

F. Glen · A. C. Broderick · B. J. Godley · G. C. Hays

## Patterns in the emergence of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtle hatchlings from their nests

Received: 20 May 2003 / Accepted: 6 October 2004 / Published online: 27 November 2004  
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**Abstract** The emergence patterns of both green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtle hatchlings were observed in great detail over three seasons at Alagadi beach, northern Cyprus. In total, 38 green turtle and 50 loggerhead turtle nests were monitored, accounting for the emergence of 2,807 and 2,259 hatchlings, respectively. We quantified these emergences into 397 green turtle and 302 loggerhead turtle emergence groups. Overall, 85.0% of green turtle and 79.5% of loggerhead turtle groups emerged at night; these accounted for 85.5 and 90.8% of hatchlings, respectively. The remaining emergences were dispersed throughout the day for green turtle nests but confined to the morning in loggerhead turtle nests. Hatchling emergence from individual nests occurred over periods of between 1 and 7 nights, with most hatchlings typically emerging on the first night. Group sizes of green turtles emerging during the day were significantly smaller than those emerging at night. Hatchlings of both species that emerged from nests during the day had longer emergence durations than those that emerged from nests at night only.

### Introduction

For sea turtle hatchlings, the timing and pattern of emergence from the nest is crucial in determining their survivorship. For example, by emerging at night, a hatchling will avoid potential diurnal predators and lethal daytime temperatures. Most hatchlings do emerge at night (Bustard 1967; Mrosovsky 1968; Witherington et al. 1990; Gyuris 1993), but some daytime emergence does occur (Bustard 1967; Mrosovsky 1971; Balazs 1974; Le Gall et al. 1985; Drake and Spotila 2002) and has been estimated at 3 and 8% of all green turtle (*Chelonia mydas*) emergences (Bustard 1967; Le Gall et al. 1985). Although studies have shown that daytime sand temperatures at sub-surface depths are important in confining hatchling emergence to night, few studies report on group dynamics during emergence (Hendrickson 1958; Bustard 1967; Mrosovsky 1968; Witherington et al. 1990; Hays et al. 1992; Moran et al. 1999; Drake and Spotila 2002; Glen 2002); indeed, the classification of an emergence event when investigating behavioural cues varies among studies. For example, group size was usually assigned as between 10 and 20 hatchlings, with those hatchlings emerging from the sand in smaller groups being omitted from subsequent analyses (Witherington et al. 1990; Gyuris 1993; Moran et al. 1999).

Hatchlings emerge from the sand typically 4–7 days after they hatch from the egg (see Godfrey and Mrosovsky 1997 for a review), often running a gauntlet of land-based and aerial predators as they move toward the sea (Stancyk 1995). This movement to the sea in groups is thought to reduce the probability of an individual being killed through predator dilution (Davenport 1997; Dehn 1990). Another anti-predator strategy includes becoming immobile and “playing dead” during an aerial attack (Bushong et al. 1996). Through natural selection, we would expect that evolution would have favoured a mass exodus from the nest over 1 or 2 nights, producing large groups of hatchlings, increasing the probability of

Communicated by R.J. Thompson, St. John's

F. Glen (✉) · G. C. Hays  
School of Biological Sciences,  
Institute of Environmental Sustainability,  
University of Wales Swansea,  
Swansea, Wales, SA2 8PP, UK  
E-mail: fglen1@hotmail.com  
Fax: +44-1792-295447

A. C. Broderick · B. J. Godley  
Marine Turtle Research Group,  
Centre for Ecology and Conservation,  
University of Exeter in Cornwall,  
Penryn, Cornwall, TR10 9EZ, UK

*Present address:* F. Glen  
16, Eshton Terrace, Clitheroe, Lancashire, BB7 1BQ, UK

an individual successfully making it to the sea. However, when reviewing the literature, although studies do record a level of synchrony in emergence (e.g. Witherington et al. 1990), that is, where predominantly all hatchlings leaving their nest in 1 night, considerable asynchrony has also been observed. Hatchlings have been recorded to emerge for periods of up to 4 days in nests of the hawksbill turtle (*Eretmochelys imbricata*) and 3–8 days for the green turtle (Balazs 1974; Diamond 1976). Loggerhead turtle hatchlings have been recorded as emerging for periods of up to 11 nights (Hays et al. 1992; Houghton and Hays 2001), a possible consequence of eggs within the same clutch being subject to different incubation temperatures. The implications of waiting in the egg chamber, post hatching, delaying emergence for an extended period are certainly not trivial, with the probability of predation, loss of energy while waiting within the egg chamber, and dipteran infestation increasing over time (Godley and Kelly 1996; Hays et al. 1992; McGowan et al. 2001).

Once at sea, inshore waters are thought to pose a significant challenge to survival of neonates, with high numbers of hatchlings being taken at many sites by bony fish, sharks, and birds (Stancyk 1995). It has been shown that aquatic predation is lowered when the number of hatchlings being released into the sea at any one time is decreased (Wyneken et al. 1998). For example, predation of green turtle hatchlings was nearly 50% higher when they were released en masse rather than in smaller groups (Pilcher et al. 2000). In Australia, aquatic predation was comparable during both day and night (Gyuris 1994), although hatchlings close inshore during the day were more likely to be taken by aerial predators (Stancyk 1995; Glen 2002). Selection, therefore, may favour asynchrony of emergence and smaller hatchling emergence groups.

The present study was based on Alagadi beach, the main nesting site for both green and loggerhead turtles in northern Cyprus (Broderick and Godley 1996; Broderick et al. 2002). The moderate number of nests laid on Alagadi, combined with the short beach length, allowed us to monitor intensively patterns of hatchling emergence from a relatively large proportion of individual nests of two marine turtle species.

## Materials and methods

### Study site

The study was conducted on Alagadi beach (35°33'N, 33°47'E) northern Cyprus, in the eastern Mediterranean (range of seasonal total of nests from 1993 to 2000: loggerhead: 38–95 per season, green: 8–111 per season). The beach consists of two short coves, 0.8 and 1.2 km long, separated by a rocky headland and backed by extensive dunes and low scrub. There is no natural shading of the beach and although there is a high level of human activity, it is confined to the water's edge, a re-

gion in which no clutches are laid. The climate is typical of the eastern Mediterranean, with virtually no rain from May to October and mean daily air temperature for each 24 h during this period ranging from 20 to 30°C (Godley et al. 2001).

Aerial and diurnal onshore predation of marine turtle hatchlings on Alagadi is negligible. Onshore nocturnal predation is more common, with the ghost crab (*Ocy-pode cursor*) and the red fox (*Vulpes vulpes*) actively taking those hatchlings on their way to the sea. Fish density off the nesting beaches is, as in much of the eastern Mediterranean, relatively low. Large predatory fish capable of taking hatchlings are occasionally caught by fishermen in the area, but their density is unknown.

