraia)	Nama Was (Mibini)	Guntai (Wando)	Blafe (Wereave)	Rema (Metafa)
Elseya branderhorsti	Medepka	M'bay	Fisor	Fisor Fifi	Rawk Rawk Sutafnarr	Chelba	Nthelon	Forr
Elseya novaeguineae			Fisor					
Emydura subglobosa	Tegma or i Anki Kan	Maro Kani	Ngani Fisor	Mani Fisor	Mare Sutafnarr	Mare Chelba	Ntharase or Mari Nthelon	Mari Forr
Chelodina parkeri	Kunkakta	Kunkakta						
Chelodina rugosa			Tomba Kofe Fisor	Mbuirr	Weya Sutafnarr	Mbroyer	Fisuwar	Tanfer Marr Forr
Chelodina novaeguineae	Magipinini	Fasar Kani		Mboro arr Garr	Mbro arr			
Carettochelys insculpta	Budu Susa	Budu Susa						
Pelochelys bibroni	Kiye Eise	Sokrere						
Emydura sp. aff. *worrelli*	Riskap Kani							

clutch (Table 3). Six of these had a set of preovulatory follicles and often also a set of additional developing follicles, indicating that another clutch or two clutches were to be laid in the future. Overall assessment indicated that one turtle would have laid one clutch, four would have laid two clutches, six would have laid three clutches, and eight would have laid four clutches in the season.

Mean egg length was 35.0 ± 0.05 mm, mean egg width was 19.0 ± 0.02 mm and estimated mean egg weight was 7.68 ± 0.20 g (n = 13 clutches). Eggs ranged in length from 28.9 to 39.1 mm and in width from 17.0 to 20.6 mm. Eggs within a single clutch varied by as much as 7.1 mm in length and 3.0 mm in width. Only egg width was significantly related to maternal body size ($F = 8.15$, d.f. = 1,10, $P < 0.02$), but the positive relationship was weak ($R^2 = 0.44$).

Clutch size varied from 4 to 11 eggs (n = 12) with an average clutch of 7 eggs. Clutch size was strongly positively related to maternal body size, as indicated by plots of egg number from each of egg counts, counts of corpora lutea on the ovary and counts of preovulatory follicles on the ovary (Fig. 3). Clutch size could be predicted from maternal CL (in centimetres) by the relationship

$$\text{Clutch size} = 1.0 \times \text{CL} - 12.2 \qquad (R^2 = 0.8),$$

established from data taken from observed clutches only. Clutch mass averaged 51.1 ± 5.2 g (n = 13) and neither clutch size ($P = 0.44$) nor clutch mass ($P = 0.36$) were related to the number of clutches to be laid by the female in the season.

From these data, we can confirm reports from local villagers that *E. subglobosa* is a late dry-season breeder that nests from August through to October. The species nests in moist peaty soils of the floating mats and levies in the extensive freshwater swamps in which it is found (Fig. 4). Exposed areas, in some cases created by small fires set by hunters, are favoured locations. The path of nesting females in the vegetation can clearly be seen, and assists the collection of eggs by the local people. Many nests are destroyed by unidentified predators soon after laying, leaving tell-tale eggshells.

Elseya branderhorsti

The breeding season of *E. branderhorsti* was nearing completion at the time of sampling. Only 6 (23.1%) of 26 mature females palpated were gravid. The species also lays white, hard-shelled ellipsoid eggs, but they were much larger than those of *E. subglobosa.* Mean egg length was 47.0 ± 0.05 mm, mean egg width was 27.0 ± 0.05 mm and estimated mean egg weight was 9.00 ± 0.90 g (n = 3 clutches). Eggs ranged in length from 43.4 to 52.6 mm and in width from 25.1 to 29.8 mm. Eggs within a single clutch varied by as much as 9.2 mm in length and 4.6 mm in width.

