

# Embryonic aestivation and emergence behaviour in the pig-nosed turtle, *Carettochelys insculpta*

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**Abstract:** Two related aspects of hatchling emergence were studied in a population of pig-nosed turtles (*Carettochelys insculpta*) in northern Australia. Using emergence phenology data, nest temperatures, historical weather data, and a developmental model, we tested the hypothesis that delayed hatching occurs in *C. insculpta*, and that such a delay would allow hatchlings to time their emergence to match the onset of the wet season. *Carettochelys insculpta* hatchlings emerged, on average, 17 days after dates predicted from a developmental model. Combined with observations of hatchlings remaining in eggs until emergence, these results confirmed delayed hatching in nature. This delay was synchronized with initial river rises associated with the onset of wet-season rains, and is consistent with published criteria for embryonic aestivation. On a diel scale, we generated predictions of two potentially competing models of nocturnal emergence in hatchling turtles based on the knowledge that air temperatures decrease with season during the emergence period. A test of these predictions for *C. insculpta* produced ambiguous results. However, further analysis indicated that *C. insculpta*, and probably other nocturnally emerging turtle species, respond to a decline in diel temperature rather than to an absolute temperature. The former would ensure nocturnal emergence, while the latter is experienced during the day as well as at night. Nocturnal emergence may be associated with nesting in open microhabitats.

**Résumé :** Nous avons étudié deux aspects interreliés de l'éclosion chez une population de Tortues palustres (*Carettochelys insculpta*) du nord de l'Australie. Nous avons utilisé des données sur la phénologie de l'émergence, les températures au nid, les conditions climatiques du passé, ainsi qu'un modèle de développement, pour tester l'hypothèse selon laquelle l'éclosion est tardive chez *C. insculpta* et qu'un tel retard permet aux petites tortues de synchroniser leur émergence avec le début de la saison humide. Les *C. insculpta* néonates ont émergé, en moyenne, 17 jours plus tard que prévu par un modèle de développement. Cette émergence tardive, combinée à l'observation de petites tortues restant dans les oeufs jusqu'à l'émergence, confirme l'émergence tardive en nature. Ce retard est synchronisé à la première crue des rivières associée au début de la saison humide et s'accorde avec les critères de la littérature sur l'estivation des embryons. Deux modèles potentiellement opposés ont généré, sur une échelle de 24 h, des prédictions d'une émergence nocturne chez les tortues néonates, tenant compte que les températures saisonnières baissent pendant la période d'émergence. Un test sur ces prédictions a produit des résultats ambigus dans le cas de *C. insculpta*. Cependant, une analyse subséquente indique que *C. insculpta*, et probablement aussi d'autres espèces à émergence nocturne, réagit à une chute de température journalière plutôt qu'à une température absolue. La chute journalière de température entraîne une émergence nocturne, alors que la température absolue est subie autant de jour que de nuit. L'émergence nocturne est peut être reliée à la nidification dans des microhabitats ouverts.

[Traduit par la Rédaction]

## Introduction

Emergence from the nest can be a critical life-history stage for hatchling turtles (Kuchling 1999). For example, during emergence and their brief crawl to the water, sea turtle hatchlings can incur high mortality (e.g., Hendrickson 1958; Diamond 1976; Pritchard and Trebbau 1984). Thus, studies on behaviour at emergence are needed because of the

probability that emergence success shapes both individual emergence behaviour and population age structure.

On a diel scale, hatchlings of several species of turtle emerge primarily at night (e.g., Anderson 1958; Witherington et al. 1990; Gyuris 1993). Nocturnal emergence in turtles is said to be adaptive, reducing the probabilities of heat stress, desiccation, and predation by visually oriented predators (Hendrickson 1958; Bustard 1967; Stancyk 1982). Support for the heat-stress factor comes from observations of scorched hatchlings that emerged during the day (Carr and Ogren 1959; Hughes and Richard 1974; Diamond 1976), while the existence of the predation factor has received little support (Witherington and Salmon 1992; Gyuris 1994). At a minimum, emergence would be detrimental during much of the day for species that nest in areas free of vegetation cover, because substrate temperatures can exceed 60°C in some areas (e.g., Georges 1992).

Thermal cues have been proposed as determinants of nocturnal emergence in sea turtles. Earlier work suggested that a threshold in absolute temperature triggered nocturnal emer-

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gence (Hendrickson 1958; Bustard 1967; Mrosovsky 1968), while more recent studies have implicated a change in temperature (Hays et al. 1992; Gyuris 1993).

The pig-nosed turtle (*Carettochelys insculpta*) is a monotypic species found in New Guinea and in the wet-dry tropics of northern Australia (Georges and Rose 1993). In Australia, *C. insculpta* nests in open sandy riparian areas from mid-July to late October (dry season) and hatches from early October to early December (late dry to early wet season) (Georges and Rose 1993; Georges et al. 2001). Although hatching has been studied in the laboratory (Webb et al. 1986), nothing is known about emergence behaviour in this species, and thus in the family Carettochelyidae.

On a seasonal scale, Webb et al. (1986) hypothesized that *C. insculpta* exhibits delayed hatching in the field after they found delayed hatching and hatching in response to anoxia in the laboratory. They suggested that such delays would allow hatchlings to synchronize emergence with the more favourable conditions of the wet season.

We investigated the emergence behaviour of *C. insculpta* during the years 1996–1998. We used emergence phenology data, nest temperatures, historical weather data, and a developmental model to test or examine the following three hypotheses associated with emergence: (1) embryonic aestivation (delayed hatching) occurs in *C. insculpta* in nature; (2) embryonic aestivation in *C. insculpta* results in synchronization between hatching/emergence and the onset of the wet season; (3) the cue used by *C. insculpta* hatchlings to emerge nocturnally is an absolute nest temperature threshold, or alternatively a change in nest temperature. We generated predictions for the two models and tested those predictions, with the ultimate goal of identifying a general thermal cue for nocturnally emerging turtles.

We also examined other behavioural aspects of emergence in *C. insculpta*, asking (i) Do hatchlings emerge in response to rainfall? (ii) Do sibling hatchlings emerge simultaneously, in small groups, or singly? (iii) Is emergence synchronized among nests within a nesting area? These questions have been difficult to answer for turtles because of logistical problems in observing emergence (Ehrenfeld 1979; Christens 1990). However, a novel remote data-collection technique allowed us to gather large amounts of emergence data with relative ease. We also review emergence data for other turtle species for comparison with our results and to elucidate any existing patterns among species.

