Non-modal Scute Patterns, Morphology, and Locomotor Performance of Loggerhead (*Caretta caretta*) and Flatback (*Natator depressus*) Turtle Hatchlings

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Non-modal scute patterns are observed more frequently in hatchlings than in adult sea turtles, which suggests greater survival of hatchlings with the modal scute pattern. Here we compare morphological parameters and fitness correlates of hatchlings of *Caretta caretta* and *Natator depressus* with the modal scute pattern against those with non-modal scute patterns. We found hatchlings with the modal scute pattern were larger and heavier than those with non-modal scute patterns; however, this size difference did not translate into a difference in crawling speed or self-righting ability for either species. There was also no difference in swim thrust produced by hatchlings of *C. caretta* over the first four hours of swimming; however, hatchlings of *N. depressus* with the modal pattern produced greater swim thrust during the first 40 minutes of swimming than those with non-modal scute patterns. This difference may affect the risk of predation and mortality at this early life stage.

T HE carapace of most turtle and tortoise species is covered by large keratinous scales known as scutes (Zangerl and Johnson, 1957). The most frequent or modal sea turtle pattern consists of five vertebral scutes along the medial line of the carapace, flanked on both sides by four to seven pairs of costal scutes. Anterior to the first vertebral scute is the nuchal scute, which is followed by 11 or 12 pairs of marginal scutes which flank the costal scutes. Posterior to the final vertebral scutes is one pair of post-vertebral scutes (Pritchard and Mortimer, 1999).

Individual variations on this modal pattern occur relatively often, particularly in hatchlings, and consist of differences in the number, shape, or arrangement of scutes, with the most common variation being additional or supernumerary scutes (Zangerl and Johnson, 1957; Mast and Carr, 1989). These variations have been observed in individuals of all species of marine turtles except *Dermochelys coriacea* (Hill, 1971; Limpus, 1971; Limpus et al., 1983; Mast and Carr, 1989; Türkozan et al., 2001; Ergene et al., 2011). Where non-modal patterns are exhibited, there is no clear trend toward symmetric or asymmetric patterns. In addition, studies which recorded the scute pattern of adult and hatchling turtles from the same population have found a higher incidence of non-modal scute patterns in hatchling turtles compared to adult turtles (Limpus, 1971; Limpus et al., 1983; Türkozan et al., 2001; Ergene et al., 2011).

Very few sea turtle hatchlings survive to breeding age (Frazer, 1986; Heppell et al., 1996), and it has been hypothesized that the lower frequency of non-modal scute patterns observed in adult turtles is due to higher initial mortality of hatchlings with non-modal scute patterns, resulting in fewer surviving to breeding age (Türkozan and Yilmaz, 2007). It is unlikely that non-modal scute patterns affect survival directly, as variations in the number of scutes generally do not affect the shape or hydrodynamics of the carapace (Pritchard, 1969); however, they may be a phenotypic expression of underlying morphological or physiological abnormalities which may adversely affect the survival of the turtle (Mast and Carr, 1989).

Hatchling sea turtles face the highest risk of predation while crossing the beach from the nest to the sea, and while swimming offshore (Bustard, 1972; Gyuris, 1994; Davenport, 1997). The longer a hatchling spends in these environments, the greater the risk of mortality (Glenn, 1998; Harewood and Horrocks, 2008), increasing to almost 50% when the hatchlings must swim over coral reefs (Gyuris, 1994; Pilcher et al., 2000). Because sea turtle hatchlings do not actively defend themselves against predators (Gyuris, 1994), hatchlings that are able to move through these environments more quickly will reduce their risk of predation. We hypothesized that hatchlings with non-modal scute patterns would have disadvantages that would cause them to spend more time in this high-predation environment (e.g., smaller size and/or reduced locomotor performance) compared to those with the modal scute pattern, thus making them more vulnerable to predation in the early stages of their life.

Most studies concerning scute patterns in hatchling sea turtles have concentrated on reporting the frequency of non-modal scute patterns, or determining the cause of these non-modal scute patterns (Suganuma et al., 1994; Türkozan and Yilmaz, 2007; Margaritoulis and Chiras, 2011). Here we compare morphological parameters and fitness correlates of Loggerhead (*Caretta caretta*) and Flatback (*Natator depressus*) turtle hatchlings with non-modal scute patterns to hatchlings with the modal scute pattern to determine whether differences in the correlates of fitness can explain the apparent differences in survival to breeding age.