Clutch size varied from 15 to 32 eggs (n = 8) with an average clutch size of 23.5 eggs. Clutch size was not related to maternal body size, though the range of female sizes examined may not have spanned the range of mature female sizes (CL 36.7–44.5 cm). Clutch mass was estimated to average 206.5 ± 57.6 g (n = 3).

Local people who hunt the gravid females during the nesting season report nesting in July and August, with two peaks in nesting activity, suggesting double clutching. The protracted nesting season, which, from our data, extends into early September, is also suggestive of multiple clutching. However, we could find no evidence of double clutching when examining ovaries (n = 8). No ovaries contained preovulatory or developing follicles or more corpora lutea than there were eggs in the oviducts. If there is double clutching, then the internesting period must be of sufficient duration for the corpora lutea from the first clutch to fully regress before the second clutch is laid.

Elseya branderhorsti deposits its nests in soil on banks adjacent to the streams or swamps it inhabits. At Kouma Swamp in the Fly drainage (08°17.65′S, 141°54.60′E, near Gukabi), the turtles moved up slope until vegetation blocked progress or the land leveled to deposit their nests in clay soil. At Tonda Creek in the Morehead drainage (08°55.80′S, 141°33.64′E, near Morehead), the females nested in small shallow offstream basins above the high-tide mark but that were likely to be inundated with the first rise in water levels at the onset of the wet season. The soil was loam overlaid by leaf litter and had ~40% overstorey cover.

Elseya novaeguineae

The breeding season for *E. novaeguineae* had not yet begun at the time of sampling. The largest immature female (n = 3) had a carapace length of 16.9 cm and the smallest mature female (n = 4) had a carapace length of 18.7 cm suggesting a size at maturity of 17–18.5 cm for females. None of the four mature females examined were gravid, nor did their ovaries have corpora lutea, though all had preovulatory follicles, indicating that breeding was imminent. Three of the four mature females had a clear set of developing follicles in addition to the preovulatory follicles, strongly suggesting that they would double clutch in the coming season. Average clutch size was estimated from these developing and preovulatory follicles to range from 9 to 14, with an average of 12 eggs. From these data, we conclude that the nesting season for *E. novaeguineae* is late September and October. Nothing is known of its egg characteristics.

Morphometric measurements for all the turtles examined in this study are shown in Table 4.

Discussion

This paper provides new information on a poorly studied group of freshwater turtles from the remote Western Province of Papua New Guinea. The distribution of *C. parkeri* is extended with new locality data for the swamps south-west of the Fly River. It was previously recorded from the freshwater swamps associated with Lake Murray and Aramia River regions (Rhodin and Mittermeier 1976;

Table 3. Reproductive parameters for three species of freshwater turtle from the TransFly region

Follicles were deemed to be preovulatory when they contained yolked ova of a size comparable to the yolk in shelled eggs. Developing follicles were enlarged, yellow, but not yet of preovulatory size. Both preovulatory and developing follicles tended to be present in size classes, presumably corresponding to pending clutches of eggs. Atretic follicles were reddish or pink in colour, resulting from the invasion of blood vessels and resorption of yolk (Georges 1983). Corpora lutea occurred in sets corresponding to the most recently laid clutch of eggs, and previously laid clutches of eggs. The first set could be reliably counted; presence of the second set was noted (+). An overall assessment of the number of clutches to be laid in the season is given as three digits (e.g. 1-1-2). The first digit gives the number of clutches laid before dissection (0 or 1), based on the number of sets of corpora lutea present minus those associated with oviducal eggs. The second digit indicates whether a clutch of eggs was in the oviducts at the time of dissection. The third digit gives an estimate of the number of clutches yet to come, based on counts of preovulatory follicles and the presence or absence of an additional set of developing follicles. Abbreviations: CL, maximum carapace length; PL, mid-line plastron length