## Materials and methods

We studied *C. insculpta* along a 30-km stretch of the Daly River in the Northern Territory, Australia. The study stretch centred on Ooloo Crossing (14°04'40''S, 131°15'00''E). The climate is typical of the wet-dry tropics of northern Australia (Taylor and Tulloch 1985), with a mean monthly rainfall of less than 7 mm from May to September, rising to a peak monthly average of 284 mm in February (Station 014139/014941, Ooloo, 1962–1985). Mean monthly maximum air temperatures range from 30.9°C in June to 36.8°C in October. Most data were collected in 1998, but some data (e.g., timing of nesting, observations on flooding) were collected in 1996 and 1997.

A standard station for monitoring sand, water, and air temperatures was set up on a small nesting bank used by *C. insculpta* in May of each of 3 years (1996–1998). Temperatures were monitored at 15-min intervals at the sand surface and at 10 cm depth in-

tervals to a depth of 50 cm. Water and air temperatures were taken in the shade. Temperatures were recorded with four-wire RTD probes fitted to a datalogger (Datataker Model DT500) calibrated against a thermometer certified as accurate by the Australian National Authority of Testing Agencies. Rainfall gauges were placed at each nesting beach and checked daily. River rises were recorded from mid-October to mid-December of 1996–1998.

We inspected nesting areas daily for turtle tracks throughout the nesting season. Nests were located by probing the sand with a 2 mm diameter spring-steel rod (after Blake 1974). Temperatures in 44 nests were monitored with either Datataker® DT500 multi-channel dataloggers ( $N = 37$ ) or Stowaway® single-channel dataloggers ( $N = 7$ ). Temperatures were recorded at 15-min intervals by the Datataker dataloggers and at 1-h intervals using the Stowaway dataloggers. Typically, three temperature probes were fitted to each nest: one immediately below the deepest egg, one in the core of the nest, and one immediately above the shallowest egg. When Stowaway dataloggers were used, often only core temperatures were recorded. The probes were fitted as soon as possible after discovery of the nest, usually within 1–3 days. The depth of each egg was measured before its removal and eggs were returned to their original positions and orientations after deployment of datalogger probes.

Nests were subsequently inspected each day throughout the period when hatching and emergence were considered likely (October–December). Emerging hatchlings leave a distinctive hole and tracks in the sand. After checking each nest, we cleared the sand surface and sprayed it with nontoxic paint to avoid double-counting. For 17 nests, emergence dates and times were recorded by Trailmaster® infrared camera systems (Doody and Georges 2000). Each system consisted of a transmitter box, a programmable receiver box with LED readout, and an automatic camera (Olympus®). Boxes were placed on either side (and just to the river side) of each nest, and the camera was attached to a metal stake (1.7 m long), which was driven into the sand. Emerging hatchlings were photographed as they crossed the beam, and both the receiver box and the photographs displayed the date and time of each emergence event. We also determined emergence dates for 46 nests without camera systems by monitoring nests daily throughout emergence. The sand was smoothed out just over the nest after each emergence to discriminate between emergence events. Incubation period is defined here as the number of days elapsed between nesting date and emergence date. For 10 nests the actual emergence date was not known and the date was estimated as the median within a known range of possible dates (Table 1). Emergence temperatures were determined by inspecting datalogger traces for temperatures corresponding to dates and times recorded by the camera systems.

Because *C. insculpta* is known to delay hatching after completing embryogenesis (Webb et al. 1986), it is difficult to determine the end point of embryonic development in natural nests without being invasive. We calculated this parameter from temperature traces using a method of summation (deCandolle 1855; Reibish 1902; A. Georges, K. Beggs, J.S. Doody, and J.E. Young, unpublished data). Gaps in the temperature traces, typically only the first few days between finding the nest and fitting the probes to it, were filled by cross-regression with traces from other nests on the same beach or traces from the standard monitoring station. The relationship between incubation temperature and developmental rate (Beggs et al. 2000; A. Georges, K. Beggs, J.S. Doody, and J.E. Young, unpublished data) was integrated along each temperature trace to estimate when embryo head width attained its maximum. A period of some days, obtained by correcting for the average terminal incubation period, was added to account for the maturation period (at 30°C it is 10 days, from attainment of maximum size to yolk internalization) (A. Georges, K. Beggs, J.S. Doody, and J.E. Young, unpublished data). Thus, for each nest we obtained a date on which emergence could occur and a date on which emergence *did* occur.

**Table 1.** Predictions of the length of incubation period by developmental model compared with observed incubation periods for *Carettochelys insculpta*.

Nest	Beach	Date laid	Earliest possible emergence date	Observed emergence date	Shortest possible incubation period (days)	Observed incubation period (days)
1	Pandanus	11 July	24 Sept.	16 Oct.	75	97
2	Oolloo	12 July	22 Sept.	16 Oct.	72	96
3	Bonfire	12 July	6 Oct.	16 Oct.	87	96
4	Triangle	14 July	3 Oct.	21–27 Oct.	82	99
5	Moyes	14 July	12 Oct.	8 Nov.	91	107
9	Snag	18 July	10 Oct.	26 Oct.	85	100
10	Experimental	17 July	20 Sept.	16–25 Oct.	66	91
11	Experimental	17 July	21 Sept.	16–25 Oct.	67	91
12	Experimental	17 July	24 Sept.	16–18 Oct.	70	91
13	Experimental	19 July	1 Oct.	16 Oct.	75	89
14	Experimental	19 July	24 Sept.	18 Oct.	68	91
15	Experimental	19 July	24 Sept.	16 Oct.	68	89
16	Experimental	19 July	23 Sept.	16–20 Oct.	67	89
17	Experimental	19 July	20 Sept.	16–25 Oct.	64	89
18	Triple A	22 July	3 Oct.	27 Oct.	75	97
21	Pandanus	22 July	8 Oct.	30 Oct.	80	100
24	Oppsalt	2 Aug.	5 Oct.	27 Oct.	66	86
26	Rapids	5 Aug.	30 Sept.	29 Oct.	58	85
27	Rapids	5 Aug.	30 Sept.	29 Oct.	58	85
29	Big bend	1 Aug.	15 Oct.	29 Oct.	77	89
30	Big bend	1 Aug.	14 Oct.	29 Oct.	76	89
31	Big bend	1 Aug.	11 Oct.	20–25 Oct.	73	93
32	Big bend	1 Aug.	9 Oct.	5 Nov.	71	109
33	Moyes	21 Aug.	28 Oct.	17 Nov.	70	88
34	Moyes	21 Aug.	26 Oct.	16 Nov.	68	87
35	Moyes	22 Aug.	19 Oct.	8 Nov.	60	78
37	Oppsalt	24 Aug.	20 Oct.	30 Oct.	59	66
41	Salty extension	23 Aug.	29 Oct.	8 Nov.	69	77
43	Big bend	21 Aug.	21 Oct.	5 Nov.	63	76
47	Triple A	31 Aug.	23 Oct.	5–7 Nov.	55	66
48	Triangle	1 Sept.	29 Oct.	5 Nov.	60	65
50	Pyramid	3 Sept.	27 Oct.	14 Nov.	56	72
52	Pyramid	2 Sept.	31 Oct.	24–26 Nov.	61	83
53	Pyramid	3 Sept.	1 Nov.	10–17 Nov.	64	68
58	Moyes	6 Sept.	2 Nov.	16 Nov.	62	71
60	Salty extension	6 Sept.	2 Nov.	13 Nov.	62	68
68	Pyramid	5 Sept.	1 Nov.	17 Nov.	62	73

