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A Comparison of Hatchling Locomotor Performance and Scute Pattern Variation between Two Rookeries of the Flatback Turtle (*Natator depressus*)

Elizabeth L. Sim¹, David T. Booth¹, Colin J. Limpus², and Michael L. Guinea³

Marine turtle species consist of several genetically discrete 'evolutionarily significant units' (ESUs) which do not interbreed. We studied Flatback turtle (*Natator depressus*) hatchlings from two rookeries (Mon Repos Conservation Park and Bare Sand Island, Australia) representing two separate ESUs. Turtles from these ESUs differ in several key life history traits, including body size, and we predicted hatchlings would also differ in locomotor performance. We also investigated the proportion of hatchlings with non-modal scute patterns to determine whether this varies between ESUs. We collected newly emerged hatchlings, and measured mass, carapace length and width, and recorded the scute pattern. We then measured self-righting ability and crawling speed. Our results confirmed a difference in hatchling size between the two ESUs, with Mon Repos rookery hatchlings being larger. However the size difference did not translate into a difference in self-righting ability or crawling speed. The Mon Repos rookery also produced a larger proportion of hatchlings with major non-modal scute pattern compared to Bare Sand Island rookery. The differences suggest hatchling survival rates may differ between ESUs, and that ESUs should be studied separately when implementing conservation measures.

MANY species exhibit variation in life history traits among populations (How et al., 1996; Tiwari and Bjørndal, 2000; Du et al., 2005). This variation is often attributed to a differential allocation of resources to optimize fitness for that population in its environment (Brockelman, 1975; McGinley et al., 1987; Stearns, 1993). Most marine turtle species have a wide distribution, comprising many nesting populations which do not interbreed (Norman et al., 1994; Bowen, 2003; Wallace and Saba, 2009). These discrete populations, referred to as 'evolutionary significant units' (ESUs [Moritz, 1994]), can be distinguished from each other on the basis of differences in genetic factors, body size, timing of nesting, and clutch size (Tiwari and Bjørndal, 2000; Limpus, 2008; Wallace and Saba, 2009).

Female marine turtles produce a large number of eggs, few of which survive to breeding age (Gyuris, 1994; Heppell et al., 2003; Chaloupka and Limpus, 2005). Differences in life history traits between ESUs may influence hatchling survival, resulting in different survival rates. Direct measurements of fitness and survival are difficult to obtain in marine turtles, due to their long lifespan, widely dispersed habitat use, and the difficulty of tracking them through their successive age classes (Booth et al., 2004). Therefore correlates of fitness such as body size and locomotor performance (self-righting ability, crawling speed, and swimming attributes) have been used in hatchling turtles (Booth et al., 2004; Freedberg et al., 2004; Ischer et al., 2009). Measures of terrestrial locomotor performance are used as fitness correlates because they can influence the amount of time a hatchling spends on the beach (Paitz et al., 2010), and increased time on the beach can lead to increased risk of desiccation and predation (Bustard, 1972; Steyermark and Spotila, 2001; Delmas et al., 2007). Consequently, hatchlings that spend more time on the beach may have low survival rates (Dial, 1987; Janzen et al., 2007). Although several studies have investigated fitness correlates of hatchling sea turtles (Booth and Astill, 2001; Burgess et al., 2006; Pereira et al., 2011), these studies have focussed on single ESUs only.

Another proposed indicator of hatchling fitness is variation in the number of scutes on the carapace. The modal scute pattern for Flatback turtles (*Natator depressus*) is 1 nuchal, 5 vertebral, 4 pairs costal, 11 pairs of marginal, and 1 pair of post-vertebral scutes (Limpus, 1971). Non-modal scute patterns have been reported for all marine turtle species (Hill, 1971; Limpus, 1971; Mast and Carr, 1989), and supernumerary scutes are the most common variation (Zangerl and Johnson, 1957). Non-modal scute patterns are generally more common in hatchling turtles than in adult turtles (Limpus, 1971; Mast and Carr, 1989; Türkozan et al., 2001). The lower proportion of individuals with non-modal scute patterns in breeding adults suggests that fewer turtles with non-modal scute patterns survive to breeding age (Türkozan et al., 2001). It is likely that non-modal scute patterns do not influence survival directly, but are indications of greater internal abnormalities (Mast and Carr, 1989). Non-modal scute patterns may be caused by genetics, environmental conditions during egg incubation, or handling of eggs (Hewavisenthi and Parmenter, 2001; Türkozan and Yilmaz, 2007; Velo-Anton et al., 2011), and therefore have the potential to vary among different rookeries.