MATERIALS AND METHODS

Study site.—This study was conducted at Mon Repos Conservation Park (24°48′S, 152°27′E) in southeast Queensland, Australia. Mon Repos is a major loggerhead rookery, with between 100 and 600 females nesting each year (Limpus, 2008) and a minor rookery for flatback turtles, with between one and 13 females nesting each year (Limpus, 2008). This beach is also the southern-most limit for nesting flatback turtles (Limpus, 2008).

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Egg collection.—In December 2010 and 2011 we collected 36 clutches of loggerhead and 13 clutches of flatback eggs by locating nesting females on the beach between dusk and dawn. After the female had laid eggs and left the beach, we uncovered the eggs and relocated them to a hatchery area of the beach using a 10 L plastic bucket. During relocation we minimized rotation of the eggs and completed the relocation within two hours. Within this time, we weighed (±0.1 g) a random sample of ten eggs from each clutch using a portable balance (AND model EK-1200A).

Hatchling collection.—In February 2011 and 2012 we collected 1496 loggerhead hatchlings from 36 clutches and 265 flatback hatchlings from 13 clutches by placing an enclosure made of plastic mesh around the top of each nest at dusk. These enclosures were checked every half hour between dusk and dawn to ensure that hatchlings were not on the surface long before being tested for locomotory performance. As soon as an emerging clutch was discovered, up to 60 hatchlings were haphazardly selected and transported to the laboratory in a 10 L bucket by foot (a five-minute procedure).

Hatchling measurements.—Once in the laboratory, each hatchling was weighed (±0.1 g) with an electronic balance (AND model EK-1200A), then the straight carapace length and width at the widest point were measured with digital callipers (±0.1 mm). Carapace size index was calculated by multiplying length by width to give a value in mm^2.

Scute pattern classifications.—The number of each type of scute was recorded and the hatchlings were photographed as a record. These records were used to classify hatchlings into three different scute pattern groups: modal, minor non-modal (variation in the number of nuchal, marginal, or post-vertebral scutes), or major non-modal (variation in the number of vertebral or costal scutes). We chose these classifications for two reasons—firstly because the nuchal, marginal, and post-vertebral scutes are much smaller in size, and secondly because variation in marginal, nuchal, and post-vertebral scutes is more common in both hatchling and adult turtles (Türkozan et al., 2001; Ergene et al., 2011; Margaritoulis and Chiras, 2011) than variation in the costal and vertebral scutes.

Correlates of fitness.—We chose three correlates of fitness: self-righting ability, crawling speed, and swimming ability. We chose self-righting ability because it has been previously recognized as an indicator of fitness in hatchling sea turtles (Booth et al., 2013) and freshwater turtles (Delmas et al., 2007). As hatchlings crawl down the beach, they often become inverted (Hosier et al., 1981). Until the hatchling has righted itself it remains vulnerable to predation, and if it is unable to right itself, it risks death by dehydration or overheating. We chose crawling speed for similar reasons, as hatchlings that can crawl more quickly down the beach are exposed to terrestrial predators for a shorter length of time. Finally we chose swimming ability because the near-shore environment can contain a gauntlet of predators (Gyuris, 1994), so hatchlings that can swim more quickly will spend less time in this environment, reducing their risk of predation.

Self-righting experiments.—Locomotor experiments were begun within an hour of first collecting emergent hatchlings.

We quantified righting performance using the same method as Booth et al. (2013). Each hatchling was placed upside down on its carapace on a flat area of sand and the time taken to self-right was measured with a stopwatch. If a hatchling failed to self-right within 10 s, it was returned to its plastron for 10 s before the next trial. This experiment was repeated until the hatchling had successfully self-righted three times, or had attempted self-righting six times, whichever came first. We gave each hatchling a righting propensity score from 0 (failed to self-right) to 6 (successfully self-righted three times out of three), then averaged self-righting time across successful self-righting events for each hatchling.

Crawling experiments.—Immediately following the self-righting experiments, we measured the plastron surface temperature of each hatchling with an infrared thermometer (Smart Sensor AR300), as performance of reptiles is correlated with body temperature (Adams et al., 1989). We then measured hatchling crawling speed using the same method as Ischer et al. (2009). We placed each hatchling at the landward end of a 2.9 m length of black plastic guttering lined with moist, lightly compacted beach sand. This runway was 10 cm wide and contained a dim light at the seaward end to attract the hatchling and ensure that it crawled in a straight line. We timed each hatchling crawling along the guttering with a stopwatch, and converted this value to cm/s.