To confirm that *C. insculpta* were exhibiting delayed hatching rather than hatching and delayed emergence, we carefully excavated to the top eggs of each nest up to three times during the period between predicted earliest hatching and observed hatching.

To examine the timing of emergence relative to the onset of wet-season flooding we obtained historical river-stage data for Dorisvale Crossing (60 km upstream of the study area) for the years 1960–1996. From these data we gleaned the dates of initial river rises of >0.3 m for each year for comparison with data on the timing of emergence. We used actual emergence dates for 1998 and predicted emergence dates by extrapolating from nesting dates and incubation period for 1996 and 1997.

Contingency-table analysis was used to examine the association between emergence and rainfall in the previous 24 h. Regression analysis was used to examine relationships among emergence date, incubation time, emergence time, emergence temperature, and cooling rate of the nest before emergence. Each emergence event within a

nest may have influenced the next, so we analysed emergence-time data twice, once using the first emergence from each nest and once using all emergence events. Single-factor ANOVA was used to test for any influence of rainfall on emergence time between sibling hatchlings. We checked that the assumptions of parametric tests were met before we performed the analyses, and we used an  $\alpha$  level of 0.05.

## Results

### Embryonic aestivation, emergence, and onset of the wet season

#### *Embryonic aestivation*

Table 1 lists the predicted dates of earliest emergence and shortest incubation periods and the observed emergence dates

and incubation periods. Data were available for 37 nests. The observed incubation period (mean = 86 days) was significantly greater ( $F_{[1,70]} = 48.74$ ,  $p < 0.001$ ) than the shortest possible incubation period (mean = 69 days). The observed incubation period ( $r^2 = 0.71$ ,  $F_{[1,34]} = 84.52$ ,  $p < 0.001$ ) and shortest possible incubation period ( $r^2 = 0.48$ ,  $F_{[1,34]} = 31.65$ ,  $p < 0.001$ ) decreased with emergence date (Fig. 1). Inspection of the top eggs of each nest at various times after the predicted hatching date confirmed that turtles were exhibiting delayed hatching rather than hatching and delayed emergence.

#### Timing of emergence and rainfall

Hatchlings emerged between 16 October and 26 November ( $N = 63$  nests). Hatchlings emerged at a greater frequency on nights after rain had fallen in the previous 24 h (0.92) than would be expected (0.60) on nights when no rainfall occurred ( $\chi^2 = 9.14$ ,  $df = 1$ ,  $p = 0.003$ ,  $N = 63$ ). In 3 of 17 nests, it appears that emergence occurred during rainfall, because the sand was visibly wet in emergence-event photographs. In one nest, hatchlings emerged as the river rose and flooded the nest chamber (Fig. 2). Rainfall in 1998 appeared to be typical in frequency and magnitude (NT Water Resources 1999).

#### Timing of emergence and the onset of the wet season

The mean onset of the wet season, as indexed by date of first river rise ( $>0.3$  m) each year during 1960–1996, was 17 November (range = 25 October – 30 November; Fig. 3). These rises were associated with a decrease in water clarity that persisted throughout the wet season. Using 1998 emergence data and extrapolating time of emergence data from time of nesting data for 1996–1997, mean first and last emergence dates of 30 October and 10 December, respectively, were obtained (Fig. 3).

#### Emergence behaviour and the cue for nocturnal emergence

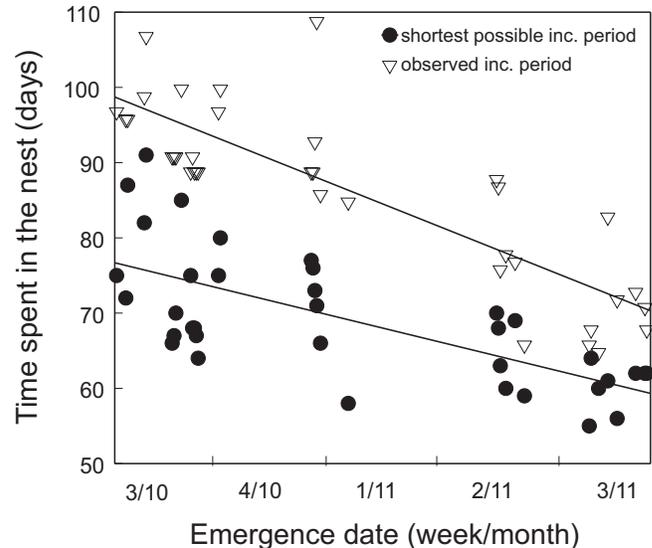
##### Emergence times

Sixty-seven *C. insculpta* hatchlings from 17 nests on seven beaches were photographed as they emerged from the nest (Fig. 2);  $4.1 \pm 1.91$  (mean  $\pm$  SD) ( $N = 17$ ; range = 2–8) hatchlings emerged from each nest. Emergence occurred at night with the exception of two hatchlings that emerged from one nest at approximately 18:00. Actual times of emergence ( $2348 \text{ h} \pm 147.4 \text{ min}$  (mean  $\pm$  SD);  $N = 67$ ; range = 1756–0456 h) were normally distributed (Fig. 4). Hatchlings that emerged later in the season did so earlier in the night when either the first emergence for each nest ( $r^2 = 0.796$ ,  $F_{[1,19]} = 6.92$ ,  $p = 0.007$ ) or all emergences ( $r^2 = 0.277$ ,  $F_{[1,56]} = 22.96$ ,  $p < 0.001$ ) were considered.