Date	Location	CL maximum (cm)	PL mid-line (cm)	Oviducal eggs	Sets of corpora lutea	Pre-ovulatory follicles	Additional developing follicles	Atretic follicles	Mean egg length (mm)	Mean egg width (mm)	Mean egg mass (g)	No. of clutches	Source
Emydura subglobosa													
4 Sept. 2005	Kouma Lagoon	–	–	7	–	–	–	–	33.3 (32.6–34.2)	18.6 (18.0–19.1)	7 (6.5–7.3)	–	Nest
7 Sept. 2005	Serki Swamps	15.3	12.3	0	1 (3,0)	2	2	0	–	–	–	1-0-2	Dissection
7 Sept. 2005	Serki Swamps	15.4	12.3	4	1 (4,0)	1	2	0	31.9 (30.9–33.2)	18.1 (17.7–18.3)	6.3 (5.8–6.6)	0-1-0	Dissection
7 Sept. 2005	Serki Swamps	15.7	12.6	0	1 (5,0)	5	3	0	–	–	–	1-0-1	Dissection
7 Sept. 2005	Serki Swamps	16.7	13.5	4	1 (4,0)	4	0	0	35.3 (33.6–36.3)	18.6 (18.1–19.1)	7.4 (6.9–8.0)	0-1-1	Dissection
7 Sept. 2005	Serki Swamps	17.6	14.2	4	2 (4,+)	5	5	0	36.9 (35.5–38.6)	19.1 (18.9–19.2)	8.1 (7.8–8.6)	1-1-2	Dissection
7 Sept. 2005	Serki Swamps	17.8	14.4	0	1 (5,0)	6	4	0	–	–	–	1-0-2	Dissection
7 Sept. 2005	Serki Swamps	18.0	14.5	0	2 (4,+)	5	5	0	–	–	–	2-0-2	Dissection
7 Sept. 2005	Serki Swamps	18.0	14.6	7	2 (7,+)	7	6	0	33.6 (31.9–34.9)	18.5 (18.1–18.9)	6.9 (6.7–7.1)	1-1-2	Dissection
7 Sept. 2005	Serki Swamps	18.5	15.0	5	1 (5,0)	7	7	0	38.8 (38.2–39.1)	19.2 (18.7–19.7)	8.7 (8.2–9.1)	0-1-2	Dissection
7 Sept. 2005	Serki Swamps	18.8	15.2	0	2 (+,+)	8	7	0	–	–	–	2-0-2	Dissection
7 Sept. 2005	Serki Swamps	19.2	15.5	4*	2 (5,+)	5[A]	4[A]	0	33.8 (33.2–34.4)	19.8 (19.6–20.1)	8.0 (7.9–8.2)	1-1-2	Dissection
7 Sept. 2005	Serki Swamps	19.6	15.9	7	2 (7,+)	8	6	0	35.6 (33.2–38)	18.4 (18–19.2)	7.3 (6.8–7.5)	1-1-2	Dissection
7 Sept. 2005	Serki Swamps	20.7	16.8	8	2 (6,+)	6	2	0	36.1 (35.2–36.9)	19.4 (19.2–19.7)	8.2 (8.1–8.4)	1-1-1	Dissection
7 Sept. 2005	Serki Swamps	20.8	16.9	8	1 (8,0)	11[B]	7[B]	0	36.3 (35.2–37.8)	20.0 (19.4–20.2)	8.7 (8.4–8.9)	0-1-2	Dissection
7 Sept. 2005	Serki Swamps	21.0	17.1	0	2 (9,+)	10	7	0	–	–	–	2-0-2	Dissection
7 Sept. 2005	Serki Swamps	21.8	17.7	0	1 (6,0)	13	0	0	–	–	–	1-0-1	Dissection
9 Sept. 2005	Tonda Creek	22.0	17.9	9	2 (8,+)	8	3	0	33.9 (28.9–36.0)	19.4 (17.0–20.0)	7.7 (5.0–8.4)	1-1-1	Dissection
13 Sept. 2005	Dufideben Swamp	19.4	15.7	8	2 (8,+)	3	0	2	36.7 (35.8–38.4)	18.3 (17.6–19.7)	7.4 (6.7–8.9)	1-1-0	Dissection
13 Sept. 2005	Morehead River	21.5	17.5	11	2 (11,+)	9	> 6	0	33.1 (32.1–34.1)	20.1 (18.6–20.6)	8.1 (6.9–8.5)	1-1-2	Dissection
Elseya branderhorsti													
7 Sept. 2005	Serki Swamps	38.4	31.5	32	1 (19,0)	0	0	2	47.9 (44.6–51.1)	27.2 (25.2–29.8)	21.6 (18.7–25.7)	0-1-0	Dissection
8 Sept. 2005	Tonda Creek	36.7	30.1	0	1 (10,0)	0	0	a+	–	–	–	1-0-0	Dissection
9 Sept. 2005	Tonda Creek	41.9	34.0	0	1 (23,0)	0	0	a+	–	–	–	1-0-0	Dissection
9 Sept. 2005	Tonda Creek	42.3	34.0	0	1 (27,0)	0	2	a+	–	–	–	1-0-0	Dissection
9 Sept. 2005	Tonda Creek	42.2	36.4	0	1 (27,0)	0	0	a+	–	–	–	1-0-0	Dissection
10 Sept. 2005	Morehead River	42.9	36.0	20	1 (20,0)	0	0	2	46.9 (43.4–52.6)	27.7 (26.8–28.9)	22.1 (19.4–25.3)	0-1-0	Dissection
2 Sept. 2005	Tonda Creek	–	–	15	–	–	–	–	46.3 (44.6–48.9)	26 (25.1–27.2)	19.2 (18–20.2)	–	Nest
14 Sept. 2005	Kouma Lagoon	40.5	32.6	0	1 (21,0)	0	0	0	–	–	–	1-0-0	Nesting, eggs eaten
4 Sept. 2005	Morehead River	44.5	35.4	23	–	–	–	–	–	–	–	0-1-0	Nesting, eggs eaten
Elseya novaeguineae													
13 Sept. 2005	Aruba Creek	28.0	21.0	0	0	14	12	0	–	–	–	0-0-2	Dissection
13 Sept. 2005	Aruba Creek	25.8	20.5	0	0	13	5	0	–	–	–	0-0-2	Dissection
13 Sept. 2005	Aruba Creek	23.0	18.7	0	0	13	0	0	–	–	–	0-0-1	Dissection
13 Sept. 2005	Aruba Creek	23.4	19.3	0	0	11	9	0	–	–	–	0-0-2	Dissection