Swimming experiments.—Immediately following crawling trials we haphazardly selected eight hatchlings from each group of 30 (four with the modal scute pattern and four with major non-modal scute patterns). We measured swimming ability using the same method as Ischer et al. (2009). Hatchlings were fitted with a Lycra harness, which contained a monofilament line which was attached to a force transducer (MLT050 ADInstruments) connected to a bridge amplifier (model ML112 ADInstruments). The output was recorded via a data acquisition system (Power Lab 8/20 ADInstruments) programmed to sample force 40 times per second. Hatchlings were swum in plastic tubs containing sea water maintained at $28°C$ for four hours. Before and after each trial the transducers were calibrated by hanging a known mass from each. Swimming performance was quantified by calculating mean thrust (mN) for each 10 min period throughout the four-hour swimming trial.

Nest excavations.—Two days after the emergence of the first group of hatchlings, the nest was excavated and all of the eggs and eggshells were removed. Any dead or live hatchlings found inside the nest were scute-counted. Any unhatched eggs were opened and large embryos were also scute-counted. Hatchlings can fail to emerge from the nest for a number of reasons which are unrelated to their quality, for example entanglement in roots, becoming trapped under rocks or hard sand, or predation by crabs and other predators (Limpus, 2008). Because of this we separated hatchlings found (live or dead) in the nest from those that died during development.

Statistics.—To test the association of frequencies of hatchlings in each hatchling type (emerged, in nest, or embryo) and each scute pattern (modal, minor non-modal, and major non-modal) we used a Poisson regression model with

Table 1. Mean proportion of unhatched embryos, hatchlings in nest, and emerged hatchlings of *C. caretta,* with modal, minor non-modal, and major non-modal scute patterns (*n* = 24 clutches).

	Modal	Minor non-modal	Major non-modal
Unhatched embryos	0.330	0.336	0.334
Hatchlings in nest	0.578	0.226	0.195
Emerged hatchlings	0.574	0.161	0.266

clutch included as a random factor. We only included the first clutch for each female and excluded any clutches in which there were no hatchlings or embryos found in the nest.

To test the effect of scute pattern variation (as a categorical variable) on hatchling mass, length, width, size index, and plastron surface temperature we used an ANOVA. Hatchlings were used as the data unit, with clutch nested within mother as random factors. We excluded any clutches which did not have at least one hatchling from all three scute pattern groups from the analysis (*n* = 2 for both species). Where there was a significant difference in mass or size between scute pattern categories, we used a Tukey *post-hoc* test to determine where those differences occurred.

To test the effect of scute pattern on self-righting ability and crawling speed we used an ANCOVA, with hatchlings as the data unit, plastron surface temperature as a covariate, and clutch nested within mother as random factors. When there was a difference detected between scute patterns, we added size index to the model as a covariate to determine if the difference could be explained by a difference in size. Where there was a significant difference between scute patterns, we used a Tukey *post-hoc* test to determine where those differences occurred.

Swim thrust data were analyzed using a repeat measures ANCOVA with the thrust produced each ten minute as the data unit and scute pattern as a fixed factor and clutch as a random factor. Again, when there was a difference detected between scute patterns, we added size index to the model as a covariate to determine if the difference could be explained by a difference in size.

Data analysis was performed using R (R Development Core Team, version 2.15.0, 2013). Data are reported as means and standard errors of means or as least squares covariate means, and statistical significance was assumed if *P* < 0.05.

RESULTS

Hatchling type and scute pattern.—For *C. caretta*, there was an association between hatchling type (unhatched embryo, in nest, emerged) and frequency of scute pattern type (modal, minor non-modal, major non-modal) (χ^2_4 = 23.88, *P* < 0.001). Closer examination of the data revealed a greater proportion of in-nest and emerged hatchlings with the modal scute pattern, whereas two thirds of unhatched embryos had either major or minor non-modal scute patterns (Table 1). There was no difference between the hatchling groups of *N. depressus* in terms of proportion of hatchlings with each scute pattern (χ^2_4 = 3.94, *P* = 0.41; Table 2).

Scute pattern, size, and locomotory performance.—Hatchlings of *C. caretta* with the modal scute pattern were heavier and had wider carapaces (and as a consequence had a greater size index) than those with major non-modal scute patterns (Table 3). There were no differences in size between the normal and minor non-modal, or minor and major non-modal groups (Table 3).

