

Twice every second year: reproduction in the pig-nosed turtle, *Carettochelys insculpta*, in the wet–dry tropics of Australia

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Abstract

The reproductive biology of female pig-nosed turtles *Carettochelys insculpta* was studied for 4 years in the wet–dry tropics of northern Australia. Females matured at around 6 kg body mass (38.0 cm curved carapace length, 30.5 cm plastron length). Turtles produced egg sizes and clutch sizes similar to that of other turtle species similar in size. Turtles reproduced every second year, but produced two clutches within years, about 41 days apart. Thus, it appeared that females were energy limited, possibly due to the low available energy content of the dry season diet (aquatic vegetation). Life-history theory predicts that some costly behaviour associated with reproduction exists, such that by skipping years turtles could reduce that cost and put the savings into future reproduction. Previous work revealed no behaviour associated with reproduction in the population. Within years, clutch mass did not differ between early (first) and late (second) clutches. However, early clutches tended to have more eggs per clutch but smaller eggs than late clutches, a new finding for turtles that has been demonstrated in lizards and other animals. Because the study spanned both years with ‘big’ and ‘small’ wet seasons, we were able to examine how the magnitude of the wet season influenced reproductive characteristics. Following big wet seasons, turtles produced larger, heavier, and more eggs per clutch than they did after small wet seasons. Relationships among body size, egg size and clutch size were evident after two big wet seasons but not apparent after two small wet seasons. Collectively, annual variation in reproductive characteristics and current life-history theory suggest that a big wet season is a time of high energy accumulation for the turtles.

Key words: reproductive frequency, clutch size, egg size, wet–dry tropics, biennial reproduction, *Carettochelys insculpta*

INTRODUCTION

Reptiles are ideal for the study of reproductive output and trade-offs between offspring size and number (Elgar & Heaphy, 1989; Gregory & Skebo, 1998). This is partly owed to their general lack of parental care after hatching or birth. Among reptiles the lack of parental care is most pronounced in turtles, which typically offer no maternal contribution after provisioning yolk to the eggs and choosing a nest site.

Patterns of reproduction in turtles have emerged, such as a negative correlation between body-size adjusted clutch size and egg mass, and the negative correlation between clutch frequency and latitude (Elgar & Heaphy, 1989; Iverson *et al.*, 1993). However, interpreting these patterns in a natural context can be complicated by environmental factors and physical constraints (Olsson & Shine, 1997a). Reproductive output can be influenced by

food availability and rainfall (James & Whitford, 1994), or by morphological constraints such as size and shape of the abdominal cavity (Vitt & Congdon, 1978; Shine, 1988, 1992), or size of the pelvic girdle through which eggs pass (reviewed in Clark, Ewert & Nelson, 2001). In particular, local environmental conditions can often dictate the specifics of reproductive output through their effects on rates of resource acquisition (Kuchling, 1999). Investigating the interactions between environmental conditions and reproduction is necessary to develop an understanding of how reproductive output contributes to life-history evolution (van Noordwijk & de Jong, 1986; Bernardo, 1996; Roosenberg & Dunham, 1997).

In practice, turtles facing annual variation in environmental conditions resulting in low energy acquisition can: (1) adjust reproductive output by reducing clutch frequency (Turner, Medica & Lyons, 1984; Bjørndal, 1985; Iverson, 1991a), clutch size and/or egg size (Swingland & Coe, 1978; Roosenberg & Dunham, 1997); or (2) defer laying eggs completely (Nieuwolt-Dacanay, 1997; Kuchling, 1999). However, few studies on turtles have linked environmental variation to reproductive characteristics (reviewed in Kuchling, 1999).

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Phenotypic plasticity in reproductive traits is likely to be more pronounced in species exposed to high or extreme annual or seasonal variation in environmental factors dictating food acquisition. One such system is the wet-dry tropics of northern Australia, which is characterized by a mean monthly rainfall of < 7 mm from May to September, rising to a peak monthly average of 284 mm in February.

We studied the ecology and sex determination in the pig-nosed turtle *Carettochelys insculpta* for 4 years in the wet-dry tropics of northern Australia. In particular, we were interested in the previously unknown female reproductive biology (Heaphy, 1990). Because the study spanned both years with 'big' and 'small' wet seasons, we were able to ask: how might the wet-dry climate shape the reproductive biology of this unique species? Specifically, how did reproductive characteristics relate to the magnitude of the wet season prior to reproduction? The study was also designed to answer fundamental questions on reproduction in *C. insculpta*, such as: what variation exists in reproductive frequency, clutch size, clutch mass and egg size?; what relationships exist among clutch characteristics?; at what size do females mature?

Two findings on the reproductive biology of female *C. insculpta* were of particular interest: biennial reproduction with double clutching and a seasonal change in egg and clutch size. We discuss these findings within a broader context of current life-history theory.

METHODS

The pig-nosed turtle is the sole surviving species of a once widespread family (Carettochelydidae) of turtles (Georges & Wombey, 1993), now restricted to New Guinea and the wet-dry tropics of northern Australia (Georges & Rose, 1993). Thus, its biology is of considerable interest due to both its restricted geographic distribution and taxonomic position. In Australia this freshwater turtle is found in a few rivers in the Top End Region of the Northern Territory (Georges & Rose, 1993; Georges, Rose & Doody, 2003).