##### Emergence temperatures

Nest temperatures at emergence were normally distributed (Fig. 4). The nest temperature at emergence was  $33.0 \pm 2.28^\circ\text{C}$  (mean  $\pm$  SD) ( $N = 64$ , range = 28.8–37.0). Hatchlings that emerged later in the season emerged at lower nest temperatures (Fig. 5) for both the first emergence from each nest ( $r^2 = 0.621$ ,  $F_{[1,19]} = 31.15$ ,  $p < 0.001$ ) and for all emergences ( $r^2 = 0.586$ ,  $F_{[1,56]} = 79.21$ ,  $p < 0.001$ ). Emergence temperature was not related to emergence time, when either

**Fig. 1.** Evidence for embryonic aestivation in *Carettochelys insculpta*. Observed incubation (inc.) period and shortest possible incubation period are regressed against emergence date. The shortest possible incubation period was calculated using the developmental model.



the first emergences for each nest ( $r^2 = 0.058$ ,  $F_{[1,19]} = 1.17$ ,  $p = 0.292$ ) or all emergences ( $r^2 = 0.05$ ,  $F_{[1,56]} = 2.72$ ,  $p = 0.105$ ) were considered. Temperatures began to decrease earlier in the day as the season progressed ( $r^2 = 0.796$ ,  $F_{[1,15]} = 58.61$ ,  $p < 0.001$ ).

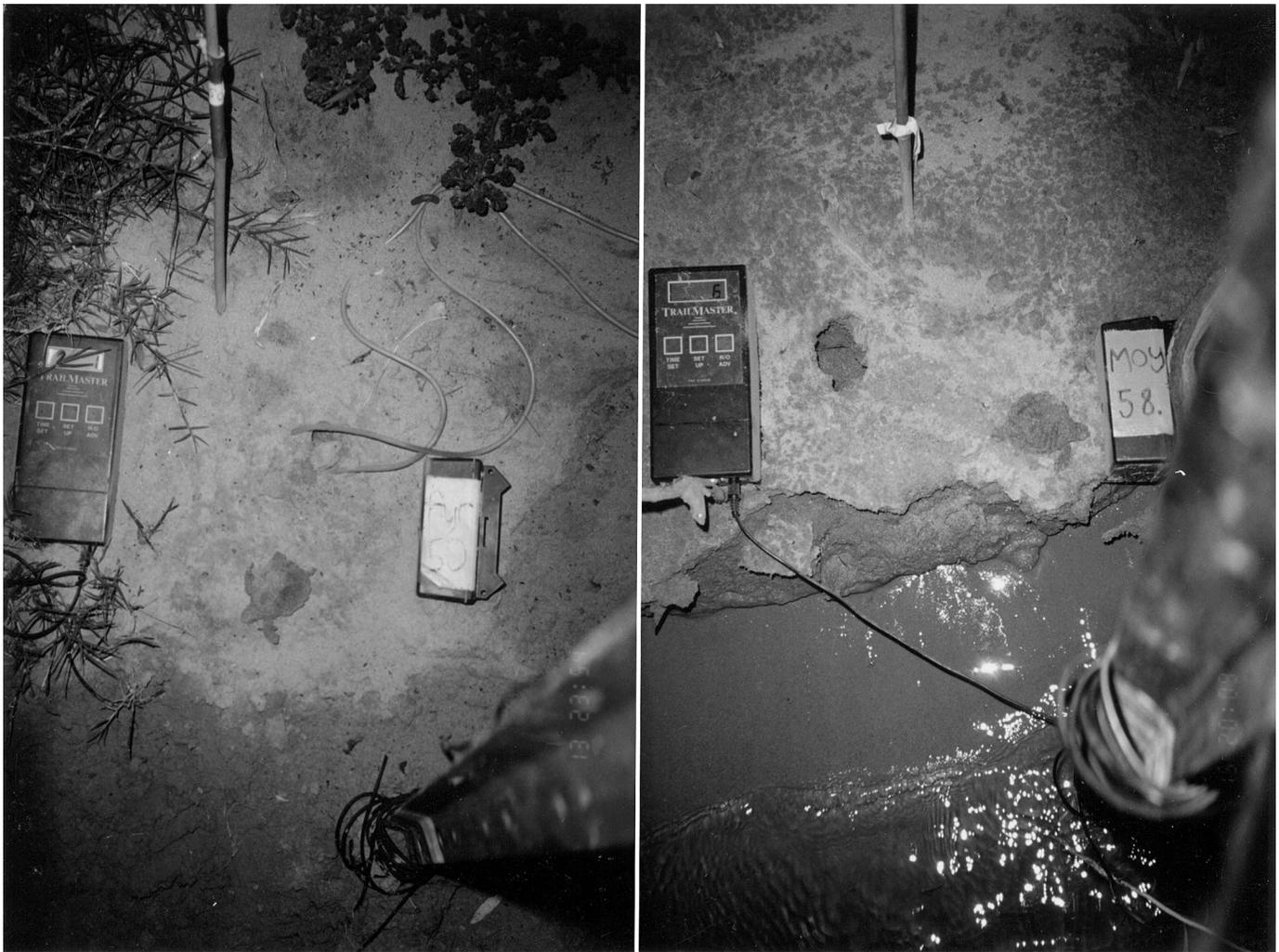
All hatchlings emerged when nest temperatures were decreasing. Figure 4 shows the number of hatchlings emerging against the cooling rate of the nest during the 3 h preceding emergence. The two outliers in this figure emerged during the day after an afternoon rain shower that resulted in a rapid decrease in nest temperature. Rate of cooling during the 3 h before emergence was not related to emergence time (first emergence,  $r^2 = 0.008$ ,  $F_{[1,19]} = 0.15$ ,  $p = 0.701$ ; all emergences,  $r^2 = 0.019$ ,  $F_{[1,56]} = 1.08$ ,  $p = 0.303$ ) or emergence temperature (first emergence,  $r^2 = 0.012$ ,  $F_{[1,19]} = 0.24$ ,  $p = 0.631$ ; all emergences,  $r^2 = 0.02$ ,  $F_{[1,56]} = 0.94$ ,  $p = 0.336$ ). Cooling rate did not change with season (Fig. 5) for either the first emergence for each nest ( $r^2 = 0.00$ ,  $F_{[1,19]} = 0.02$ ,  $p = 0.998$ ) or all emergences ( $r^2 = 0.01$ ,  $F_{[1,56]} = 0.30$ ,  $p = 0.590$ ).