### Data collection

Hatchling emergence patterns were observed in 1997 and 1998 for green turtles, and in 1997 and 1999 for loggerhead turtles. Nesting of both species on Alagadi occurs between May and August. During this period, the beach was monitored nightly from 2100 to 0800 hours (+2 h GMT) by three pairs of observers. Once a nesting female was encountered, the species established, and egg deposition was complete, the position of the nest was recorded by triangulating to marker posts at 50-m intervals at the back of the beach. To prevent predation by dogs and foxes, a numbered 1.5×1.5-m anti-predation wire screen was placed over each nest.

Incubation periods for the green turtle on Alagadi beach are known to be from 43 to 60 days (Broderick et al. 2000) and for the loggerhead from 42 to 58 days (Godley et al. 2001). Forty days after egg deposition, a circular wire-mesh corral of 1.6 m diameter and 35 cm depth (mesh size 1×2 cm) was placed around the nest to prevent emergent hatchlings from making their way to the sea. Previous screening that had been placed over nests into the sand immediately after laying was lifted and placed on top of the circular cage, thus acting as a cover to prevent predation. Once caged, the sand inside the corral was not disturbed.

Throughout the study, Alagadi beach was monitored constantly from 2000 to 0800 hours every night, during which each cage was checked every 20 min for hatchling activity. Once hatchling activity was observed, the nest was monitored constantly. Between 1930 and 2000 hours every night the circular cages were closed, the surrounding area checked for tracks of hatchlings that might have emerged during the day, and placements checked to ensure their integrity as a barrier. At 0800 hours the cages were re-opened, forming a U-shape with the exit facing the sea. Opening of the cages was a necessary precaution as daytime emergent hatchlings, emerging into a closed cage during the day, would certainly have perished. To counter this possibility, nests that had produced hatchlings after 0500 hours were monitored by pairs of observers throughout the following day. Any hatchlings that emerged after

0600 hours were kept and released that evening. We classified nocturnal emergence as that occurring between 2100 and 0600 hours.

Hatchling heads were often found to be slightly protruding through the sand, remaining in situ for periods of up to 4 h (personal observation and Bustard 1967). We recorded the time of emergence of each hatchling once it had completely emerged from the sand. All hatchlings were left to emerge without assistance. Excavation of the nest contents was undertaken once 48 h had elapsed with no hatchling emergence. Depth to the top and bottom of the egg chamber was measured, unhatched eggs and hatched shell fragments were enumerated, and clutch size and hatch success were determined. Occasionally, tracks leading away from nests indicated that hatchlings had emerged eccentrically outside the corral and had made their way to the sea unimpeded. Nests in which this happened were omitted from the study. We were confident that for the nests used in the analysis, all hatchling emergences were recorded, as we were able to compare the number of hatchlings observed with the number of eggshell fragments counted upon excavation (Paired  $t$  test:  $t_{87} = -0.82$ ,  $P > 0.05$ ).

### Statistical analysis

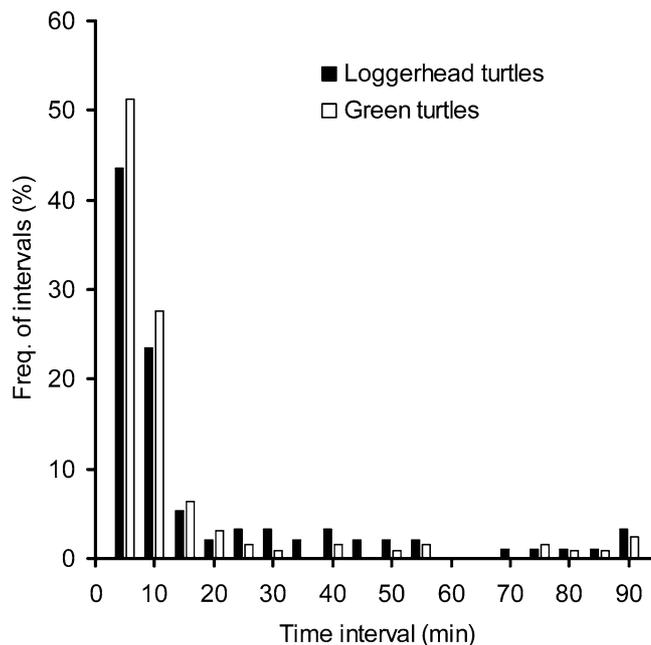
Data were analysed using MINITAB version 11.21. Non-parametric analyses included the Mann–Whitney  $U$  test and the Kolmogorov–Smirnov two-sample test. Differences were considered significant at  $P < 0.05$ .

### Defining an emergence group

Although hatchlings emerged in groups, each hatchling emerged at a discrete point in time: often these were so close together in time that they were indistinguishable from others. However, discrete intervals were recorded and to define objectively a hatchling emergence group with a level of biological reality, we plotted the frequency histogram of time intervals. There was a clear cut-off point, with 78.7% of all intervals for green turtles, and 67.0% of all intervals for loggerhead turtle hatchlings being 10 min or less (Fig. 1). Therefore we classified a group as those hatchlings whose emergences were separated by intervals equal to or less than 10 min.

### Defining synchrony of emergence

The length of time for which a nest produces hatchlings can be defined in numerous ways; for example, the number of nights between the first and last emergence is the “emergence duration”. However, as this may include nights when very few or no hatchlings emerged, it does not provide a clear picture of the level of synchrony of hatchling emergence. We therefore calculated an index



**Fig. 1** Frequency histogram of all the time intervals between consecutive emergences throughout the study period for green turtle hatchlings (open bars) in both 1997 and 1998 and loggerhead turtle hatchlings (filled bars) in both 1997 and 1999

of emergence synchrony using the following equation, where  $h$  is the number of hatchlings that emerge on night  $i$ , divided by the total number of hatchlings that emerge over the entire nest emergence period. A value of 1 represents all hatchlings emerging on night 1.

$$\text{Index} = \frac{\sum_{i=1}^{i=n} (h_i \times i)}{h_{\text{total}}}$$

## Results

### Green turtles

#### Study nests

Hatchling emergence was monitored in 9 nests in 1997 and 29 nests in 1998; the basic nest parameters are provided in Table 1. No significant inter-seasonal difference was observed in medians of clutch size, emergence success, incubation duration, depth of the eggs, and the number of live/dead hatchlings found in the egg chamber upon excavation (Table 1; Mann–Whitney  $U$  test,  $P > 0.05$  in all cases).