We studied *C. insculpta* in the Daly River, a spring-fed system characterized by shallow depths and clear water during the dry season (May–October), and deep turbid water during the wet season. *Carettochelys insculpta* nest in the dry season (Georges & Rose, 1993). Data were collected as part of a sex determination study which spanned 3 dry seasons, from 1996 to 1998.

The study area was a 30 km stretch of the Daly centred around Oolloo Crossing (14° 04' 40" S, 131° 15' 00" E), Northern Territory (NT). The climate is typical of the wet-dry tropics of northern Australia (Taylor & Tulloch, 1985) with a mean monthly rainfall < 7 mm from May to September, rising to a peak monthly average of 284 mm in February (Stn 014139/014941, Oolloo, 1962–85). Mean monthly maximum air temperatures range from 30.9 °C in June to 36.8 °C in October. Water flows continuously through the study site throughout the year, with water

levels rising to an average peak of 13.6 m (5.8–21.7 m) above dry season levels in March.

We captured turtles nearly every day from August to October 1996 and from July to October in 1997–98. Turtles were captured with dipnets from a motorboat, by snorkeling, and with baited hoopnets. Captured turtles were measured, weighed and females were X-rayed for the presence of shelled eggs using a portable X-ray machine (EXCELRAY®). Radiographs were developed in a makeshift darkroom in the field. Turtles were marked with passive transponder (PIT) tags and with cattle ear tags, the latter of which were attached by drilling a hole in the rear carapacial edge. Cattle ear tags allowed identification from the boat. Turtles were held in a large tub (2000 l) and released within 24 h of capture.

Clutch frequency (within and among years) was determined by: (1) compiling X-ray records of individuals throughout the 3-year study; (2) by determining the proportion of gravid turtles during the period in which turtles were found to be gravid. Radiograph histories were considered to be sufficient for determining within-year clutch frequency when the interval between successive radiographs for an individual was < 12 days. This number was based on data from 2 turtles in which both the egg-shelling date and the subsequent nesting date were known. In 5 turtles, X-rays revealed that the eggs were in the process of being calcified, as evidenced by faint images of the eggs (see also Turner *et al.*, 1986). Fresh nests with known laying dates were subsequently found for 2 of these turtles, 17 and 18 days after the eggs were being calcified. Thus, we estimated conservatively that X-rays every 12 days would ensure that a complete reproductive history was known. Repeated X-rays for the same individuals allowed us to estimate minimum egg retention times for some individuals. Size at maturity for female *C. insculpta* is defined herein as the size of the smallest gravid female.

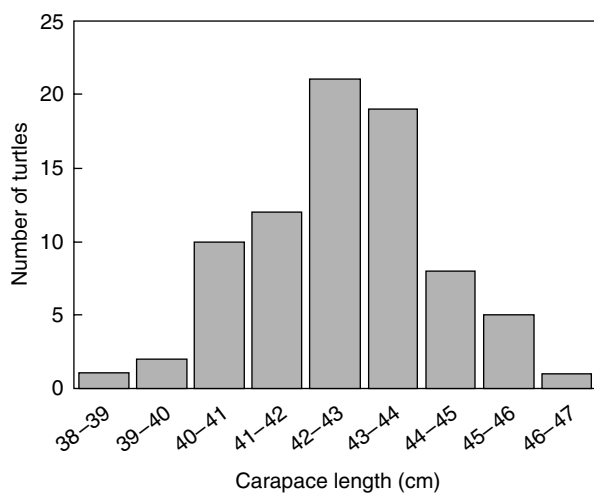
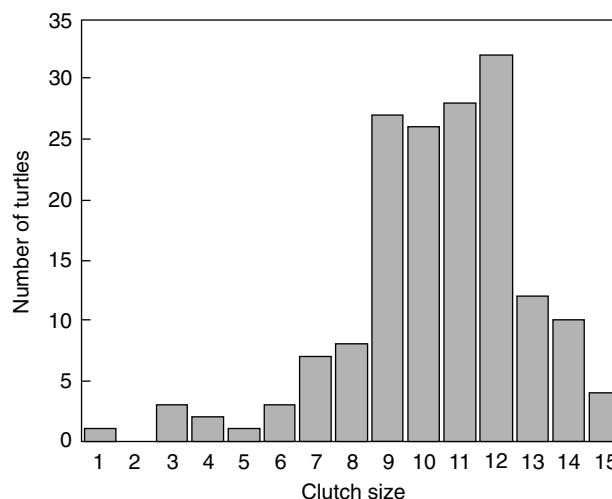
In Australia, *C. insculpta* nests on sandy banks and beaches adjacent to the river (Georges, 1992; Georges & Rose, 1993). We surveyed for nests daily by boat, and nests were found by noting tracks in the sand and probing for the eggs with a spring steel rod. Eggs were carefully removed from each nest and counted, weighed and measured. *Carettochelys insculpta* lays eggs that appear spherical, but are actually slightly oblong or elongate. We measured egg length and width with calipers to the nearest 0.05 mm. Eggs were then returned to their original depths and positions in the nest. Datalogger probes were placed in most nests to measure continuous temperatures for a concurrent study.