##### Other behaviour

For 49 of 62 nests (79%) all siblings within a nest emerged on the same night. Siblings that emerged on different nights generally did so on 2 nights, usually separated by 1 or 2 nights. Outliers included one nest in which siblings emerged on 2 nights 20 days apart, and another in which siblings emerged on 4 different nights. Siblings generally emerged through the hole created by the first emerging hatchling, but in 6 nests multiple holes were made.

Siblings emerged singly, not in groups. Only 9 of 67 photographs showed more than one hatchling on the surface at one time. When only nests in which all hatchlings emerged on the same night were considered, and three outliers were removed, the emergence interval between siblings was  $12.0 \pm 3.57 \text{ min}$  ((grand) mean  $\pm$  SE) ( $N = 14$  nests; range = 0.7–

**Fig. 2.** Photographs of *C. insculpta* hatchlings emerging from the nest, taken by remote cameras mounted above. In each photograph, a single hatchling (positioned between infrared transmitter and receiver boxes in each photograph) has broken the infrared beam, triggering the camera. The photograph on the left shows datalogger probes emanating from the nest. The photograph on the right shows emergence associated with a river rise and subsequent flooding of the nest chamber. Note the clear exit hole in this photograph.



46.3 min). A single-factor ANOVA revealed that rainfall during the previous 24 h did not significantly influence the mean emergence interval between siblings ( $F_{[1,16]} = 4.54$ ,  $p = 0.613$ ).

Emergence from nests on the same beach during the same night was observed on six occasions (in groups of 7, 7, 4, 2, 2, and 2 nests). Most synchronous emergence among nests within a beach was explained by nesting date (i.e., in 15 of 19 nests, nesting dates were within 2 days of hatchlings emerging from the other nest(s) that night).

## Discussion

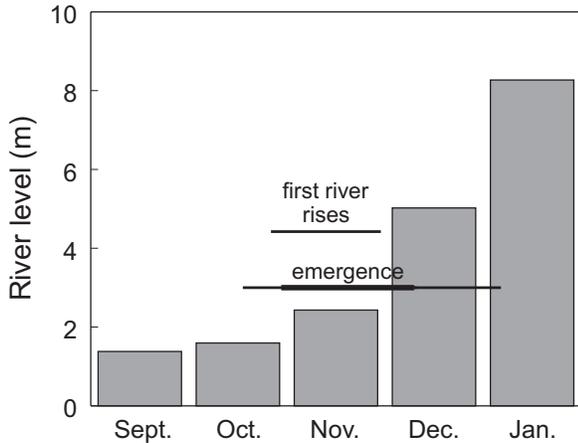
### Timing of emergence, embryonic aestivation, and onset of the wet season

*Carettochelys insculpta* hatchlings were more likely to emerge after rainfall. Emergence associated with rainfall has been documented for sea turtles (Carr 1984) and a few freshwater species (Hammer 1969; Alho and Padua 1982; DePari 1996; Kuchling 1999). Hatchlings of some turtle species

may depend on rainfall to soften or degrade the nest chamber so that they can emerge (DePari 1996). However, *C. insculpta* clutches are deposited in sand, and hatchlings are likely to be able to emerge without such softening. This is supported by our observations of hatchlings from 8 nests that emerged following rainless periods of 2–4 days. Butler and Graham (1995) found that rainfall during the previous 24 h was not necessary for inducing emergence in *Emydoidea blandingii*. Similarly, DePari (1996) found an imperfect association between rainfall and emergence in *Chrysemys picta*, and Tucker (1997) found no association between the presence or magnitude of rainfall and the emergence of *Trachemys scripta* hatchlings.

For Australian *C. insculpta*, however, rainfall also signals the onset of the wet season, which follows a long period of extremely dry conditions (e.g., mean monthly rainfall for May–September is 7 mm). After finding delayed hatching and hatching in response to anoxia in *C. insculpta* eggs in the laboratory, Webb et al. (1986) hypothesized that similar delays in nature would allow hatchlings to emerge and dis-

**Fig. 3.** Timing of emergence in *C. insculpta* is consistent with the first river rises of the wet season. Mean monthly river-stage data (histograms) and the period during which the first river rises occur (indicated by the extent of the upper horizontal bar) are for the years 1960 to 1996. Emergence data are from 1996–1998; in 1996–1997 these data were extrapolated from nesting dates. For emergence, the thicker line spans the range of mean first and last emergence dates for the 3 years, while the thinner line indicates the total range.



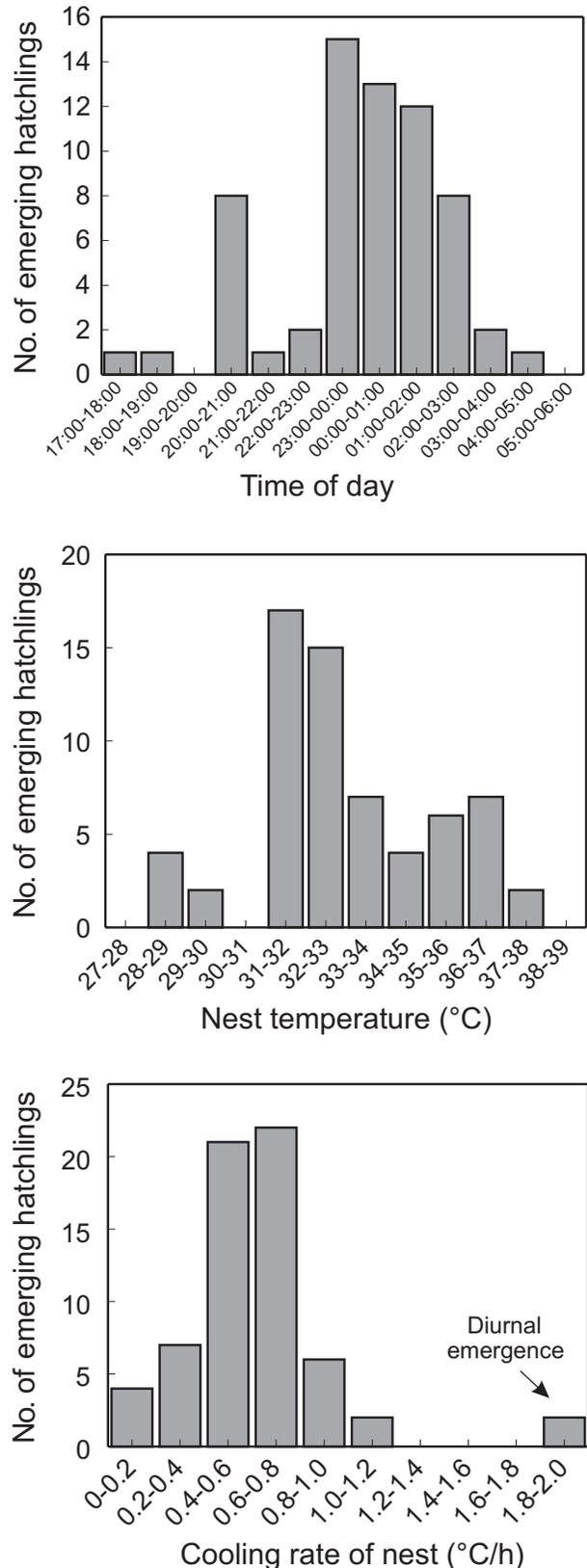
perse under the more favourable conditions of the wet season (flood waters). The results of the present study support both of these hypotheses.