#### Temporal pattern of emergence

In 1997, 785 hatchlings in 90 emergence groups were recorded (Fig. 2a, b). In total, 2,022 hatchlings were observed in 1998 (Fig. 2c), in 307 emergence groups (Fig. 2d). Despite a statistically significant difference in

**Table 1** Basic parameters of nests monitored in this study. Distance to the high water mark (HWM) is only available for nests laid in 1998 and 1999

	Green turtles			Loggerhead turtles			Mann-Whitney test
	Mean $\pm$ SD (Range)		Mann-Whitney test	Mean $\pm$ SD (Range)		Mann-Whitney test	
	1997 <i>n</i> = 9 nests	1998 <i>n</i> = 29 nests		1997 <i>n</i> = 21 nests	1999 <i>n</i> = 29 nests		
Clutch size	129.1 $\pm$ 26.9 (80–171)	109.4 $\pm$ 24.4 (51–155)	<i>W</i> = 542.0, <i>P</i> = 0.06	72.3 $\pm$ 18.5 (25–100)	71.0 $\pm$ 21.3 (12–110)	<i>W</i> = 666.0, <i>P</i> = 0.9	
Incubation duration (days)	49.9 $\pm$ 3.3 (46–57)	48.1 $\pm$ 3.1 (43–54)	<i>W</i> = 459.0, <i>P</i> = 0.1	47.6 $\pm$ 2.5 (42–51)	47.0 $\pm$ 2.9 (43–55)	<i>W</i> = 558.0, <i>P</i> = 0.2	
Emergence success (%)	70.2 $\pm$ 27.0 (1.2–97.4)	73.8 $\pm$ 30.2 (1.5–100)	<i>W</i> = 517.0, <i>P</i> = 0.5	79.2 $\pm$ 25.8 (42.6–98.8)	78.2 $\pm$ 30.0 (13.3–100)	<i>W</i> = 604.0, <i>P</i> = 0.2	
Depth to the top of the eggs (cm)	68.8 $\pm$ 10.2 (45–85)	66.0 $\pm$ 9.6 (45–83)	<i>W</i> = 548.0, <i>P</i> = 0.5	38.0 $\pm$ 7.6 (26–55)	34.1 $\pm$ 8.8 (14–50)	<i>W</i> = 603.5, <i>P</i> = 0.2	
Depth to the bottom of the eggs (cm)	91.4 $\pm$ 7.7 (81–109)	85.1 $\pm$ 10.4 (68–106)	<i>W</i> = 486.0, <i>P</i> = 0.1	51.6 $\pm$ 7.4 (34–66)	51.3 $\pm$ 7.9 (37–69)	<i>W</i> = 648.5, <i>P</i> = 0.8	
No. of live hatchlings counted upon nest excavation	17.2 $\pm$ 30.3 (0–106)	16.3 $\pm$ 26.5 (0–115)	<i>W</i> = 575.5, <i>P</i> = 0.9	5.7 $\pm$ 11.2 (0–49)	4.8 $\pm$ 8.3 (0–33)	<i>W</i> = 687.0, <i>P</i> = 0.6	
No. of dead hatchlings counted upon nest excavation	8.3 $\pm$ 15.4 (0–55)	5.9 $\pm$ 8.0 (0–30)	<i>W</i> = 576.0, <i>P</i> = 0.9	1.9 $\pm$ 2.7 (0–8)	6.5 $\pm$ 13.5 (0–60)	<i>W</i> = 692.5, <i>P</i> = 0.5	
Distance to HWM (m)		18.4 $\pm$ 14.7 (3.5–62.0)			9.9 $\pm$ 8.1 (2.2–43.2)		

the temporal patterns of emergence between the two years, it can be seen that in both years, the majority of emergence occurred at night [Kolmogorov–Smirnov two-sample test, group distribution:  $D_{1,47} = 0.19$ ,  $P < 0.05$ ; hatchling distribution:  $D_{1,47} = 0.19$ ,  $P < 0.05$ ; Fig. 2, hatchling distribution: 1997:0330, interquartile (IQ) range: 0130–0500; 1998:0130, IQ range: 2330–0430; group distribution: 1997:0400, IQ range: 0300–0530; 1998:0300, IQ range 0000–0630). Nocturnal emergence accounted for 85% of the total number of hatchlings in both years. Although dispersed throughout the day, the remainder, accounting for 30% of group emergences, occurred diurnally in both years.

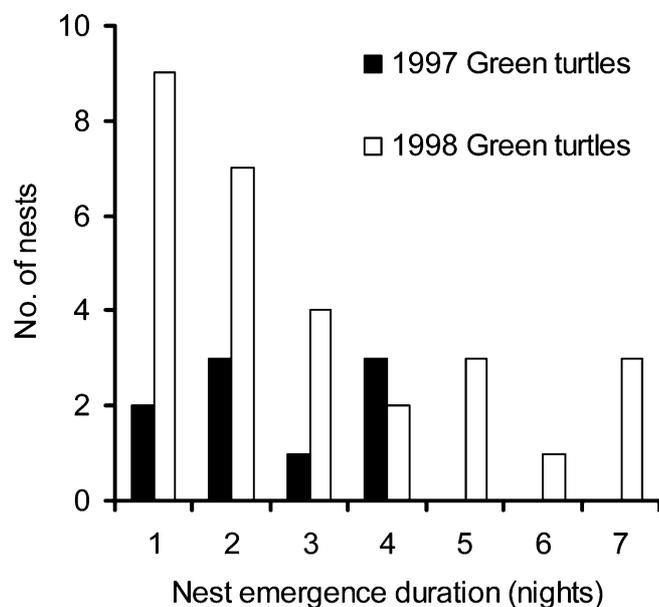
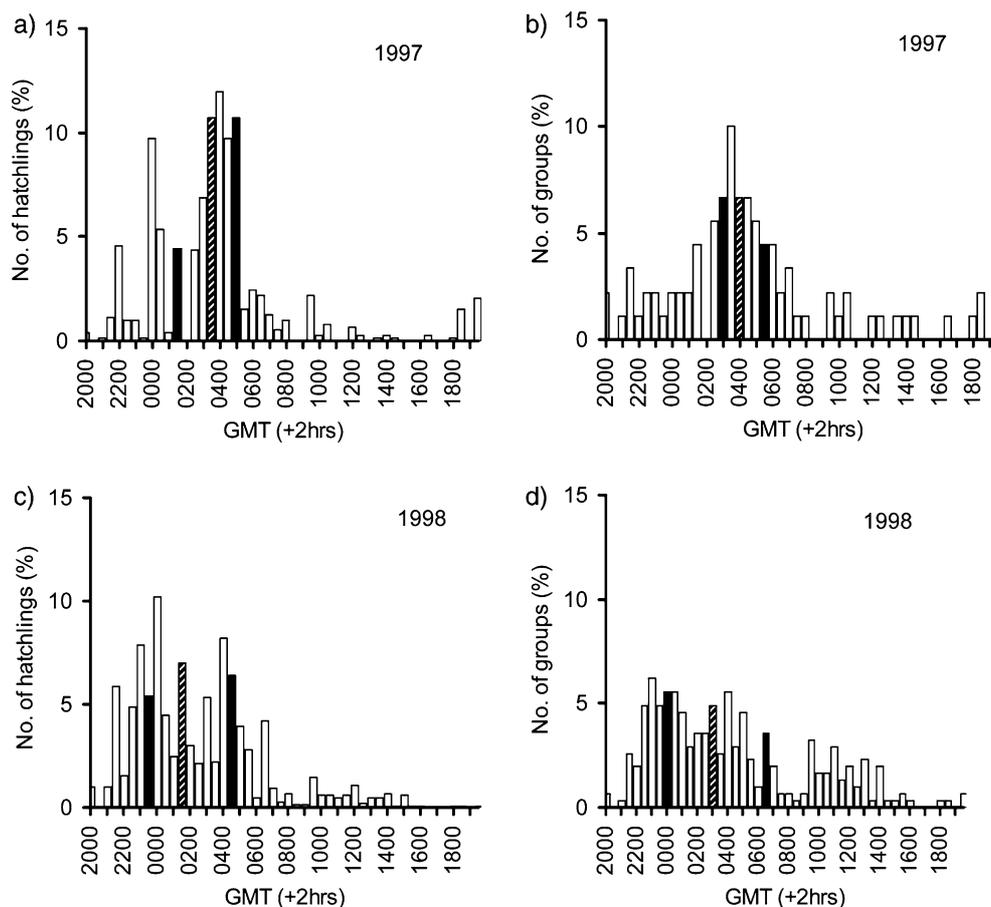
#### Duration and synchrony of emergence