Mean inter-nesting intervals were determined by subtracting the mean/median nesting date of first clutches from that of second clutches. This was appropriate because a distinct bimodal temporal distribution of nests was found (pers. obs.).

We used mean monthly river levels as an index of the magnitude of each wet season during the study years. River stage data were from Dorisvale Crossing (60 km upstream of the study area), and are routinely collected by Northern Territory Water Resources. To assess how typical the size of the wet season was, these data were compared to

Table 1. Annual variation in reproductive characteristics of *Carettochelys insculpta*. Data are means \pm 1 SD, except egg size data, which are grand means \pm 1 SE. Sample sizes (number of clutches) are in parentheses. Inter-nesting intervals are presented as means/medians

Attribute	1996	1997	1998	All years
Nests (<i>n</i>)	65	51	75	191
Percentage gravid	51 (83)	36 (59)	42 (55)	44.0 (197)
Inter-nesting interval (days)	36/36 (57)	46/48 (38)	42/46 (56)	40/42 (145)
Egg length (mm)	39.2 \pm 0.15 (47)	39.1 \pm 0.74 (47)	40.2 \pm 0.18 (69)	39.6 \pm 0.21 (156)
Egg width (mm)	38.3 \pm 0.15 (47)	38.8 \pm 0.14 (47)	38.9 \pm 0.10 (69)	38.7 \pm 0.07 (156)
Egg mass (g)	34.0 \pm 0.42 (44)	35.5 \pm 0.34 (44)	35.9 \pm 0.25 (69)	35.2 \pm 0.20 (153)
Clutch size	9.8 \pm 2.46 (50)	10.7 \pm 2.62 (45)	10.6 \pm 2.34 (69)	10.4 \pm 2.47 (164)
Clutch mass (g)	327.0 \pm 98.41 (44)	376.1 \pm 94.30 (40)	369.1 \pm 99.20 (69)	360.9 \pm 7.79 (152)

**Fig. 1.** Frequency distribution of mature female *Carettochelys insculpta*, based on radiograph data. CL, curved carapace length.**Fig. 2.** Clutch size distribution of *Carettochelys insculpta* for 1996–98 combined.

38-year averages of mean monthly river levels calculated for the years 1960–98.

We also analysed data on the onset of nesting, egg size and clutch size collected by AG during 1986. These data were not included in all analyses due to missing information (e.g. first clutch vs. second clutch). Methods for finding nests and handling eggs in 1986 were identical to those described above.

RESULTS

Number of nests and radiographed turtles

A total of 210 adult females was X-rayed 491 times during the study. One hundred and ninety-one nests were found between 1996 and 1998 (see Table 1 for breakdown by year).

Size at maturity

Size distribution of reproductive females is given in Fig. 1. The smallest mature female *C. insculpta*, based on radiography, measured 38.0 cm (curved carapace length, CL), 30.5 cm (plastron length) and 5.9 kg (mass).

Clutch frequency

Proportions of gravid turtles each year, determined by radiography between the dates of the first and last gravid turtles, are given in Table 1. Tracking individuals, 28 of 34 (82%) turtles with adequate X-ray profiles followed a pattern consistent with biennial reproduction, while five turtles (15%) skipped more than 1 year, and one turtle (3%) nested in consecutive years. Of 20 turtles with sufficient X-ray records to determine clutch frequency *within* a year, 16 (80%) nested twice in a year while four (20%) nested once.

Clutch size, egg size, clutch mass and clutch number

Data on egg size, clutch size and clutch mass of *C. insculpta* are presented in Table 1. Clutch size distribution for 1996–98 combined is shown in Fig. 2. Taken from radiographs, clutch size generally increased with carapace length (linear regression; 1996, $F_{1,49} = 2.97$, $P = 0.091$, $r^2 = 0.06$; 1997, $F_{1,21} = 4.50$, $P = 0.047$, $r^2 = 0.18$; 1998, $F_{1,21} = 7.97$, $P = 0.011$, $r^2 = 0.28$). Clutch size did not differ between radiographs and nests (ANOVA; $F_{1,265} = 1.36$, $P = 0.25$). Clutch size did not differ significantly among years (ANOVA; $F_{3,190} = 1.27$, $P = 0.286$).

Table 2. Influence of clutch (first vs. second) on reproductive attributes in *Carettochelys insculpta* in 1996–98. Data are means \pm SD for clutch size and clutch mass, and grand means \pm SE for measures of egg size. Numbers of clutches are in parentheses. Significance is from single-factor ANOVA. *, $P < 0.05$, **, $P < 0.01$