First, delayed hatching was observed in nearly all nests (Fig. 1). On average, hatchlings spent 17 days in the ground at a hatchable stage, according to the developmental model that predicted the earliest date of completed development (Table 1, Fig. 1). The laboratory findings of Webb et al. (1986) indicated that turtles spent this time in the egg rather than as hatchlings. This was confirmed in our study by (i) inspection of eggs after the predicted hatching date and (ii) spontaneous hatching of eggs that were removed for sex determination for a concurrent study. Webb et al. (1986) also found that after yolk internalization, *C. insculpta* embryos cease developmental growth and the metabolic rate decreases precipitously. Thus, using the terminology of Ewert (1985), we conclude that *C. insculpta* exhibits embryonic aestivation.

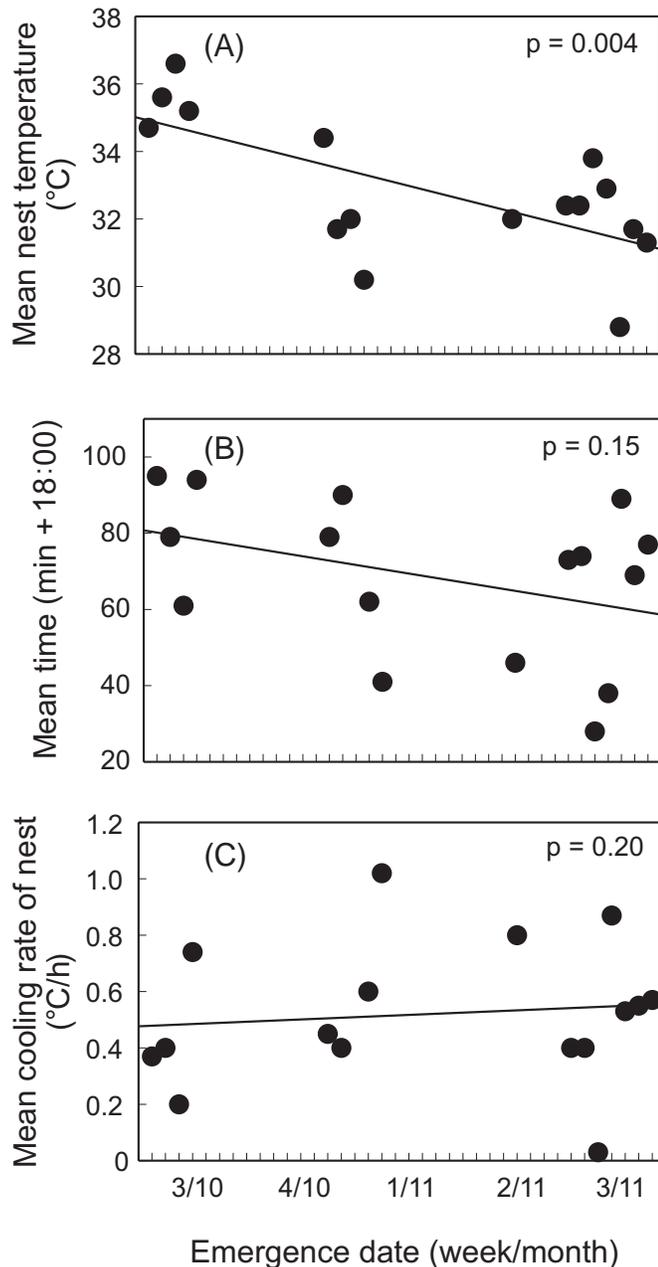
Second, historical river-stage data for 37 years and emergence data for 3 years indicate that most hatchlings emerged as river levels were rising (Fig. 3). Thus, embryonic aestivation may have evolved as a mechanism for optimizing timing of emergence and hence fitness, provided that hatchling survival or growth is favoured under wet-season conditions. From the results of the present study we cannot distinguish between the two proposed survival mechanisms (namely, a reduction in predator detection due to decreased water clarity, and lower hatchling densities because of greater water volume) proposed by Webb et al. (1986). We found that river rises of >0.3 m were invariably associated with a reduction in water clarity. Water visibility of 1–4 m during the dry season was reduced to a few centimetres by December.

The primary benefit of delayed emergence in turtles is said to be the “sanctuary offered during a period when growth benefits are likely to be outweighed by predation or mortality resulting from harsh environmental conditions” (Gibbons

**Fig. 4.** Emergence times, temperatures, and cooling rates of nests in relation to emergence of *C. insculpta* hatchlings. The cooling rate applies to the 3-h period prior to emergence.



**Fig. 5.** Tests of the three predictions generated from hypotheses concerning nocturnal emergence. Mean nest temperatures at emergence (A), mean emergence times (B), and mean cooling rates of nests preceding emergence (C) are plotted against emergence date. Cooling rates were measured across the 3 h prior to emergence.



and Nelson 1978). In a review of turtles known to exhibit different types of developmental arrest, Ewert (1985) concluded that in species with embryonic aestivation, late incubation is often associated with hot, dry conditions. Although these conditions persisted throughout incubation and aestivation in *C. insculpta*, it is unclear how they might affect

hatchlings in the river. It seems more likely that embryonic aestivation in *C. insculpta* has evolved to allow hatchlings to exploit early wet season survival or growth benefits rather than to avoid any particular stress caused by late dry season conditions.