Natator depressus is endemic to the Australian continental shelf (Limpus, 1971) and has been classified into four different ESUs: the Eastern Australian ESU, the Gulf of Carpentaria and Torres Strait ESU, the Western Northern Territory ESU, and the North-West Shelf ESU (Limpus, 2008). Several key differences separate these ESUs in terms of size of eggs, hatchlings, and females, and timing of nesting. For example, the Western Northern Territory ESU consists of smaller adult females that lay smaller eggs and produce smaller hatchlings than the Eastern Australian ESU (Limpus, 1971; Whiting and Guinea, 2003). In addition, *N. depressus* in the Western Northern Territory ESU nest in the Austral winter (June–August; Whiting and Guinea, 2003), whereas *N. depressus* in the Eastern Australian ESU nest in the Austral spring/summer (November–January; Limpus, 1971).

This paper compares hatchling fitness correlates and proportion of non-modal scute patterns of *N. depressus* from

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the Eastern Australian and Western Northern Territory ESUs. We predicted that Eastern Australian ESU hatchlings would be faster at crawling than Western Northern Territory ESU hatchlings, because larger hatchlings have been found to crawl faster than smaller ones from the same clutch (Wren et al., 1998; Chu, 2008; Ischer et al., 2009). We predicted that Western Northern Territory ESU hatchlings would be able to self-right more quickly and more often due to their smaller size making them more maneuverable (Booth et al., 2013). Finally, we predicted that the proportion of hatchlings with non-modal scute patterns would differ between the two rookeries because of genetic and environmental differences. Both of these factors have previously been proposed as causes of non-modal scute patterns (Hewavisenthi and Parmenter, 2001; Velo-Anton et al., 2011).

MATERIALS AND METHODS

Study sites.—We sampled the Eastern Australian ESU at Mon Repos Conservation Park in south-east Queensland (24°48'S, 152°27'E). This beach is a minor rookery of *N. depressus*, with between one and 13 nesting females per year (Limpus, 2008) and is also the southern limit of nesting for *N. depressus* in eastern Australia (Limpus, 1971). We sampled the Western Northern Territory ESU on Bare Sand Island in the Northern Territory (12°32'S, 130°25'E). This island is a major rookery of *N. depressus*, with up to 20 nesting females per night during peak nesting months of June and July (Whiting and Guinea, 2003).

Hatchling collection.—At Mon Repos we relocated nine clutches laid by seven females into a hatchery area in December 2010. After the nests had been incubating for 50 days, we placed a plastic enclosure around the top of each nest each night at dusk. We checked the enclosures every half hour between dusk and dawn. As soon as we discovered an emerging clutch, we randomly selected up to 30 hatchlings from the first emergence, which we transported to the laboratory in a bucket by foot (a five-minute journey). When two clutches emerged simultaneously, we kept each clutch in a separate bucket. We collected a total of 184 hatchlings from these clutches during February 2011.

At Bare Sand Island we sampled 129 hatchlings from seven emerging clutches that we located by patrolling the beach between dusk and dawn during July 2011. Because the clutches emerged over a ten-day period, and the mean re-nesting interval for this ESU is 14.8 days (Hope and Smit, 1998), we assumed that they were laid by different females. We transported hatchlings in separate buckets for each clutch by foot to a central location on the beach, a journey of less than 10 min.