Attribute	Year	First clutch	Second clutch	Significance
Clutch size	1996	9.4 \pm 2.54 (20)	10.2 \pm 2.39 (30)	$F_{1,49} = 4.04, P = 0.250$
	1997	11.5 \pm 2.34 (24)	9.8 \pm 2.66 (21)	$F_{1,44} = 4.07, P = 0.025^*$
	1998	11.1 \pm 2.31 (35)	10.1 \pm 2.29 (34)	$F_{1,68} = 3.98, P = 0.068$
Egg mass (g)	1996	34.4 \pm 0.58 (14)	34.0 \pm 0.53 (29)	$F_{1,42} = 0.21, P = 0.652$
	1997	34.5 \pm 0.44 (19)	36.4 \pm 0.45 (21)	$F_{1,39} = 8.84, P = 0.005^{**}$
	1998	35.4 \pm 0.39 (31)	36.3 \pm 0.32 (38)	$F_{1,68} = 2.98, P = 0.091$
Egg length (mm)	1996	39.3 \pm 0.26 (14)	39.2 \pm 0.18 (33)	$F_{1,46} = 0.13, P = 0.716$
	1997	39.5 \pm 0.16 (19)	38.7 \pm 1.41 (21)	$F_{1,39} = 0.31, P = 0.583$
	1998	40.0 \pm 0.25 (31)	40.4 \pm 0.25 (38)	$F_{1,68} = 1.02, P = 0.316$
Egg width (mm)	1996	38.4 \pm 0.24 (14)	38.3 \pm 0.20 (33)	$F_{1,46} = 0.13, P = 0.716$
	1997	38.4 \pm 0.18 (19)	39.2 \pm 0.17 (21)	$F_{1,39} = 10.33, P = 0.003^{**}$
	1998	38.5 \pm 0.14 (31)	39.1 \pm 0.12 (38)	$F_{1,68} = 10.34, P = 0.002^{**}$
Clutch mass (g)	1996	295.9 \pm 103.21 (14)	341.5 \pm 94.34 (30)	$F_{1,43} = 2.10, P = 0.155$
	1997	393.2 \pm 78.28 (19)	360.5 \pm 106.26 (21)	$F_{1,39} = 1.21, P = 0.279$
	1998	393.7 \pm 87.82 (31)	349.1 \pm 104.46 (38)	$F_{1,67} = 2.73, P = 0.104$

A two-factor ANOVA revealed no significant effect of year ($F_{2,158} = 2.14, P = 0.12$) or early vs. late season clutch ($F_{1,158} = 2.85, P = 0.09$) on clutch size taken from nests. However, a significant interaction was found ($F_{2,158} = 3.60, P = 0.03$). In 1997 and 1998 clutch size was significantly higher in the first clutch, while in 1996 clutch size did not differ between first and second clutches (Table 2).

Mean egg size differed significantly among years (Table 1; Fig. 3). However, egg dimensions differed in different ways. Egg length was significantly different among years (ANOVA; $F_{3,178} = 4.22, P = 0.007$), and a Tukey's HSD showed a significant difference between 1986 and 1998 ($P = 0.007$; Fig. 3). Egg width varied significantly among years ($F_{3,176} = 10.16, P < 0.001$). Generally, eggs were wider in years following 'big' wet seasons (1997, 1998) than in years following 'small' wet seasons (1986, 1996) (Fig. 3). A Tukey's HSD revealed wider eggs in 1986 than in 1996 ($P = 0.034$), 1997 ($P < 0.001$), and 1998 ($P < 0.001$), and wider eggs in 1998 than in 1996 ($P = 0.026$). Egg mass also differed significantly among years ($F_{3,175} = 17.34, P < 0.001$; Table 1; Fig. 3). Eggs were lighter in 1986 than in all other years (1996, $P = 0.009$; 1997, $P < 0.001$; 1998, $P < 0.001$), and eggs were also lighter in 1996 than in 1997 ($P = 0.033$) and 1998 ($P < 0.001$) (Fig. 3). No measure of egg size differed significantly between 1997 and 1998 (Table 1; Fig. 3).

We were not able to examine the influence of female body size on egg size because we could only link a few nests to their respective females, and because egg size in radiographs is confounded by error associated with eggs positioned at different (unknown) depths in the turtle. However, egg mass was significantly negatively correlated with clutch size in years after big wet seasons (1997, $r = -0.320, P = 0.044$; 1998, $r = -0.254, P = 0.035$), but not in years after small wet seasons (1986, $r = 0.165, P = 0.411$; 1996, $r = 0.098, P = 0.514$).

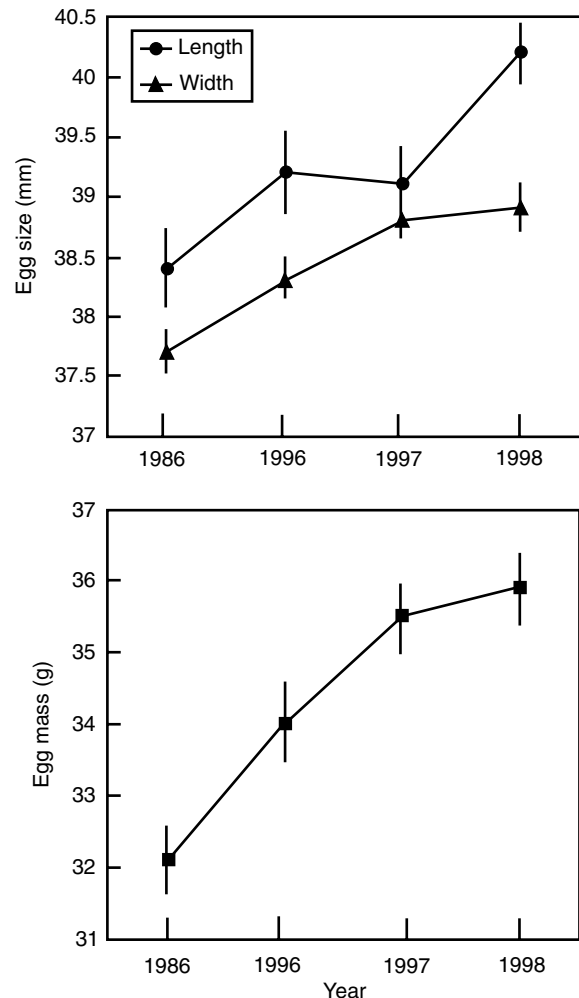


Fig. 3. Annual variation in egg dimensions of *Carettochelys insculpta* for the years 1986 and 1996–98. Bars represent ± 1 SE.