[A]Only one functional ovary.

[B]Distinction between pre-ovulatory and other follicles unclear.

Iverson 1992). We confirm its presence in similar habitat south and west of the Fly River (the TransFly region), but within the Fly drainage basin. Our study confirms that *C. rugosa* (formerly *C. seibenrocki*) in the Western Province is restricted to the coastal swamps. Its habitat is consistent with that found in Australia – seasonally dry *Melaleuca* swamps where it survives the dry season by burying in mud or seeking refuge in adjacent small permanent streams (in this case, tidal streams). This habitat is very different from the swamps occupied by *C. parkeri*, dominated by inundated grasses and extensive floating mats, subject to seasonal reduction but complete drying only in exceptionally dry seasons. It appears that habitat preferences maintain effective spatial separation between these two closely related species (Rhodin and Mittermeier 1976).

Carettochelys insculpta is reported to be widespread in southern New Guinea, but in the region we visited substantial populations occurred only in the Fly River drainage. It was occasionally caught in the Morehead and Bensbach drainages but, with the exception of Daraia, the villagers there do not have a name for it. When it has been caught, it is so unfamiliar that it has been released in the belief that it is a turtle spirit. In northern Australia, *C. insculpta* is sometimes caught in minor drainages such as the Adelaide River, but substantial populations occur only in the major drainages of the Daly River and Alligator Rivers region. It appears that the same may be true in New Guinea, with substantial populations in the Fly, Kikori and Purari (Georges and Rose 1993) and exceptionally low populations in smaller rivers such as the Morehead and Bensbach. It is impossible to judge whether this is due to harvesting of populations, unsustainable by virtue of smaller population sizes, as some local people believe. *P. bibroni* is widespread but rare in southern New Guinea (Rhodin *et al*. 1993) so our failure to obtain any specimens was expected.