Hatchling measurements.—At both rookeries, we weighed the hatchlings (± 0.1 g) with a portable balance (AND model EK-1200A), measured the straight carapace length and width (± 0.1 mm) at the widest point with digital callipers (Sontax 150 mm digital calliper, China), and calculated the carapace size index (length \times width; Ischer et al., 2009). We counted the number of carapace scutes, and photographed the carapace scute pattern. We classified hatchlings into three groups: modal scute pattern, minor non-modal patterns (variation in the number of nuchal, marginal, and/or post-vertebral scutes), or major non-modal scute patterns (variation in the number of vertebral and/or costal scutes; Sim et al., 2014).

Locomotor performance tests.—Within the first hour of collection, we began locomotor performance tests. We placed each hatchling upside down on its carapace on a flat area of sand and, using a stopwatch, measured the time taken to self-right. Following previous experimental protocol, hatchlings that failed to self-right within 10 s were returned to their plastron for 10 s, a period long enough for the hatchling to become re-oriented and begin vigorous crawling again, before the next trial (Booth et al., 2013). Trials continued 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 to 6 using the same method as Booth et al. (2013), where 0 = no self-rightings in six attempts, 1 = one self-righting in six attempts, 2 = two self-rightings in six attempts, 3 = three self-rightings in six attempts, 4 = three self-rightings in five attempts, 5 = three self-rightings in four attempts, and 6 = three self-rightings in three attempts. We averaged self-righting time across successful self-righting events for each hatchling. Twelve hatchlings from nine clutches failed to self-right at all, and they were excluded from the self-righting time data.

Immediately following the self-righting experiment, we measured the plastron surface temperature of the hatchling with an infra-red thermometer (Smart Sensor AR300, $\pm 1.5^\circ\text{C}$) to control for the effect of body temperature on locomotor performance (Hutchison et al., 1966; Adams et al., 1989; Elnitsky and Claussen, 2006). We then measured crawling speed using a 2.9 m length of black plastic guttering as a raceway (Ischer et al., 2009). The raceway was lined with moist, lightly compacted beach sand and contained a dim light at the seaward end to attract the hatchling and ensure that it crawled in a straight line. If a hatchling did not begin to move within three minutes, we aborted the trial and excluded that hatchling from the analysis. A total of two hatchlings from one clutch were excluded. We timed each hatchling crawling along the guttering. We subjected each hatchling to self-righting and crawling tests (2–3 minutes) before moving on to the next hatchling to ensure plastron surface temperature measurements remained relevant throughout the trials.

Statistics.—We used an ANOVA to test for a difference in hatchling size and mass between the two ESUs, with clutch nested within mother as random factors. To test for a difference in locomotor performance between the two ESUs, we used an ANCOVA with ESU as a fixed factor, clutch nested within mother as random factors, and plastron surface temperature as a covariate. We removed non-significant interactions from the model. To determine whether there was a learning response at the population level, we used a paired t-test to determine whether there was a difference between the timing of the first and third self-righting trials.

To test for differences in the proportion of hatchlings with non-modal scute patterns between the two ESUs, we calculated the proportion of hatchlings with the modal, minor non-modal, and major non-modal scute patterns for each clutch. We transformed the data using an arcsine transformation and used an ANOVA with ESU as the fixed factor and mother as a random factor. We performed data analysis using R (version 2.15.0; R Development Core Team, 2013). We report data as means and standard errors of means or as least squares covariate means and assume statistical significance if $P < 0.05$.

Table 1. Mean (\pm SE) mass, carapace length, width, and size index and body temperature of hatchlings of *Natator depressus* from Mon Repos ($n = 184$ from nine clutches) and Bare Sand Island ($n = 129$ from seven clutches) rookeries. Significant differences between ESUs are indicated in bold font.