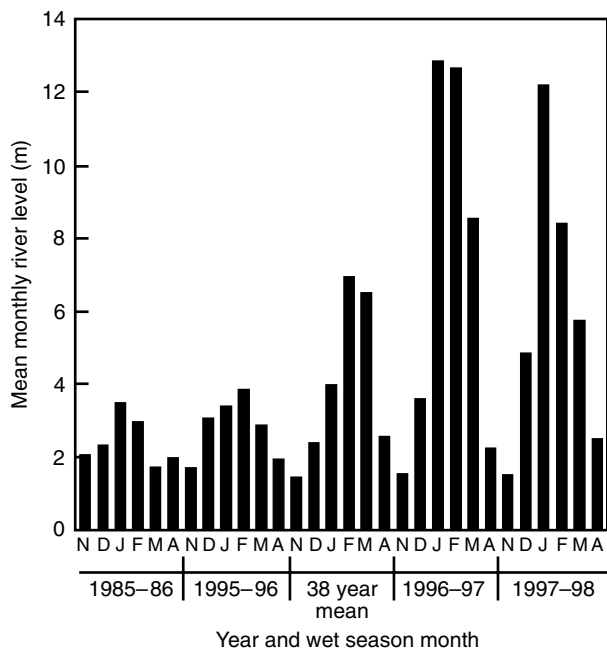


Fig. 4. Annual variation in the magnitude of the wet season (Nov–April), as indexed by mean monthly river levels prior to each year of the study (1995–96, 1996–97, 1997–98), in the year preceding the first year of the study (1994–95), in the year prior to data collection in 1986, and a 38-year average (1960–98). Note that 1985–86 and 1995–96 were ‘small’ wet seasons and that 1996–97 and 1997–98 were ‘big’ wet seasons.

Mean egg mass was higher in later (second) clutches than in earlier (first) clutches in 1997 and 1998, although the difference only approached significance in 1998 (Table 2). No significant difference in mean egg size between early and late clutches existed in 1996 (Table 2). Egg width was significantly larger in later clutches than in earlier clutches in 1997 and 1998, but not in 1996 (Table 2). Egg length did not differ between early and late clutches in any year (Table 2).

Clutch mass did not differ significantly among years ($F_{3,176} = 2.55, P = 0.057$; Table 1). However, the difference approached significance, and clutch mass was larger in years after big wet seasons (1997, 1998) than in years following small wet seasons (1986, 1996). Clutch mass did not differ between early and late clutches in any year (Table 2).

Magnitude of the wet season

Annual variation in the magnitude of the wet season during the study, as indexed by mean monthly river levels, is shown in Fig. 4. A ‘small’ wet season characterized 1986 and 1996, while ‘big’ wet seasons occurred in 1997 and 1998 (record rainfall totals for the catchment in both years). Also shown is the 38-year average level for each month during the years 1960–98, which is intermediate in magnitude.

Inter-nesting intervals and egg retention

The estimated inter-nesting interval, based on the time elapsed between mean nesting dates of the first and second clutch, was 41.3 days (see Table 1 for breakdown by years). Two turtles retained their first clutch for a minimum of 52 days each. One of these turtles laid her first clutch when most turtles were laying their second clutch. The other turtle and her nest were not recovered.

DISCUSSION

Some aspects of reproduction in female *C. insculpta* were similar to other turtles. Females matured at around 82% of their maximum size (CL). This is high but just within the range found for other turtles species (reviewed in Shine & Iverson, 1995). The eggs and clutches produced by *C. insculpta* in the present study were similar in size to those produced by other turtle species of similar size and at similar latitudes (see Iverson *et al.*, 1993). Comparing clutch frequency (CF) of *C. insculpta* to other turtles is more difficult, because data are not available for many species, and because of difficulty in interpretation. For example, CF = one for both *C. insculpta* and four species of *Clemmys*, despite the fact that *Clemmys* spp. generally lay one clutch per year (reviewed in Forsman & Shine, 1995) and *C. insculpta* lays two clutches every other year. Nevertheless, CF in *C. insculpta* is consistent with the prediction of multiple clutching (within years) in tropical species (Fitch, 1981).

Biennial reproduction and multiple clutches within years

In contrast to the above reproductive attributes, *C. insculpta* females exhibited two unusual patterns of egg production. First, females produced eggs every second year, but produced two clutches within years. Second, turtles laid smaller numbers of larger eggs in their season’s first clutch than they did in their second clutch of the season.