Hatchlings of *N. depressus* with the modal scute pattern were heavier, longer, wider, and larger than those with major non-modal scute patterns (Table 4). Hatchlings with minor non-modal scute patterns were also wider (and as a consequence had a larger size index) than those with major non-modal scute patterns (Table 4).

Despite these size differences there was no difference in righting propensity, average time taken to self-right, or crawling speed between the hatchlings with the modal scute pattern and those with minor or major non-modal scute patterns in either *C. caretta* or *N. depressus* (Tables 3, 4). There was also no difference in plastron surface temperature between the scute groups (Tables 3, 4).

Mean thrust produced by swimming hatchlings decreased over time for hatchlings of both *C. caretta* and *N. depressus* (Fig. 1). There was no difference in the thrust produced between hatchlings of *C. caretta* with the modal scute pattern and those with major non-modal scute patterns ($F_{1,140}$ = 0.25, *P* = 0.62; Fig. 1). Hatchlings of *N. depressus* with the modal scute pattern produced greater thrust than those with major non-modal scute patterns, but only for the first 40 minutes of swimming (*P* = 0.005; Fig. 2). This difference persisted even after size was controlled for by using carapace size index as a covariate (*P* = 0.01).

DISCUSSION

Hatchling type and scute pattern.—Sixty percent of the emerged hatchlings of *C. caretta* in this study exhibited the modal scute pattern, which is higher than that reported for hatchlings of *C. caretta* in Turkey (34%; Ergene et al., 2011), but well within the range recorded for other species of sea

Table 2. Mean proportion of unhatched embryos, hatchlings in nest, and emerged hatchlings of *N. depressus*, with modal, minor non-modal, and major non-modal scute patterns (*n* = 9 clutches).

	Modal	Minor non-modal	Major non-modal
Unhatched embryos	0.528	0.111	0.361
Hatchlings in nest	0.507	0.081	0.412
Emerged hatchlings	0.451	0.177	0.371

Table 3. Hatchling morphological and locomotory parameters (±SE) for 1407 hatchlings of *C. caretta* with the modal (A), Minor (B), and major (C) non-modal scute patterns (*n* = 34 clutches).

Attribute	Modal (*n* = 821)	Minor non-modal (*n* = 220)	Major non-modal (*n* = 366)	*F*-statistic	*P*-value	Comparison of treatments
Mass (g)	19.9±0.1	19.8±0.1	19.7±0.3	5.60	<0.001	A = B, B = C, A > C
Length (mm)	43.4±0.1	43.3±0.1	43.3±0.2	2.62	0.07	A = B = C
Width (mm)	35.2±0.1	35.1±0.1	35.0±0.2	3.36	0.03	A = B, B = C, A > C
Size index (mm²)	1529±4	1523±6	1517±13	3.87	0.02	A = B, B = C, A > C
Righting time (s)	2.9±0.04	2.9±0.1	2.9±0.1	0.0002	0.99	A = B = C
Righting propensity score	5.7±0.01	5.6±0.01	5.6±0.01	0.58	0.56	A = B = C
Crawling speed (cm/s)	5.3±0.1	5.3±0.1	5.4±0.1	+	+	N/A
Plastron surface temperature (°C)	26.3±0.1	26.3±0.1	26.4±0.3	1.49	0.22	A = B = C

turtle all over the world (59–87%; Mast and Carr, 1989; Suganuma et al., 1994; Özdemir and Türkozan, 2006; Ergene et al., 2011).

Unfortunately, no substantial data were available in the literature with which to compare the data collected from the emerged hatchlings of *N. depressus*; however, the proportion (49%) of hatchlings with the modal scute pattern was lower than all recorded proportions except for the population of *C. caretta* in Turkey (Ergene et al., 2011). There is some evidence that low incubation temperatures cause a greater proportion of hatchlings with non-modal scute patterns in *N. depressus* (Hewavisenthi and Parmenter, 2001), and since Mon Repos is the southernmost limit for nesting of this species, this rookery may have a greater proportion of hatchlings with non-modal scute patterns than other rookeries.

Several studies suggest that non-modal scute patterns can be caused by nest relocation or rough handling of the eggs (Mast and Carr, 1989; Türkozan and Yilmaz, 2007); however, none of the authors have suggested a mechanism by which this occurs, or compared relocated and *in situ* eggs from the same clutch. All nests in this study were relocated with minimal rotation and all within two hours of being laid, as per Limpus et al. (1979).