Nests produced hatchlings for between 1 and 4 nights in 1997, and between 1 and 7 nights in 1998 (Fig. 3). In total, 66 and 69% of nests produced hatchlings for periods of 3 nights or less in 1997 and 1998, respectively. No significant difference between years was observed in the emergence duration (1997: median = 2, IQ range = 1.5–4.0; 1998: median = 2, IQ range = 1.0–4.5, Mann–Whitney *U* test  $W = 172.5$ :  $P = 0.9$ ) or the emergence synchrony (1997: median = 1.1, IQ range = 1.0–1.3; 1998: median = 1.1, IQ range = 1.0–1.9, Mann–Whitney *U* test  $W = 506.5$ :  $P = 0.8$ ) of the study nests.

When both the 1997 and 1998 data sets were combined, neither nest emergence duration nor emergence synchrony was influenced by incubation duration, depth to the top or bottom of the clutch, emergence success, clutch size, or the number of live and dead hatchlings found in the nest upon excavation (Table 2). Distance of each nest to the high water mark was available for 1998, although no relationship was observed between this measurement and emergence duration or the index of emergence synchrony (Table 2).

In each season, over half of the nests produced hatchlings both at night and during the day, with hatchlings emerging only at night from 41% (1997) and 44% (1998) of nests. No nests produced hatchlings during the day only. However, when both years were pooled, nests that had hatchlings emerging during the day and night were less synchronous than those nests that produced hatchlings at night alone (Index of synchrony: day and night: median = 1.7, IQ range = 1.1–2.1; night only: median = 1.0, IQ range = 1.0–1.1, Mann–Whitney *U* test  $W = 126.0$ ,  $P < 0.001$ ; Emergence duration: day and night: median = 3.7, IQ range = 2.0–5.0; night only: median = 1.0, IQ range = 1.0–2.0, Mann–Whitney *U* test  $W = 111.5$ ,  $P < 0.001$ ). However, there was no significant difference between the two types of nests in incubation duration ( $W = 266.0$ ,  $P = 0.14$ ), depth to the top ( $W = 248.5$ ,  $P = 0.95$ ) or bottom ( $W = 195.5$ ,  $P = 0.18$ ) of the clutch, emergence success ( $W = 233.0$ ,  $P = 0.88$ ), clutch size ( $W = 220.0$ ,  $P = 0.45$ ) and the number of hatchlings, both live ( $W = 207.0$ ,  $P = 0.26$ ) and dead ( $W = 266.5$ ,  $P = 0.57$ ) found in the nest upon excavation.

**Fig. 2** Temporal distribution of all green turtle hatchling emergence condensed into half-hour intervals in **a** 1997 ( $n=9$  nests; 785 hatchlings) and **c** 1998 ( $n=29$  nests; 2,022 hatchlings), and all hatchling groups in **b** 1997 ( $n=90$  groups) and **d** 1998 ( $n=307$  groups). Hashed bars indicate the median, and solid bars the upper and lower quartile ranges of the proportion of hatchlings or group emergences



**Fig. 3** The number of nights over which green turtle nests had hatchlings emerging in 1997 (solid bars,  $n=9$  nests) and 1998 (open bars,  $n=29$  nests)

#### Group size

In general, the greatest proportion of hatchlings emerged from their nest on night 1 (1997:83.5% Fig. 4a;

1998:71.8% Fig. 4c), with a general pattern of progressively smaller proportions of hatchlings emerging on each subsequent night. The majority of hatchling emergence groups were small, with groups of 1–5 hatchlings constituting 59.3% of groups in 1997 and 71.0% of groups in 1998. However, these groups only accounted for 15.7 (1997) and 19.8% (1998) of hatchlings (Fig. 4b, d). In both years, 46% of hatchlings emerged in groups of 21 or more hatchlings, which only constituted 11.0 (1997) and 7.4% (1998) of groups.

Diurnally emergent groups were smaller in size (1997 median = 2, IQ range 1–8; 1998 median = 1, IQ range 1–3) than those emerging at night (1997: median = 4, IQ range 2–16; 1998 median = 3, IQ range 1–8; Mann–Whitney 1997:  $W=3105.0$ ,  $P<0.05$ ; 1998:  $W=33148.0$ ,  $P<0.0001$ ).

#### Loggerhead turtles

##### Study nests

In 1997, loggerhead hatchling emergence was monitored from 21 nests, and in 1999, a further 29 loggerhead nests were monitored. Nest parameters are provided in Table 1. No significant inter-seasonal difference was observed in medians of clutch size, emergence success, incubation duration, depth of the eggs, and the number

**Table 2** Relationship between emergence duration/synchrony and nest parameters (results obtained through regression analysis)