Both individual and population data strongly suggest that female *C. insculpta* in the Daly River follow a biennial breeding cycle. Indeed, only one individual produced eggs in consecutive years. Gregory (1982) concluded that biennial (or less frequent) reproductive cycles were not known in oviparous reptiles. However, sea turtles are known to possess a multi-year vitellogenic cycle and skip years (Moll, 1979; Limpus & Reed, 1985; Johnson & Ehrhart, 1994; Miller, 1997), and a few studies have since recorded biennial cycles in oviparous reptiles (e.g. Cree, Cockrem & Guilette, 1992; Kuchling, 1993). Among freshwater turtles, only *Erymnochelys madagascariensis* is known to have a biennial cycle (Kuchling, 1993). Although other studies on freshwater turtles have reported some individuals to skip years, in those studies most individuals in each population reproduced annually (reviewed in Kuchling, 1999).

According to Kuchling (1999) female animals exhibiting multi-year cycles either fail to initiate or sustain a vitellogenic cycle each year (Kuchling & Bradshaw, 1993), or fail to ovulate despite a normal annual vitellogenic cycle (Moll, 1979). We have no data to indicate which might be the case for *C. insculpta*. In either case, multi-year reproductive cycles presumably reflect an energy accumulation problem at some stage of the cycle (Bull & Shine, 1979). We suggest that the energy accumulation problem lies in the dry season diet of the population. During the dry season Daly River *C. insculpta* consume mainly aquatic vegetation, such as *Vallisneria nana* (Heaphy, 1990; Welsh, 1999), which is low in available energy content (Spencer, Thompson & Hume, 1998; Tucker, 2000a). Dry season home ranges of females in the population, the largest known in freshwater turtles, may have reflected the need to cover extensive river stretches to acquire sufficient food for reproduction (Doody, Georges & Young, 2002).

Bull & Shine (1979) reviewed animals exhibiting biennial reproduction, producing an adaptive hypothesis for why animals would skip opportunities to reproduce. They hypothesized that in these animals an energy-expensive behaviour associated with reproduction exists, such that animals could increase lifetime reproductive success (LRS) by skipping years and putting the savings into future reproduction. Examples of these accessory behaviours were brooding, live bearing and migration. Animals exhibiting this pattern were generally long-lived, and were food- or season-limited (Bull & Shine, 1979). While brooding and live-bearing are not features of turtles, *C. insculpta* could theoretically expend energy in migrations associated with nesting. However, the results of a concurrent movements study were equivocal. Most gravid *C. insculpta* nested within their home ranges, and did not occupy significantly larger home ranges than non-gravid females (Doody *et al.*, 2002). However, females moved farther between fixes while gravid than while spent (Doody *et al.*, 2002). An ultimate test of this idea would require knowledge of energy expenditure associated with searching for a nesting beach and nest site (e.g. Congdon & Gatten, 1989).

Alternatively, biennial reproduction in the population may simply reflect phenotypic plasticity in clutch frequency. A negative energy balance caused by poor habitat quality or low available energy may have forced biennial reproduction (Congdon *et al.*, 1987). Well-fed, captive green sea turtles produce eggs annually (Wood & Wood, 1980), compared to wild individuals that usually skip years (Mortimer & Carr, 1987; Limpus & Nicholls, 1988).

Turtles in the present study produced two clutches every second year, a pattern previously unknown in non-marine turtles. Why produce two clutches every second year rather than one clutch each year? Our data are not sufficient to answer this question. Sea turtles skip years and lay multiple clutches within years, but do so irregularly, putatively due to variation in length of nesting migrations (Bjorndal, 1982). No such migrations occur in *C. insculpta* (Doody *et al.*, 2002), which appear to skip years regularly but produce two clutches each year. If there is a consistent

energy accumulation problem, why not lower the threshold needed to produce a clutch of eggs, thereby producing one clutch annually? Future work should focus on this question.

Seasonal changes in clutch size and egg size

An unusual finding of the present study was that later (second) clutches contained fewer but larger eggs than earlier (first) clutches of each female (Table 2), despite no difference in clutch mass between the two clutches. This pattern is not previously known in turtles (but see seasonal decrease in clutch size reviewed in Tucker & Frazer, 1994). Seasonal changes in clutch and egg size occur in some lizards (reviewed in Nussbaum, 1981) and have been reported for other animals (e.g. Wolda & Kreulen, 1973). Nussbaum (1981) discussed theoretical underpinnings of this pattern, in which he critiqued an existing hypothesis (parental investment model) and proposed another (bet-hedging model).

The parental investment model predicts that females are selected to increase egg size, at the cost of clutch size, late in the season in order to produce larger and competitively superior hatchlings at a time when food for hatchlings is low and juvenile density is high (Ferguson, Brown & DeMarco, 1982; Ferguson, Snell & Landwer, 1990; see also review of similar models in Nussbaum, 1981). The key assumption of this optimal offspring model is a late season reduction in offspring fitness (Landa, 1992), related to food availability. No data exist on diet or food availability in hatchling *C. insculpta*. However, juveniles are reported to have a catholic diet (Welsh, 1999), including ribbonweed *Vallisneria spiralis*, which is abundant relative to body size of juveniles (pers. obs.). There is little change in late season environment compared to early season at the Daly River (mean inter-nesting interval = 6 weeks); dry season conditions persist throughout this period, and river levels are stable (Doody *et al.*, 2001). Lastly, the difference in timing between early and late clutches is reduced by both a seasonal increase in air temperatures (increasing developmental rate and reducing incubation period), and by embryonic aestivation in the egg (Doody *et al.*, 2001). Thus, there is no indication that the observed decline in clutch size in *C. insculpta* supports the parental investment hypothesis.