Caretta caretta that died during embryonic development had a much higher incidence of non-modal scute patterns than both the in-nest and emerged hatchlings, which suggests that hatchlings with non-modal scute patterns are more likely to die during development. It is unlikely that the non-modal scute patterns themselves are the cause of this; however, they may be indicative of low-quality hatchlings

with other internal abnormalities (Mast and Carr, 1989). We did not find a difference in frequency of non-modal scute patterns between hatchlings and embryos that died during development in *N. depressus;* however, this is likely due to the much smaller sample size in terms of number of clutches and also number of eggs in each clutch.

A previous study which investigated non-modal scute patterns in Kemp's ridley turtles (*Lepidochelys kempi*) did not find a difference in proportion of hatchlings with non-modal scute patterns between emerged hatchlings and dead in-nest and unhatched embryos (Mast and Carr, 1989). However, the authors did not separate dead emerged hatchlings and unhatched embryos into two separate groups like we did, which may have masked a difference between hatched and unhatched hatchlings.

Hatchling size.—In both species hatchlings with the modal scute pattern were heavier than those with major non-modal scute patterns. There are two possible explanations for this observation; either smaller eggs are more likely to produce hatchlings with non-modal scute patterns, or hatchlings with non-modal scute patterns leave more material behind in the eggs at hatching. The first possibility could be tested by looking at whether there is a correlation between egg size and frequency of non-modal scute patterns. The second possibility could be tested by weighing the remaining shell and its remnants after the turtle has hatched and correlating this mass with the frequency of non-modal scute patterns. A heavier mass may mean a larger yolk to provide energy for the first few days of the

Table 4. Hatchling morphological and locomotory parameters (±SD) for 254 hatchlings of *N. depressus* with the modal scute pattern (A), minor non-modal (B), and major non-modal (C) scute patterns (*n* = 11 clutches).

Attribute	Modal (*n* = 119)	Minor non-modal (*n* = 54)	Major non-modal (*n* = 81)	*F*-statistic	*P*-value	Comparison of treatments
Mass (g)	43.1±0.3	42.9±0.4	42.0±0.8	4.63	0.01	A = B, B = C, A > C
Length (mm)	60.8±0.3	60.7±0.3	60.2±0.6	3.14	0.045	A = B, B = C, A > C
Width (mm)	53.6±0.3	53.5±0.4	52.4±0.5	6.84	0.001	A = B, B > C, A > C
Size index (mm²)	3262±28	3256±35	3162±59	6.56	0.002	A = B, B > C, A > C
Righting time (s)	3.9±0.2	3.8±0.2	3.9±0.2	0.46	0.63	A = B = C
Righting propensity	4.6±0.2	4.7±0.2	4.8±0.2	0.03	0.97	A = B = C
Crawling speed (cm/s)	6.7±0.2	7.1±0.3	6.9±0.3	1.27	0.28	A = B = C
Plastron surface temperature (°C)	26.0±0.2	26.0±0.2	26.1±0.5	0.65	0.52	A = B = C
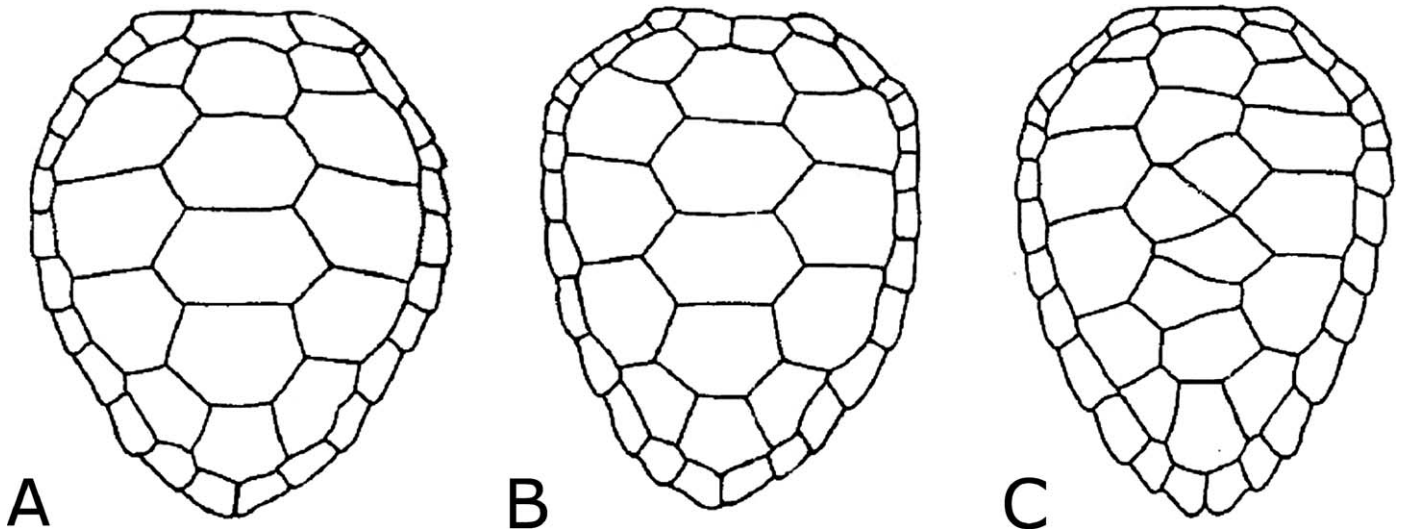
Fig. 1. Examples of scute patterns of *C. caretta*: (A) modal scute pattern, (B) minor non-modal scute pattern (additional nuchal scute), and (C) major non-modal scute pattern (additional vertebral and costal scutes). Modified from Coker (1910).