	Green turtles		Loggerhead turtles	
	1997 and 1998		1999	
	<i>n</i> = 38 nests	<i>n</i> = 21 nests	<i>n</i> = 29 nests	<i>n</i> = 29 nests
	Emergence duration	Emergence synchrony	Emergence duration	Emergence synchrony
Incubation duration (days)	$F_{1, 37} = 1.85, P = 0.18$	$F_{1, 37} = 1.46, P = 0.24$	$F_{1, 20} = 27.8, P < 0.05,$ $r^2 = 0.59$	$F_{1, 28} = 4.67, P < 0.05,$ $r^2 = 0.13$
Depth to the top of the clutch (cm)	$F_{1, 37} = 0.72, P = 0.56$	$F_{1, 37} = 0.55, P = 0.47$	$F_{1, 20} = 3.73, P = 0.07$	$F_{1, 28} = 1.50, P = 0.23$
Depth to the bottom of the clutch (cm)	$F_{1, 37} = 0.59, P = 0.48$	$F_{1, 37} = 1.13, P = 0.30$	$F_{1, 20} = 0.76, P = 0.40$	$F_{1, 28} = 1.77, P = 0.20$
Emergence success	$F_{1, 37} = 0.09, P = 0.76$	$F_{1, 37} = 0.29, P = 0.60$	$F_{1, 20} = 0.03, P = 0.86$	$F_{1, 28} = 1.93, P = 0.18$
Clutch size	$F_{1, 37} = 0.07, P = 0.80$	$F_{1, 37} = 0.0, P = 0.99$	$F_{1, 20} = 3.47, P = 0.08$	$F_{1, 28} = 2.72, P = 0.11$
No. of live hatchlings counted upon nest excavation	$F_{1, 37} = 0.13, P = 0.72$	$F_{1, 37} = 1.04, P = 0.32$	$F_{1, 20} = 0.28, P = 0.60$	$F_{1, 28} = 1.41, P = 0.25$
No. of dead hatchlings counted upon nest excavation	$F_{1, 37} = 1.41, P = 0.24$	$F_{1, 37} = 0.02, P = 0.89$	$F_{1, 20} = 4.35, P = 0.06$	$F_{1, 28} = 0.01, P = 0.96$
Distance to HWM (m)	$F_{1, 28} = 0.08, P = 0.80$	$F_{1, 27} = 0.27, P = 0.60$		$F_{1, 28} = 1.90, P = 0.20$
				$F_{1, 27} = 0.76, P = 0.40$

of live and/or dead hatchlings found in the egg chamber upon excavation of the nest (Table 1; Mann–Whitney *U* test,  $P > 0.05$  in all cases).

#### Temporal pattern of emergence

In 1997, the emergence of 1,069 hatchlings (Fig. 5a) was classified as occurring in 96 groups (Fig. 5b); in 1999, 1,190 hatchlings (Fig. 5c) emerged in 206 groups (Fig. 5d). Although there was a significant difference in emergence patterns between the two years (Kolmogorov–Smirnov two-sample test: hatchling distribution  $D_{1,29} = -0.22, P < 0.05$ ; group distribution  $D_{1,29} = -0.17, P < 0.05$ ), emergence predominantly occurred at night in both years, with patterns broadly similar between the two years (hatchling emergence patterns: 1997 median: 0230, IQ range: 0100–0330; 1999 median: 0130, IQ range: 0030–0300; group emergence patterns: 1997 median: 0200, IQ range: 0030–0430; 1999 median: 0230, IQ range: 0130–0500, Fig. 5). Diurnal emergence did occur, although not past 1030 hours in either year, accounting for 8 and 12.5% of hatchling emergences in 1997 and 1999, respectively.

#### Duration and synchrony of emergence

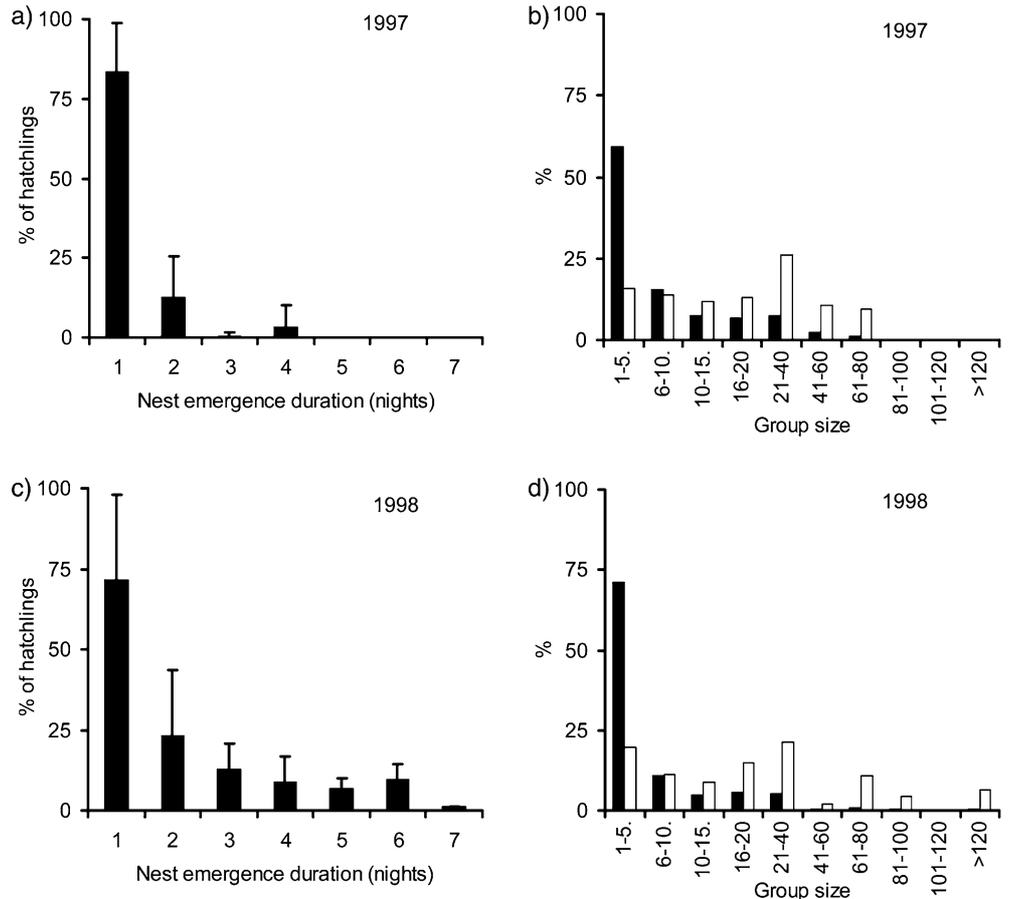
Nests produced hatchlings for 1–7 nights in 1997 and 1–6 nights in 1999 (Fig. 6). A total of 76.2 and 69.0% of nests produced hatchlings for 3 nights or less in 1997 and 1999, respectively. A significant difference between years was observed in both emergence duration and emergence synchrony, where nests in 1999 had longer emergence durations and were more asynchronous than those in 1997 (emergence duration: 1997: median = 2.7, IQ range = 2.0–4.0; 1999: median = 2.1, IQ range = 1.0–3.0, Mann–Whitney *U* test:  $W = 409.5, P < 0.05$ ; index of synchrony: 1997: median = 1.0, IQ range = 1.0–2.7; 1999: median = 1.2, IQ range = 1.0–2.9, Mann–Whitney *U* test:  $W = 769.0, P < 0.05$ ).