The bet-hedging model claims that the amount of food available to females for the production of late season clutches is unpredictable, and that selection has favored conservatively small clutches in the late season to insure that each egg is minimally provisioned (Nussbaum, 1981). Nussbaum argued that when faced with an optimal clutch size that is fractional, lizards are likely to opt for the smaller integral clutch size and adjust their investment by increasing egg size. Nussbaum outlined five predictions of this model: (1) both small and large clutches will have variable egg sizes among years, depending on annual variation in resource levels; (2) within years, small clutches will have larger eggs than large clutches because unanticipated resources are divided among fewer

eggs (Smith & Fretwell, 1974); (3) the largest mean difference among egg sizes should occur between eggs of very small and very large clutches sampled at the same time and place; (4) large-egged clutches will seldom consist of sufficient surplus yolk, compared to clutches of equivalent size with average-sized eggs, to provision an additional egg of minimal size; (5) this model would most likely apply to species that cannot afford to miss an opportunity to reproduce in the late season, i.e. those with very high adult mortality, even in the absence of reproduction.

Prediction (1) is upheld in *C. insculpta*, with egg sizes of small and large clutches varying considerably among and within years (Fig. 3). Presumably, these differences are at least partially due to resource uptake. Predictions (2) and (3), involving a trade-off between clutch and egg size, are evident in 2 of 3 years (Table 2). Prediction (4) could not be examined in the present study, as yolk content was not determined. Prediction (5), that the model would most likely apply to species with high adult mortality that cannot afford to skip opportunities for reproduction, is not consistent with *C. insculpta*. Although adult mortality data are unavailable for *C. insculpta*, turtles are generally characterized by high adult survival (Gibbons, 1987; Iverson, 1991b; Shine & Iverson, 1995), and the present study has demonstrated that *C. insculpta* in the Daly River do skip opportunities for reproduction.

Nussbaum (1981) noted that the bet-hedging model would be falsified if a late-season increase in egg size was, on average, large enough to account for one or more additional eggs of the smaller size, thereby providing evidence that clutch size was sacrificed for egg size. For an average late season clutch of *C. insculpta*, the percentage increase in egg size would have to exceed the critical value of 10% (clutch size of 10). In 1997 and 1998 the mean percentage late-season increase in egg size was 9.5% and 9.7%, respectively. Although these values do not exceed 10%, they are very close; thus, according to Nussbaum (1981), there is evidence that clutch size is sacrificed for egg size in *C. insculpta*. Therefore, several of the bet-hedging model's predictions are not upheld in our data for *C. insculpta*.

The wet season and reproduction

Numerous studies on lizards, mostly desert-adapted species, have shown that annual variation in reproductive output is associated with rainfall amounts that dictate food availability (reviewed in Ballinger, 1977; Judd & Ross, 1978; Vitt, van Loben Sels & Ohmart, 1978; Dunham, 1981; Trauth, 1983; Ferguson *et al.*, 1990; James & Whitford, 1994; Smith, Ballinger & Rose, 1995; Abell, 1999). Less evidence exists for environmental control of reproductive output in turtles. In the herbivorous turtles *Geochelone gigantea* and *Gopherus agassizii*, reproductive output (clutch size) is strongly influenced by primary production, which is in turn influenced by rainfall (Swingland & Coe, 1978; Swingland & Lessells, 1979; Henen, 1997). Two other species have been shown

to abort reproduction in dry years (Kuchling, 1993, 1999; Nieuwolt-Dacanay, 1997). Other studies suggest links between rainfall and reproductive output (Tucker, 2000b) and still others report no annual variation in reproductive characteristics (Rowe, 1994). Nearly all of these studies were in temperate climates.

Is the wet season a favourable time for *C. insculpta* females? The wet season in the Australian wet-dry tropics is generally thought to be a plentiful time for reptiles, based on seasonal studies of diet, activity, growth and energetics of lizards and snakes (Christian & Green, 1994; Christian *et al.*, 1995; Griffiths & Christian, 1996; Madsen & Shine, 1996; Shine & Madsen, 1997; Christian, Bedford & Shultz, 1999; Christian *et al.*, 1999; but see Vitt, 1982; James & Shine, 1985). Pig-nosed turtles may experience increased food uptake during the wet season, taking advantage of the availability of food such as fruits, leaves and flowers. Populations of *C. insculpta* in the Alligator River system have been shown to have varied diets (reviewed in Georges & Rose, 1993). Six juvenile *C. insculpta* in the Daly River grew significantly faster during the wet season than did seven juveniles during the dry season (Heaphy, 1990).

However, the opposite argument is reasonable for *C. insculpta*. In the dry season *C. insculpta* prefer to eat *Vallisneria*, which although patchy and relatively nutrient-poor (Heaphy, 1990; Tucker, 2000a), is in abundance in the Daly. During the wet season the river is often in continuous flood, precluding the turtles from eating that vegetation. Radiotelemetry during a fly-over in the wet season indicated that turtles were not in the river channel where the *Vallisneria* beds are located, but were in flooded riparian forest (Doody *et al.*, 2002). Further, river levels fluctuate, and the strictly aquatic nature of *C. insculpta* means that turtles would be constrained in many cases to follow those fluctuations.