	Mon Repos	Bare Sand Island	F statistic	P value
Mass (g)	42.2 \pm 1.4	33.1 \pm 1.0	39.59	<0.001
Carapace length (mm)	60.5 \pm 0.8	57.4 \pm 0.6	14.15	0.002
Carapace width (mm)	53.2 \pm 1.1	49.6 \pm 0.8	10.77	0.006
Carapace size index (mm ²)	3227 \pm 103	2855 \pm 74	12.94	0.004
Body temperature ($^{\circ}$ C)	26.2 \pm 1.0	27.3 \pm 0.7	1.28	0.280
Self-righting propensity	4.7 \pm 0.1	5.0 \pm 0.1	1.35	0.267
Self-righting time (s)	3.5 \pm 0.1	3.3 \pm 0.1	0.76	0.401
Crawling speed (m/s)	7.5 \pm 0.2	6.9 \pm 0.3	0.58	0.461

RESULTS

Hatchlings of *N. depressus* from Mon Repos were greater in mass ($F_{1,297} = 39.59$, $P < 0.001$), and longer ($F_{1,297} = 14.15$, $P = 0.002$) and wider ($F_{1,297} = 10.77$, $P = 0.006$) in carapace than hatchlings from Bare Sand Island (Table 1). Plastron surface temperature, self-righting propensity, mean self-righting time, and crawling speed did not differ between the two ESUs (Table 1). There was no difference in self-righting time between the first and the third trial ($t(256) = 1.42$, $P = 0.16$).

A higher proportion of hatchlings from Mon Repos nests exhibited major non-modal scute patterns than at Bare Sand Island ($F_{1,12} = 13.42$, $P < 0.01$; Table 2), whereas there was no difference in the proportion of hatchlings with minor non-modal scute patterns and proportion of hatchlings with the modal scute pattern between the ESUs (Table 2).

DISCUSSION

Size.—Hatchlings of *N. depressus* from Mon Repos were significantly heavier and had longer, wider carapaces than hatchlings from Bare Sand Island, something that has been reported previously (Limpus, 1971; Whiting and Guinea, 2003). Nesting females also have a longer carapace at Mon Repos (mean of 92.3 cm; Limpus, 1971) than at Bare Sand Island (mean of 86.4 cm; Whiting and Guinea, 2003). Similar differences in both hatchling and nesting female size between different ESUs have also been found in Loggerhead (*Caretta caretta*), Green (*Chelonia mydas*), and Leatherback (*Dermochelys coriacea*) turtles (Tiwari and Bjorndal, 2000; Limpus, 2008; Eckert et al., 2012).

Within a species, female turtles with a longer carapace length generally lay larger eggs, which produce larger hatchlings (Bjorndal and Carr, 1989), implying there is a positive relationship between maternal size and offspring size. Within a clutch, hatchling size can be affected by incubation temperature, with eggs incubated at cooler temperatures producing larger hatchlings and eggs incubated at warmer temperatures producing smaller hatchlings (Booth and Astill, 2001; Hewavisenthi and Parmenter, 2001; Maulany et al., 2012). However, all of these studies found no difference in hatchling mass between the warm and cool nests, suggesting that more yolk is converted into hatchling tissue during the longer development time at lower

Table 2. Mean proportion (\pm SE) of hatchlings of *Natator depressus* with the modal, minor non-modal, and major non-modal scute pattern variation from Mon Repos ($n = 9$ clutches) and Bare Sand Island ($n = 7$ clutches) rookeries. Significant differences between ESUs are indicated in bold font.

	Mon Repos	Bare Sand Island	F statistic	P value
Modal scute pattern	0.42 \pm 0.08	0.65 \pm 0.08	3.64	0.08
Minor non-modal scute patterns	0.17 \pm 0.05	0.32 \pm 0.09	2.41	0.15
Major non-modal scute patterns	0.41 \pm 0.08	0.04 \pm 0.03	13.45	0.003

temperatures (Ischer et al., 2009). Mon Repos is the southern-most breeding limit for *N. depressus* (Limpus, 2008), so it is likely that the nests there experienced lower incubation temperatures than nests on Bare Sand Island. However, since we did observe a large difference in mass between the two ESUs, the difference in body size is probably not solely due to differences in incubation temperature.