For either year, neither emergence duration nor emergence synchrony was significantly influenced by the depth to the bottom or top of the clutch, emergence success, or the number of live and/or dead hatchlings counted upon excavation of the nest (Table 2). However, in both years, nests with long emergence durations were observed to have short incubation durations and lower indices of emergence synchrony (see Table 2 and Fig. 7b, d).

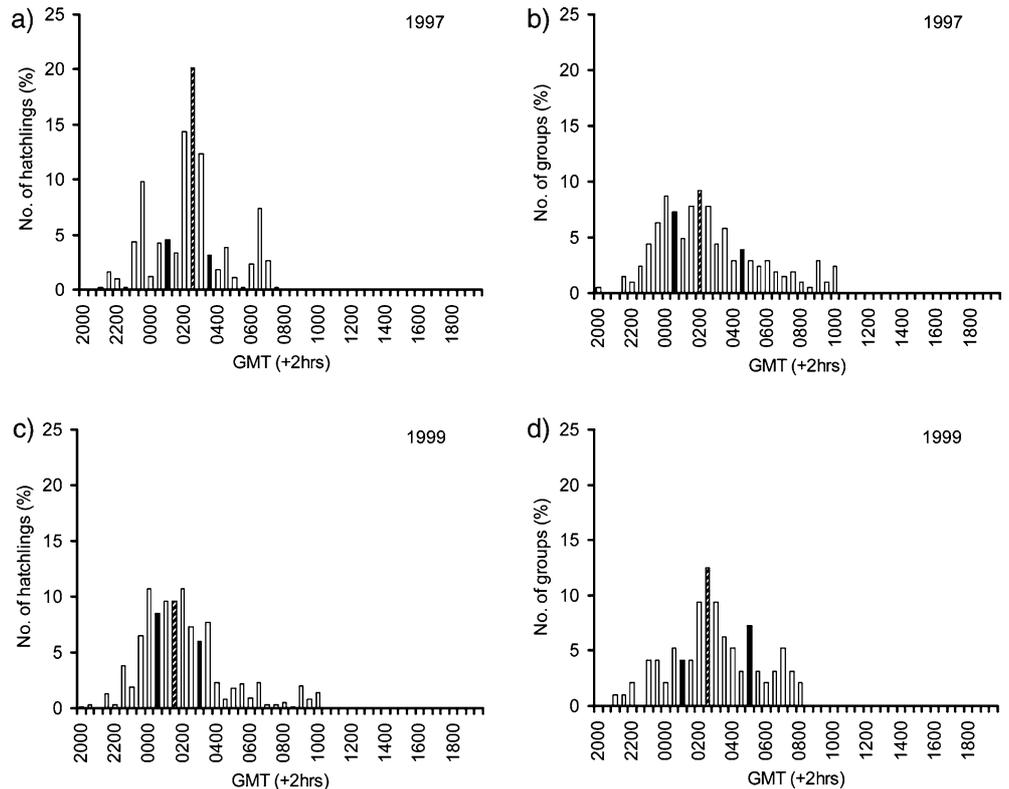
Positional data were available for those nests laid in 1999. However, no relationship was observed between distance to the high water mark and emergence duration nor the level of synchrony in emergence (Table 2).

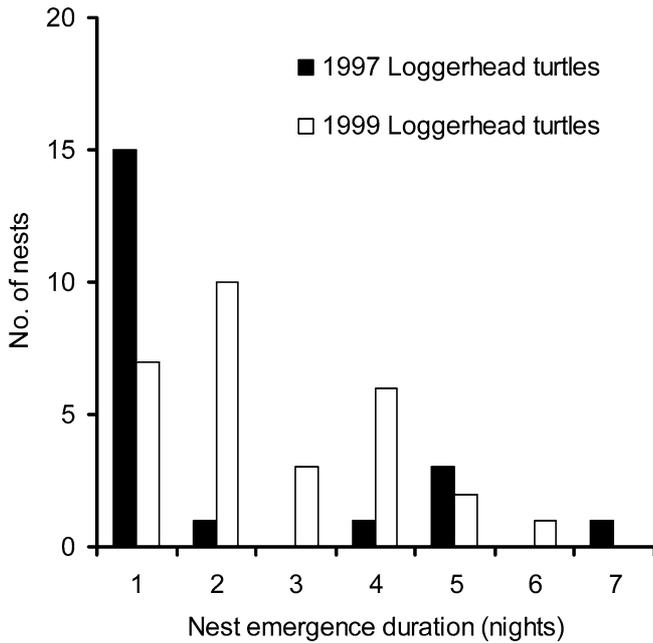
Daytime emergence occurred both years: in 26% of nests in 1997 and 44.4% in 1999. For those nests that produced hatchlings during the day and night, emergence duration was longer (Mann–Whitney 1997:  $W = 89.0, P < 0.05$ ; 1999:  $W = 211.5, P < 0.05$ ) and nests contained more dead full-term hatchlings (Mann–Whitney 1997:

**Fig. 4** The mean percentage of green turtle hatchlings that emerged on each night of emergence during **a** 1997 and **c** 1998. *Error bars are  $\pm 1$  SD.* The percentage of groups (*solid bars*) and hatchlings (*open bars*) that emerged within groups of different sizes **b** 1997 and **d** 1998



**Fig. 5** Temporal distribution of all loggerhead turtle hatchling emergence condensed into half-hour intervals in **a** 1997 ( $n = 21$  nests; 1,069 hatchlings) and **c** 1999 ( $n = 29$  nests; 1,190 hatchlings), and all hatchling groups in **b** 1997 (96 groups) and **d** 1999 (206 groups). *Hashed bars* indicate the median, and *solid bars* the upper and lower quartile ranges of the proportion of hatchlings or group emergences





**Fig. 6** Hatchling emergence duration of loggerhead turtle nests in 1997,  $n=21$  nests (solid bars) and in 1999,  $n=27$  nests (open bars)

$W=135.0$ ,  $P<0.05$ ; 1999:  $W=241$ ,  $P<0.005$ ) than nests that produced hatchlings at night alone.