Is a bigger wet season better? Annual variation in the magnitude of the wet season can have considerable impacts on reproduction. For example, the strength of the Southern Oscillation, a correlate of wet season magnitude in the Australo-Papuan region where sea turtles feed, predicted the number of nesting sea turtles *Chelonia mydas* in the Great Barrier Reef, Australia (Limpus & Nicholls, 1988). The present study indicates that the magnitude of the wet season influences the female reproductive biology of *C. insculpta* in the Daly River in several ways. The study spanned one 'small' wet season and two very 'big' wet seasons, and we analysed data from 1986, which followed a small wet season (Fig. 4). Several reproductive patterns aligned themselves according to this difference in wet season magnitude, including the onset of nesting (pers. obs.), egg size, clutch mass, a seasonal decrease in clutch size/increase in egg size, the trade-off between clutch and egg size (not standardized for body size), and the influence of body size on clutch size (Tables 2 & 3; Fig. 4). Clutch size and egg size were smaller after small wet seasons, and many studies have shown that these attributes are influenced by food uptake in reptiles and other animals (e.g. Drent & Daan, 1980; Ford & Seigel, 1989; Rohr, 1997). In addition, nesting

Table 3. Summary of annual variation in reproductive patterns and flood mortality of *Carettochelys insculpta*, and magnitude of the wet season during 1996–98. Timing of nesting, flood mortality, and hatchling sex ratio data are unpublished

Attribute	1986	1996	1997	1998
'Big' wet season	no	no	yes	yes
Early clutch size larger than late clutch size	–	no	yes	yes
Early clutch eggs smaller than late clutch eggs	–	no	yes	yes
Trade-off between clutch size and egg size	no	no	yes	yes
Clutch size influenced by female body size	–	no	yes	yes
Early nesting	no	no	yes	yes
Flood mortality	–	yes	no	no
Female-biased hatchling sex ratios	–	yes	no	no

began 4–5 weeks earlier after big wet seasons compared to small wet seasons (pers. obs.). Direct evidence of food uptake influencing the laying date is lacking for reptiles, but body condition influenced lay date in the sand lizard (Olsson & Shine, 1997b). In birds, lay date advances in years of high food availability, findings confirmed by food supplementation experiments (see reviews in Drent & Daan, 1980; Rowe, Ludwig & Schluter, 1994). A concurrent study found that late nesting in *C. insculpta* can be disadvantageous in two ways. First, late nesting in 1996 resulted in 20% nest mortality due to early wet season flooding (pers. obs.). Second, late nesting led to a female-biased hatchling sex ratio, compared to sex ratios near unity following big wet seasons in 1997 and 1998 (pers. obs.). Based on these findings, and current life-history theory, we hypothesize that a big wet season has a positive impact on *C. insculpta* reproduction, relative to a small wet season.

Because *C. insculpta* appear to need 2 years to accumulate enough energy to produce eggs, the magnitude of the *two* wet seasons prior to nesting may be important, rather than just the preceding wet season. Examining the two previous wet seasons gives the same result – after big wet seasons turtles produce larger eggs earlier in the year, exhibit trade-offs between clutch and egg size, show seasonal changes in clutch and egg size, and generate female-biased hatchling sex ratios.

Although collectively our data indicate that a big wet season is advantageous for turtle reproduction, direct evidence is lacking, and a study of the wet season diet and/or field energetics of *C. insculpta* would be required to test our supposition. Not all of our findings are consistent with those on other reptiles in terms of the influence of annual weather patterns on reproduction. For example, in the lizard *Sceloporus woodi* seasonal shifts in, and trade-offs between, egg and clutch size were only evident in a drought year (DeMarco, 1989), a finding opposite to ours. Variation in energy accumulation among females can obscure clutch size–egg size trade-offs (van Noordwijk & de Jong, 1986; Bernardo, 1996). We suggest that annual variation in energy uptake can have a similar obscuring effect. However, the specific impact of this effect based on previous studies is equivocal. This may be owed to the complexity of 'capital' vs. 'income' breeding (Bonnet *et al.*, 2001), and/or to a diversity of functional responses (i.e. energy allocation) in reproductive characteristics to

environmental variation among different taxa. Finally, some of the trends we have outlined may be spurious due to sample size; our data spanned 4 years only. Further work is needed to confirm the influence of the strongly seasonal environment on the reproductive biology of *C. insculpta*.

In summary, the present study suggests that: (1) considerable phenotypic plasticity exists in reproductive traits of *C. insculpta*, manifested in clutch characteristics influenced by annual variation in the magnitude of the wet season; (2) the species exhibits biennial reproduction, which may be a result of the low available energy content in the dry season diet. A study of the field energetics in both wet and dry seasons, coupled with information on the wet season diet, would provide confirmation of the latter of these hypotheses. Such a study might also provide the answer to why the turtles nest twice every second year rather than once each year, a novel enigmatic question in the reproductive life-history of reptiles.

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