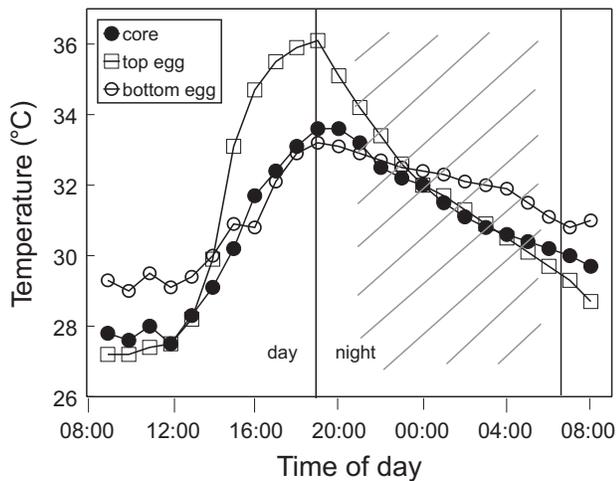
#### Emergence behaviour and the cue for nocturnal emergence

*Carettochelys insculpta* hatchlings emerged primarily at night. Nocturnal emergence in turtles is said to be adaptive, reducing the probability of heat stress, desiccation, and predation (Hendrickson 1958; Bustard 1967; Stancyk 1982). Support for the heat-stress mechanism comes from observations of hatchlings that emerged during the day and were scorched (Hughes and Richard 1974; Diamond 1976), and possibly in the behaviour of *Malaclemys terrapin* hatchlings, which head for cover immediately after diurnal emergence (Burger 1976). But how do hatchlings in the nest know when it is nighttime, assuming that they do not penetrate the surface? What signal could they use to emerge nocturnally?

Thermal cues were first implicated as the trigger for nocturnal emergence in sea turtle hatchlings, based on indirect evidence of inhibition of activity at some temperature threshold (Hendrickson 1958; Bustard 1967, 1972; Mrosovsky 1968, 1980; Heath and McGinnis 1980; O'Hara 1980). Earlier models suggested that hatchlings could avoid diurnal emergence by emerging below some absolute temperature (Hendrickson 1958; Bustard 1967; Mrosovsky 1968). More recently, Witherington et al. (1990) suggested that a rapid decrease in temperature may be an important thermal cue for *Caretta caretta*. In support of this, Hays et al. (1992) found that cooling rates of sand at 15 cm depth were linked to emergence times in that species. They added that diel and seasonal variations in sand temperatures made it doubtful that a single absolute temperature cue could reliably ensure nocturnal emergence. Gyuris (1993) also challenged the absolute temperature threshold hypothesis, producing a "thermal gradient model" to explain nocturnal emergence in *Chelonia mydas*. That work showed that the difference between sand temperatures at the surface and 10 cm depth was a more reliable predictor of darkness than an absolute temperature threshold. For the purpose of this discussion, cooling rates and thermal gradients are lumped into a "decreasing temperatures" model. Both are a way of describing a pulse of lower temperatures moving down through the sand, which is measured as a decrease in temperature at any given depth.

A goal of the present study was to determine which of these two models (absolute temperature threshold and decreasing temperatures) could better explain nocturnal emergence in *C. insculpta*. We generated the following predictions for each model, based on the knowledge that for our study population, throughout emergence air temperatures decline as the season progresses (because of an increase in cloud cover and rainfall). (i) If turtles were responding to an absolute temperature, a seasonal decrease in air temperatures would be likely to result in a shift of emergence to times earlier in the night so that hatchlings could emerge at the same temperature(s). (ii) On the other hand, if turtles were responding to a change in temperature, then the seasonal decline in air temperatures might result in a concordant decline

**Fig. 6.** Typical temperature trace from a *C. insculpta* nest relative to day/night. Data are taken from Georges (1992).



in emergence temperatures but no change in emergence times, because (iii) the cooling rate of sand does not change with season.

Our data fully support only one of these predictions: cooling rate did not change with season (Fig. 4). A seasonal decrease in air temperatures was associated with both lower emergence temperatures and earlier emergence (Fig. 4). Our data, therefore, were not sufficient to reject either model. However, subsequent analyses revealed that as the season progressed, temperatures began to drop earlier in the evening, probably because of increased cloud cover or rainfall. This would explain the apparent failure of the prediction of “no change” in emergence times with season generated for the decreasing-temperatures model.

We also found evidence refuting the fit of the absolute-temperature model to *C. insculpta* and, indeed, to other shallow-nesting turtles. In *C. insculpta*, higher nest temperatures are roughly symmetrical about dusk (Fig. 6), though heating rates are faster than cooling rates because there is a time lag in the pulse of heat moving down through the substrate. If an absolute temperature threshold existed, it would be reached twice in a 24-h period, once during the day and once at night (Fig. 6). In other words, nest temperatures are no higher during the day than at night. Thus, no absolute temperature threshold can serve as a nocturnal cue for emergence of *C. insculpta* hatchlings. Other nest-temperature data available in the literature indicate that the eggs of other shallow-nesting turtle species similarly do not experience an appreciable decline in temperature until near dusk (e.g., *Chelydra serpentina* in northeastern and central U.S.A., Wilhoft et al. 1983; Packard et al. 1985; *Emydura macquarii* and *Chelodina longicollis* in southeastern Australia, Thompson 1988; Palmer-Allen et al. 1991; *Podocnemis unifilis* in western Brazil, de Souza and Vogt 1994; *Kinosternon subrubrum* and *Pseudemys floridana* in southeastern U.S.A., Bodie et al. 1996). Thus, it appears that in most turtle nests a decline in temperature can serve as a reliable cue for nocturnal emergence, rainfall events notwithstanding. In agreement with this hypothesis, emergence in *C. insculpta* was restricted to times when nest temperatures were decreasing (Fig. 4).

Our results suggest that emerging *C. insculpta* hatchlings and those of other nocturnally emerging species are likely to be responding to either a particular rate of nest cooling, or simply a decrease in nest temperature. The latter alone could prevent diurnal emergence on hot, rainless days. As noted by Hays et al. (1992), the use of nest cooling as an emergence cue would explain the occasional diurnal emergence reported in sea turtles after rainfall (Carr 1984; Witherington et al. 1990).

The models are not necessarily mutually exclusive. There may be a temperature threshold above which activity is inhibited (e.g., in the present study no hatchlings emerged at nest temperatures  $>37^{\circ}\text{C}$ ), setting an upper limit on emergence temperatures, in addition to a nocturnal cue of decreasing temperature. Manipulation of the thermal environment of eggs, particularly using constant temperatures, would be useful for revealing the importance of a decrease in temperature to nocturnal emergence.