#### Group size

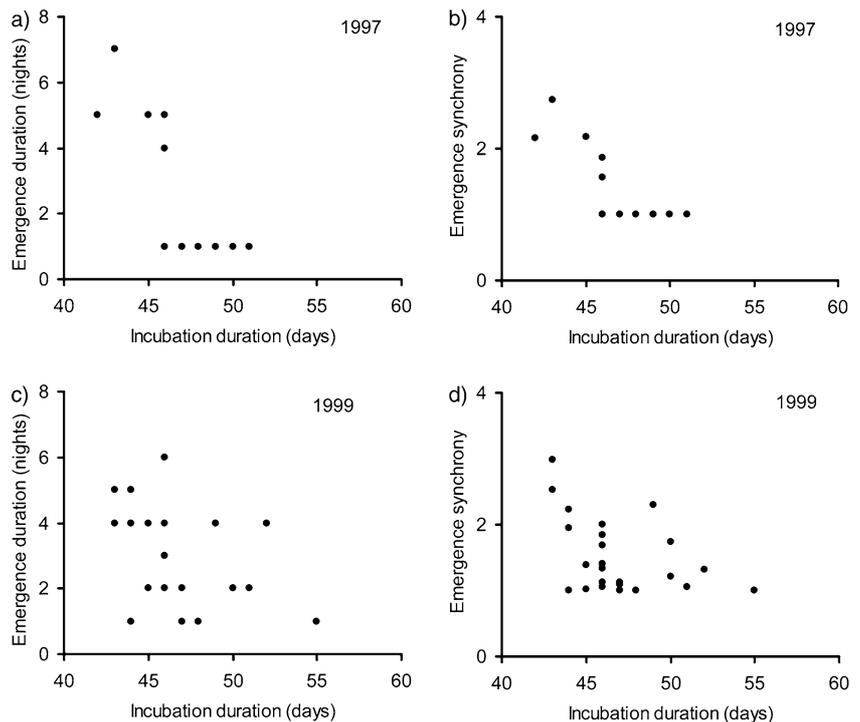
Most hatchlings emerged from their nest on night 1 (1997: 82.6%, Fig. 8a; 1998: 67.3%, Fig. 8c), with numbers decreasing over subsequent nights. The most

frequently occurring group size was that containing one to five hatchlings (Fig. 8b, d), accounting for 11.7% in 1997 and 21.7% in 1999 of the total amount of hatchling emergences. However, in 1997, most hatchlings emerged in groups containing 21 hatchlings or more (73.2% Fig. 8b), although hatchlings were more evenly dispersed among group sizes in 1999 (Fig. 8d). No significant difference was observed in group size among nights 1–7 in 1999 (Kruskal–Wallis,  $P>0.05$ ). However, in 1997, hatchlings emerged in larger groups on night 1 than on successive nights (Kruskal–Wallis  $H_{1,5}=16.4$ ,  $P<0.01$ ). The difference in the size of groups that emerged during the day or at night was not significant (Mann–Whitney,  $P>0.05$ ).

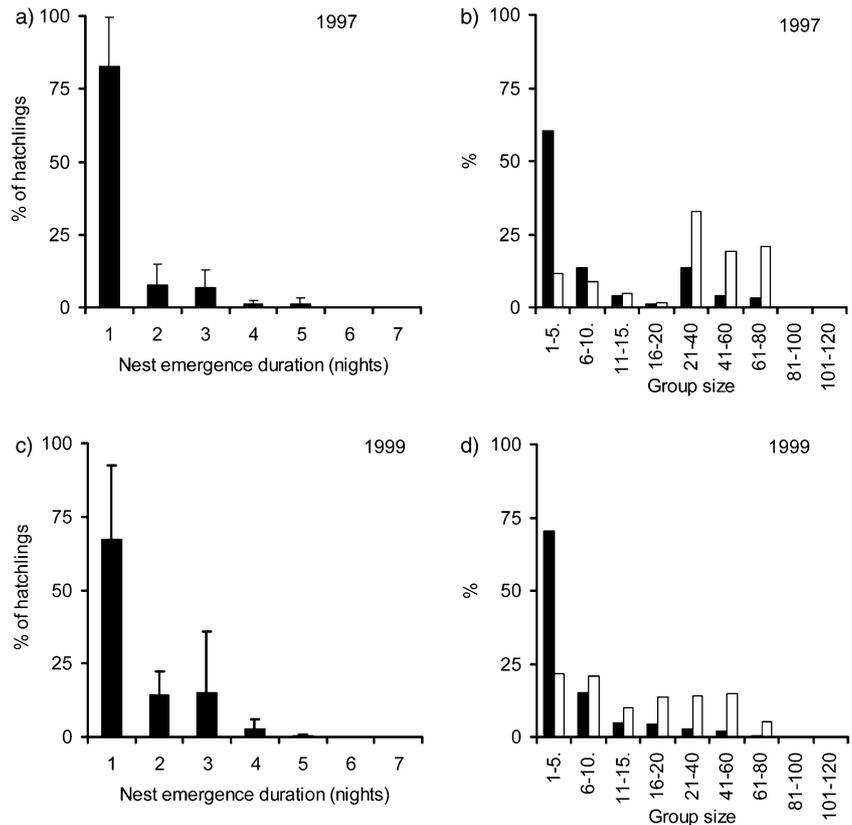
#### Discussion

In this study we compared the emergence patterns of individual nests in two species at the same study site. In both species, although some hatchlings emerged during the day, most emerged and made their way to the sea by night. The temporal distribution of nocturnally emerging green turtle hatchlings observed in the more substantial data set of this study (1998;  $n=29$  nests) were similar to the distributions observed by Gyuris (1993) in Australia, and at Ascension Island (Glen 2002), where a peak at the start of the night was followed by a gradual decline in the proportion of emergences throughout the night. Temporal distributions observed in loggerhead turtle hatchlings in this study were similar to those found in North Carolina (Neville et al. 1988) and Florida (Witherington et al. 1990).

**Fig. 7** A negative relationship existed between incubation duration (ID) and emergence duration in **a** 1997 and **c** 1999 (regression analysis: 1997:  $r^2=0.59$ ,  $F_{1,20}=27.80$ ,  $P<0.05$ , emergence duration =  $-0.59$  ID + 30.3; 1999:  $r^2=0.60$ ,  $F_{1,28}=4.67$ ,  $P<0.05$ , emergence synchrony =  $-0.21$  ID + 12.4). Higher indices of emergence synchrony occurred in clutches with shorter incubation durations in **b** 1997 and **d** 1999 (regression analysis: 1997:  $r^2=0.60$ ,  $F_{1,20}=4.72$ ,  $P<0.05$ , emergence duration =  $-0.16$  ID + 9.06; 1999:  $r^2=0.60$ ,  $F_{1,28}=4.67$ ,  $P<0.05$ , emergence synchrony =  $-0.09$  ID + 5.53)



**Fig. 8** The mean percentage of loggerhead turtle hatchlings that emerged on each night in **a** 1997 and **c** 1999. Error bars are  $\pm 1$  SD. The percentage of loggerhead groups (solid bars) and the percentage of hatchlings (open bars) that emerged within that size class in **b** 1997 and **d** 1999