In this paper we provide new information on the reproduction of three of the eight species we collected. *E. branderhorsti*, *E. novaeguineae* and *E. subglobosa* were selected because they were engaged in breeding activity at the time of our visit. Reproductive patterns in chelid turtles have been classified as temperate (typically nesting at the time of the austral spring and early summer) and tropical (typically nesting at the time of the austral winter) (Legler 1981, 1985). Both patterns were evident in the species we examined. *E. branderhorsti* exhibited the tropical pattern also expressed in other species of the *Elseya dentata* group (*sensu* Georges and Adams 1992, 1996) and the *Chelodina rugosa* group (*sensu* Georges *et al*. 2002). *E. subglobosa* and *E. novaeguineae* exhibited the temperate pattern also expressed in *Emydura* generally, *Elusor*, *Pseudemydura*, *Rheodytes*, the *Chelodina longicollis* group and the *Elseya latisternum* group. The multiple clutching demonstrated in *E. subglobosa* and *E. novaeguineae*, and not eliminated as a feature of the biology of *E. branderhorsti*, is typical of chelid turtles

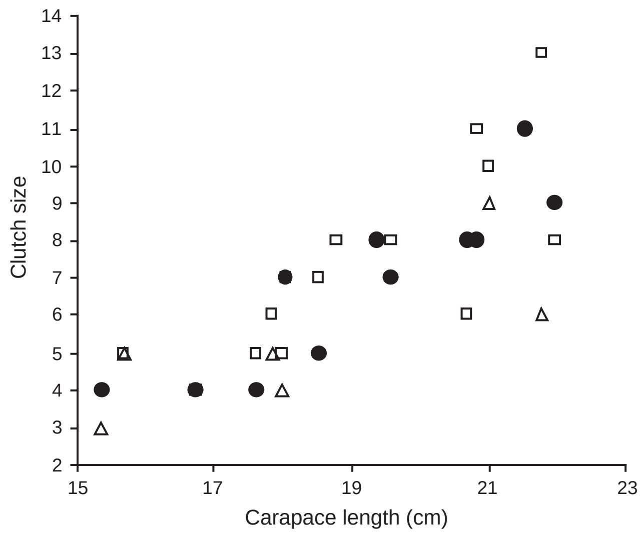

Fig. 3. Clutch size as a function of carapace length for *Emydura subglobosa*. Clutch size was estimated from counts of oviducal eggs (●), corpora lutea (△), and preovulatory follicles (□).

residing at latitudes with relatively long activity seasons (Georges 1983; Legler 1985).

Exploitation of freshwater turtles in New Guinea is thought to have increased in recent times (Rose *et al*. 1982; Georges and Rose 1993). More people moved to live along riverbanks as tribal warfare ceased, and the population of Papua New Guinea has doubled since 1971. Modern technologies have improved access, especially the introduction of outboard motors, and modern fishing gear has increased catch rates. In the Western Province, the impact of these factors is greatly moderated by the scarcity and cost of fuel and the lack of fundamental infrastructure to facilitate travel and transport of goods. The Asian turtle trade, feeding new and expanding markets in China, is resulting in often dra-

Fig. 4. Typical nesting habitat for *Emydura subglobosa* in the Suki/Aramba Swamps. In this case, the nest was deposited in moist peat on a floating mat (arrow). The eggs and the substrate in which they were laid are shown as an inset. Photos: 5 September 2005, late dry season.