hatchling's life, therefore increasing probability of survival (Gyuris, 1994; Booth et al., 2004).

While there was no difference in carapace length between hatchlings of *C. caretta* with modal and non-modal scute

Fig. 2. Mean thrust produced by (A) swimming hatchlings of *C. caretta* with the modal scute pattern (*n* = 100) and major non-modal scute patterns (*n* = 62), and (B) hatchlings of *N. depressus* with the modal scute pattern (*n* = 28) and major non-modal scute patterns (*n* = 16).

patterns, hatchlings of *N. depressus* with the modal pattern were on average 0.7 mm longer than those with major non-modal scute patterns. Larger hatchlings have the advantage of evading gape-limited predators (Bustard, 1972; Janzen, 1993) and previous work on green turtle hatchling predation has shown that hatchlings with a carapace length of greater than 51.0 mm were less likely to be predated than those with a carapace length of less than 47.0 mm (Gyuris, 2000). Since hatchlings of *N. depressus* spend their entire life in the near-shore environment (Bolten, 2003), being larger would be more important to them than to *C. caretta*.

Hatchlings of *C. caretta* with the modal scute pattern had a wider carapace than those with major non-modal scute patterns, by an average of 0.2 mm, whereas hatchlings of *N. depressus* with the modal scute pattern were on average 1.2 mm wider than those with major non-modal scute patterns. While the *C. caretta* difference is statistically significant, it is so small that it is unlikely to be biologically relevant. Natural variations in hatchling width within the same clutch of greater than 0.6 mm have been reported for hatchlings of *C. caretta* (Chu, 2008). However, the difference for hatchlings of *N. depressus* is greater than the maximum range of variation in carapace width reported in Hewavisenthi and Parmenter's (2001) study (0.8 mm).

Hatchling locomotor performance.—Despite the size differences we observed, particularly for *N. depressus*, we did not detect any difference in self-righting ability or crawling speed between modal and major and minor non-modal hatchlings in either species. In the case of the hatchlings of *C. caretta*, this was expected because the size differences between the groups were reasonably small; however, we expected to see a difference in hatchlings of *N. depressus* due to the greater size difference.