A few species of turtles, particularly sea turtles, deposit eggs in deeper nests by “body pitting,” or making a form in the substrate prior to constructing a nest cavity. In these nests only the topmost eggs may experience appreciable declines in diel temperature (e.g., see Fig. 5 in Maloney et al. 1990). However, because social facilitation is known in these species (Carr and Ogren 1960; Carr and Hirth 1961), it seems intuitive that the uppermost hatchlings could make the “decision” as to when to emerge, with hatchlings from deeper in the nest following their lead. This idea is supported by experiments with *C. mydas* by Bustard (1967), who found that by removing the topmost hatchlings from the nest he could induce the others to emerge in daylight. Carr and Hirth (1961) reported that the entire group of hatchlings moves upwards as they dig away at the roof of the nest chamber. In this scenario, hatchlings from the bottom would move up into a zone experiencing temperature declines associated with nighttime. Mrosovsky (1968) documented that the uppermost hatchlings emerge from a depth of about 10 cm. This is very similar to the depth to the top egg in *C. insculpta* nests. We suggest, therefore, that hatchlings of turtles that emerge primarily at night do so from a depth which allows them to perceive a decline in temperature associated with nighttime.

### Other behaviour

Timing-of-emergence (diel) data for turtles are sparse (Table 2), and are biased in favour of sea turtles and turtles nesting in open habitats (free of vegetation), where nests are easier to find. Despite few data, a pattern may exist. In Table 2, the eight species emerging in open habitats do so at night (and in the early morning), while the three species emerging in (at least partially) vegetated habitats emerge during the day. Data regarding the two *Graptemys* species are difficult to interpret because hatchlings emerged near the vegetated edge of large open sandbars. Although these two species would eventually have to traverse open sand, they appeared to have the option of moving into vegetation. It is worth noting that two of the three daytime-emerging species, *Malaclemys terrapin* and *E. blandingii*, headed for vegetation immediately after emergence or release at midday (Burger 1976; Butler and Graham 1995). Species or populations that nest in vegetated areas may be freed of the “constraint”

**Table 2.** Primary emergence times and nesting habitats of various turtle species gleaned from the literature.

	Primary emergence	Nesting habitat	Investigation(s)
<i>Caretta caretta</i>	Night	Open	Witherington et al. 1990; Hays et al. 1992
<i>Chelonia mydas</i>	Night	Open	Hendrickson 1958; Gyuris 1993
<i>Lepidochelys olivacea</i>	Night/early morning	Open	Hughes and Richard 1974
<i>Eretmochelys imbricata</i>	Night	Open	Diamond 1976; Limpus 1980
<i>Dermochelys coriacea</i>	Night	Open	Carr and Ogren 1959
<i>Apalone mutica</i>	Night/early morning	Open	Muller 1921; Anderson 1958
<i>Podocnemis expansa</i>	Night/early morning	Open	Alho and Padua 1982; Rose 1964
<i>Malaclemys terrapin</i>	Day	Vegetated	Burger 1976
<i>Trachemys scripta</i>	Day	Vegetated	Tucker 1997
<i>Emydoidea blandingii</i>	Day	Vegetated	Congdon et al. 1983; Butler and Graham 1995
<i>Chelydra serpentina</i>	Day	Open/vegetated	Congdon et al. 1999
<i>Graptemys pulchra</i>	Nocturnal	Open/vegetated	Anderson 1958
<i>Graptemys oculifera</i>	Nocturnal	Open/vegetated	Anderson 1958
<i>Carettochelys insculpta</i>	Nocturnal	Open	This study

of nocturnal emergence by being able to remain in vegetation until conditions are suitable for moving to the water. While these findings are consistent with an adaptive explanation for nocturnal emergence, emergence data for more species are needed to facilitate a comparative study of any potential adaptive advantage.

*Carettochelys insculpta* siblings usually emerged on the same night, but in several nests emergence spanned 2 or more nights, roughly agreeing with the results of studies on sea turtles (e.g., Peters et al. 1994; but see Hays et al. 1992), *C. serpentina* (Congdon et al. 1987), and *M. terrapin* (Burger 1976). Congdon et al. (1983) found that roughly half of *E. blandingii* hatchlings emerged the same night, while Butler and Graham (1995) found that *E. blandingii* siblings emerged over several days.

Carr and Hirth (1961) suggested that mass emergence, often observed in sea turtles, would be advantageous because emerging hatchlings stimulate one another to crawl more quickly to the ocean. *Carettochelys insculpta* siblings that emerged the same night did not emerge simultaneously in one group or a few groups, but generally trickled forth from the nest one at a time, usually separated by intervals of at least 1 min. These data, combined with the short distance (<4 m) hatchlings traverse to the water, do not support adaptive mass emergence within or among clutches in *C. insculpta*. However, the data presented in our study are from 1 year only. In years when rainfall events are more intense and coincide with the presence of mature hatchlings in the nest, hatching synchrony within and among nests may be more evident. In 1986, for example, seven mature clutches of *C. insculpta* eggs were placed in artificial nests. None hatched following a rain shower of 29.2 mm on 10 November, but 4 of the 7 nests hatched after a rain shower of 52.2 mm on 19 November (A. Georges, unpublished data). No rainfall events of this intensity were experienced during the majority of emergence events that occurred in the present study.

Emergence in small groups has also been documented in sea turtles (e.g., Christens 1990; Witherington et al. 1990), and *E. blandingii* hatchlings are known to emerge singly (Butler and Graham 1995). The logistical difficulty in monitoring emergence has resulted in a paucity of such data, especially for freshwater turtles (Ehrenfeld 1979; Christens

1990; Kuchling 1999). Future studies may show single emergence in other freshwater species.

In summary, *C. insculpta* hatchlings exhibit embryonic aestivation in nature, a characteristic that has probably evolved to synchronize emergence with the onset of wet-season conditions. On a diel scale, we erroneously predicted that season would not influence emergence times under the decreasing-temperatures model because we were unaware that temperatures begin falling earlier in the day later in the season. Absolute nest temperatures were no lower at night than during the day. Based on published nest-temperature data, temperatures in turtle nests worldwide begin to decrease late in the evening. We suggest that in nocturnally emerging species this decrease triggers emergence. As emergence data for turtles are scarce, few comparisons can be made at this time. However, we hope that the remote photographic technique we used will be adopted for investigations into the emergence behaviour of other turtle species.

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