Table 4. Maximum carapace length and midline plastron length of specimens of each species represented in our sample
n, sample size

Species	Sex	Maximum carapace length (cm)			Mid-line plastron length (cm)		
		Mean ± s.e.	Range	*n*	Mean ± s.e.	Range	*n*
Carettochelys insculpta	Female	37.1 ± 11.22	29.2–45.1	2	29.2 ± 7.31	24.0–34.3	2
	Male	30.2 ± 5.68	23.7–41.3	7	24.3 ± 4.37	18.7–32.3	7
Chelodina novaeguineae	Male	14.3		1	11		1
Chelodina parkeri	Female	28.9 ± 2.69	25.2–35.3	15	22.3 ± 1.69	19.8–25.2	15
	Male	25.4 ± 1.53	23.4–27.4	7	19.2 ± 1.52	17.3–21.2	7
Chelodina rugosa	Female	30.3 ± 1.26	28–32	7	23 ± 1.14	21.3–24.5	7
	Male	25.1 ± 1.32	23.1–26.7	5	18.3 ± 0.79	17.4–19.6	5
Elseya branderhorsti	Female	41.3 ± 3.91	29.8–48.1	22	33.7 ± 3.21	25–39	22
	Male	36.2 ± 2.62	30.6–40.2	21	29.1 ± 1.82	25.3–32	21
	Juvenile	19.7 ± 4.22	13.3–30.5	18	16.2 ± 3.62	10.2–25.3	18
Elseya novaeguineae	Female	25 ± 2.29	23–28	4	19.9 ± 1.04	18.7–21	4
	Male	20.1 ± 0.78	19.3–20.9	3	15.9 ± 0.62	15.3–16.6	3
	Juvenile	20.6 ± 1.34	19.1–21.6	3	16.2 ± 1.06	15–16.9	3
Emydura subglobosa	Female	18.9 ± 2.3	15.2–25.5	71	15.2 ± 1.96	12.1–20.9	71
	Male	14.9 ± 1.18	13.3–17.3	20	11.8 ± 0.94	10.5–13.9	20
	Juvenile	14.6 ± 1.48	10.4–17.4	46	11.6 ± 1.25	8.2–14	46
Emydura sp. aff. *worrelli*	Female	20.9		1	16.7		1

matic declines in freshwater turtle populations in the broader region (van Dijk *et al*. 2000), including neighbouring Indonesia which has legalised trade and set generous quotas for a range of species common to both Papua New Guinea and Indonesian Papua (Samedi and Iskandar 2000). Prices of up to $US2000 for specimens of the chelid turtle *Chelodina mccordi* coupled with a legal quota of 450 animals rapidly sent this species to commercial extinction and threatened it with biological extinction in its natural habitat on Roti (Rhodin and Genorupa 2000; Samedi and Iskandar 2000). High commercial value for species found in Papua New Guinea provides motivation and proximity provides opportunity for illicit trade in turtles across the Papua New Guinea/Indonesian border, trade that may lead to local population declines. Such trade has been well documented (Rhodin and Genorupa 2000), and is a major concern to the wildlife authorities in Papua New Guinea (Barnabas Wilmot, personal communication, 2005). In the regions we visited, exploitation at a rate driven higher by trade opportunities with Indonesia was limited to villages close to the Indonesian border. The Papua New Guinea Department of Environment and Conservation has received applications to legalise turtle trade, in much the same way as harvest trade in *Crocodylus novaeguineae* is legal and regulated (Hall 1990). There is insufficient demographic information on any New Guinea turtle species to make a reasoned judgment on the level of harvest that would be sustainable. Nor is there sufficient information on captive rearing for most species, and where it is available (e.g. for *C. rugosa*: Fordham *et al*. 2004), it is not accessible by local villagers. These knowledge gaps need to be addressed and factored in to management plans that are implemented before local populations can capitalise on the commercial opportunities provided by the turtle fauna without risking collapse of the resource and the implications for their concurrent subsistence economy that would follow.

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