A substantial minority (15% of green turtles, 8–12.5% of loggerhead turtles) of hatchlings in this study were observed to emerge by day. The pattern was different between species with green turtles emerging throughout the day, whereas diurnally emerging loggerhead turtle hatchlings were restricted to the morning. Sub-surface sand temperature recordings taken at standardised monitoring sites throughout the three seasons (Glen 2002) showed that hatchlings of both species emerged whilst experiencing sand temperatures above all previous upper critical threshold temperatures proposed in green turtles (33°C Hendrickson 1958; 28.5°C Mrosovsky 1968; 31°C Bustard 1967), and in loggerhead turtles (32°C Hays et al. 1992; 32.4°C Moran et al. 1999). Upper thermal limits of 38 and 36°C may have inhibited emergence of green and loggerhead turtles, respectively (Glen 2002). However, some hatchlings were emerging either voluntarily or because they were pushed out by those hatchlings ascending from beneath at temperatures reaching 44°C, exceeding the previously proposed critical thermal maximum limit (41.3°C) of hatchling sea turtles (Drake and Spotila 2002). In general, both species were able to survive throughout the day when their heads were protruding from the sand surface, although we did not notice uncoordinated movements or gaping and snapping of jaws as reported by Drake and Spotila (2002). It has been well established that incubation temperatures at Alagadi are very high (Broderick et al. 2000; Godley et al. 2001) and this may lead to the toleration of high temperatures by hatchlings

at this site. Geographical variation in thermal tolerance has been shown within some lizards, for which a positive correlation existed between the range of stress temperature and the average temperature of a niche inhabited (Ulmasov et al. 1992). Perhaps the differences in the upper thermal maxima of both green and loggerhead hatchlings are indicative of variation in the temperature at which heat shock proteins are expressed within marine turtles (Feder and Hofmann 1999).

Throughout the monitoring periods over the last 12 years, aerial predation of hatchlings has not been observed on Alagadi beach. Whether this is due to the combination of low-density nesting and comparatively few daytime emergences, such that aerial predators are not attracted to the area, we cannot be sure. However, around the coastline of northern Cyprus, aerial predation of hatchlings is rarely observed. Therefore, due to this lack of aerial predation and with sand surface temperatures only becoming lethal to hatchlings after mid-morning (personal observation), all diurnally emergent loggerhead hatchlings recorded in this study were likely to have successfully made it to the sea. However, for green turtle hatchlings the probability of reaching the sea when emerging diurnally would be very low between 1000 and 1600 hours.

Nest placement on Alagadi beach occurs above the high water mark; consequently hatchlings would have to cross at least 2 m of sand before reaching the sea. Why, then, do green turtle hatchlings emerge by day when they are less likely to survive? A number of hypotheses

are plausible, for example, the irregular daytime emergence observed in green turtles suggests that hatchlings may be pushed out by siblings ascending from below. On the other hand, sand surface temperatures may become so high during the day that waiting hatchlings in sub-surface layers of sand would die in situ, and therefore a mechanism is enacted where diurnal emergence is the best option for survival.

In general, most hatchlings in this study emerged from their nest on night 1, with decreasing numbers emerging on subsequent nights. As the effect of nest predation or infestation (Godley and Kelly 1996; McGowan et al. 2001) will be minimised as few hatchlings are left in the nest, it is not surprising that similar patterns of emergence from nests were observed in both species. Despite generally emerging on the first night, in both species, large group emergences were infrequent, and although in some years they accounted for the emergence of most hatchlings, small group emergences were prevalent. Terrestrial nocturnal predation of hatchlings on Alagadi can occur en route to the sea, where the ghost crab can drag hatchlings into their burrows. The red fox also will take hatchlings emerging from the nest and those moving towards the sea. Marine predators have not been described at this site but are undoubtedly present. It is interesting to note that large group size has the paradoxical potential to show a predator dilution effect on land but increase predation in the sea (Wyneken et al. 1998; Pilcher et al. 2000). Thus, it may not be surprising that although hatchlings emerge in groups, they do not consist of the whole clutch, or even all the hatchlings emerging on a particular night.

A number of factors were found to be correlated with the duration of emergence and the level of synchrony of individual nests. Nests of both species, which produced hatchlings both in the day as well as night, were found to have longer emergence durations and higher indices of synchrony than those that had hatchlings emerging at night alone. It may be that these clutches become somehow dysfunctional when it comes to hatchling emergence, which as well as leading to daytime emergence increases duration and reduces synchrony. For loggerhead turtles, nests with longer emergence durations were found to have a higher number of dead hatchlings. The significance of this was only apparent upon excavation, when occasionally a layer of dead hatchlings was found in the sub-surface layers of the sand that may have acted as a barrier, inhibiting the emergence of siblings from underneath. This, however, was not observed in green turtle nests. Houghton and Hays (2001) had previously suggested that within loggerhead nests, an increased thermal range across the egg mass leads to prolonged emergence duration. Thus we might expect a correlation between depth parameters of nests and level of synchrony. No such relationship, however, was apparent.

We were not able to correlate emergence synchrony and duration to green turtle nest characteristics in this study, but within loggerhead turtle nests we discovered a

negative relationship between incubation duration and emergence synchrony and emergence duration. In general, within green and loggerhead nests, short incubation durations are indicative of high incubation temperatures (e.g. Miller 1996). As hatchling size and consequently fitness (e.g. Janzen 1993) has been shown to be affected when eggs are incubated at high temperatures, we suggest that those hatchlings leaving hot, quickly incubating clutches are less vigorous than conspecifics, resulting in longer emergence durations and higher levels of emergence asynchrony.

As already mentioned, previous studies have classified an emergence event as groups containing 10 or more (Witherington et al. 1990; Moran et al. 1999) or 20 or more (Gyuris 1993) hatchlings. Within this study, 27.5 and 31.3% of green hatchlings in 1997 and 1998, respectively, and 19.9 and 36.9% of loggerhead hatchlings in 1997 and 1999, respectively, emerged in groups of fewer than 10 hatchlings. More importantly, these hatchlings accounted for 71–80% of all emergence groups in both species. These numbers are striking and it should be noted that by defining an emergence event in a specific way, large proportions of data may be lost. In comparative studies, observed variation in emergence patterns may in some way be a reflection of the number of hatchlings included/omitted from the analysis (e.g. Drake and Spotila 2002).

In summary, this study, as a result of the great detail of data collection, has given new insights into the natural history of hatchling emergence in two species of marine turtle. We have highlighted the fact that hatchling emergence is far from a simplistic scenario. Additional comparative studies under different thermal and predation scenarios are needed, and experimental/mathematical approaches will be essential to determine the thermal mechanisms responsible for the timing of hatchling emergence.

**Acknowledgements** We thank all the members of the Marine Turtle Conservation Project, the Department of Environmental Protection, and the Society for the Protection of Turtles in Northern Cyprus. This work was undertaken as part of expeditions supported by British Chelonia Group, British Ecological Society, European Commission (DG1B/1A), Kibris Turkish Airlines, MEDASSET UK, People's Trust for Endangered Species. BG is supported by an NERC fellowship. ACB is supported by a grant from the FCO Environment fund for the Overseas Territories. The experiments comply with the current laws of the country in which they were performed. The manuscript was improved by the constructive review of two anonymous referees.

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