The first 30–60 minutes of a sea turtle hatchling's life are when it is most vulnerable to predation, as it crawls from the nest to the sea and then swims through the shallow coastal waters (Gyuris, 1994; Pilcher et al., 2000). Therefore the ability to quickly self-right after becoming inverted, to crawl quickly and to swim quickly should all affect hatchling survival because they will minimize the time that hatchlings are exposed to these high-risk environments.
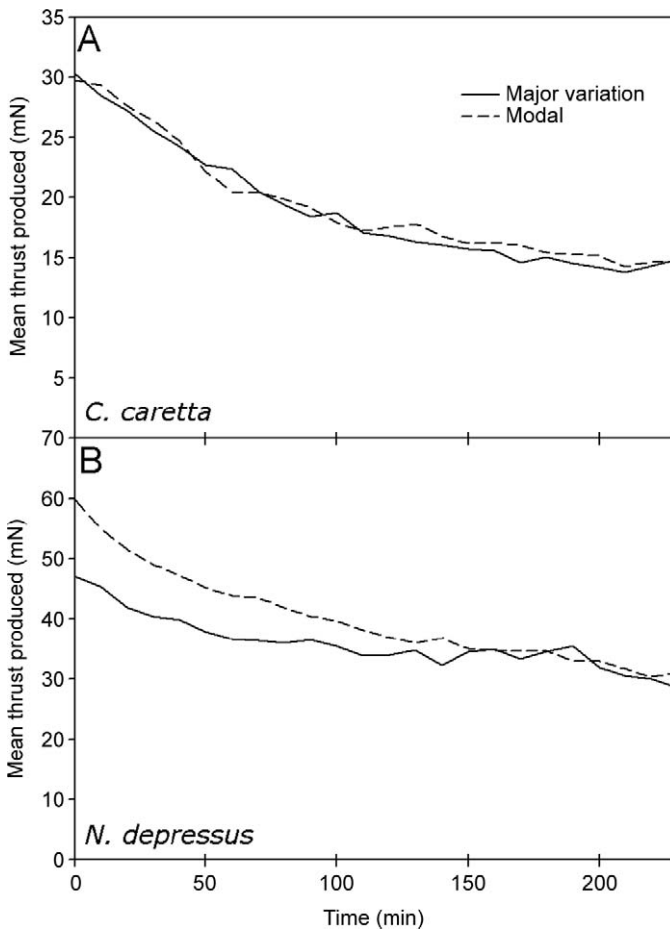
Sea turtle hatchling terrestrial locomotion has been described as ''inefficient and stereotypic'' (Davenport, 1997), and several studies have observed hatchlings becoming inverted by beach flotsam and depressions in the sand (Hosier et al., 1981; Davenport, 1997; Steyermark and Spotila, 2001; Triessnig et al., 2012). Hatchlings of *C. caretta* in Turkey overturned on average 2.1 times during the crawl from the nest to the sea, which increased the time spent crawling by an average of 40.5 seconds (Triessnig et al., 2012). Previous studies have shown larger hatchlings of *C. caretta* are faster and more likely to self-right within 10 s (Wood, 2010); however, that study investigated a larger range of sizes than we observed in this study.

While other studies have found that hatchling size is positively correlated with crawling speed (Janzen, 1993; Wren et al., 1998; Janzen et al., 2000a, 2000b), we did not find a difference in this study. This could be because of the small range of sizes observed in this study, or due to other factors that affect crawling speed. Since we did not observe any difference between the modal and non-modal groups, selection against non-modal scute patterns is likely either occurring after the hatchlings leave the beach, or is due to an attribute we did not measure.

Hatchling size has been positively correlated with swimming force in hatchlings of *C. caretta* (Chu, 2008) and *C. mydas* (Burgess et al., 2006; Ischer et al., 2009). However, similarly to self-righting ability and crawling speed, there was no difference in swim thrust produced in the first four hours between hatchlings of *C. caretta* with the modal scute pattern and those with major non-modal patterns. However, hatchlings of *N. depressus* with the modal pattern produced significantly more swimming thrust than those with major non-modal scute patterns, but only for the first 40 minutes of swimming. This might be explained by a difference in life history: hatchlings of *C. caretta* have an oceanic migration period, whereas *N. depressus* remain on the continental shelf (Bolten, 2003). Hatchlings of *N. depressus* also have a less intense frenzy period, and their swimming effort decreases more quickly than hatchlings of *C. caretta* and *C. mydas* (Pereira et al., 2011).

The first 40 minutes is likely to be the most important in terms of predation avoidance, as predation risk decreases as the hatchling moves further away from the shore. (Salmon et al., 2009; Pereira et al., 2011). By swimming more quickly during the first 40 minutes, hatchlings with the modal pattern will not only be able to out-swim predators, but also move out of the predator-rich near shore environment more quickly.

The lack of a difference in swimming performance of hatchlings of *C. caretta* suggests that selection against non-modal scute patterns may happen sometime after the first four hours of swimming. Non-modal scute patterns are generally more common in hatchlings than in breeding adult turtles; however, the period between these two life stages is decades (Limpus, 2008). There are a number of other factors that influence hatchling survival over this period, and those with the modal scute pattern may be better or more efficient foragers, may grow faster or may be better at navigating ocean currents.

ACKNOWLEDGMENTS

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