The difference in body size between the ESUs may be due to several factors. Possible explanations include increased predation pressure at Mon Repos Conservation Park causing selection for larger-sized turtles, or a greater amount or more nutritious food available to the Mon Repos nesting turtles, allowing them to grow larger and produce larger eggs and hatchlings. Hatchling size can affect survivorship due to its effect on locomotory ability or avoidance by gape-limited predators. For example, when turtle hatchlings of *C. caretta* and *N. depressus* occur on the same beach, the smaller hatchlings of *C. caretta* are predated by Silver Gulls (*Chroicocephalus novaehollandiae*), whereas the larger hatchlings of *N. depressus* are ignored (Limpus, 1973). Experiments on *C. mydas* have suggested that larger hatchlings are less likely to be predated by fish in the near-shore environment (Gyuris, 2000). Hatchlings of *N. depressus* are unique in that they remain in the near-shore environment instead of migrating into the open ocean like other sea turtle species (Limpus, 1971; Walker and Parmenter, 1990). Therefore larger hatchlings may also be able to maintain their position in coastal waters, and avoid being swept away by currents.

Locomotory ability.—Due to differences in hatchling size between the two rookeries, we predicted that smaller hatchlings from Bare Sand Island would have a greater propensity to self-right and would self-right more quickly; however, we found no difference in self-righting ability between the two ESUs. Hatchlings of *C. mydas* self-right by flexing their heads against the substrate, which allows the carapace to be raised off the ground, and the hatchling to flip upright (Booth et al., 2013). We observed similar behavior in hatchlings of *N. depressus*, and also that the hatchlings often needed to push several times against the substrate with their neck before gaining enough momentum to flip over, which has been observed previously in freshwater turtles (Finkler and Claussen, 1997). Although a weak negative correlation between carapace size and time taken to self-right has been observed in *C. mydas*, several other studies have suggested incubation temperature or maternal effects are the main drivers of self-righting ability (Steyermark and Spotila, 2001; Delmas et al., 2007; Booth et al., 2013). It is likely that self-righting ability is governed by physiological,

morphological, and behavioral components and cannot be solely attributed to one variable like body size.

We also found no difference in crawling speed between the larger hatchlings from Mon Repos and the smaller hatchlings from Bare Sand Island. Larger hatchlings typically crawl more quickly, presumably due to their greater stride length (Wren et al., 1998; Chu, 2008; Ischer et al., 2009). However all of these studies focused on a single ESU only, rather than comparing ESUs that differ in body size. The lack of a difference in crawling speed in our study suggests that the smaller hatchlings from Bare Sand Island compensate for their smaller stride length, most likely by having a greater stride rate.

Scute pattern variation.—We found nests from Bare Sand Island had a lower proportion of hatchlings with major non-modal scute patterns than nests from Mon Repos. A previous study showed that hatchlings of *N. depressus* and *C. caretta* with non-modal scute patterns performed similarly to hatchlings with the modal scute pattern in terrestrial locomotor performance trials, but hatchlings of *N. depressus* with the modal scute pattern out-performed those with major non-modal scute patterns during the first 20 minutes of swimming (Sim et al., 2014). This suggests that selection against non-modal scute patterns occurs after the hatchlings reach the sea, and could mean that a greater number of hatchlings from Mon Repos are succumbing to predation or exhaustion during their swim through the near-shore environment.

Several hypotheses have been suggested to explain non-modal scute patterns, including genetic factors, inbreeding, disturbance to eggs, pollution, and incubation temperature (Mast and Carr, 1989; Hewavisenthi and Parmenter, 2001; Velo-Anton et al., 2011). Several of these apply to the current study, most importantly incubation temperature (as mentioned above) and movement of eggs, as the Mon Repos clutches were relocated and the Bare Sand Island ones were not. Constant temperature experiments on *N. depressus* have suggested that non-modal scute patterns are produced at lower temperatures (Hewavisenthi and Parmenter, 2001). As it is likely that incubation temperatures were lower at Mon Repos than at Bare Sand Island during our study, this could explain the higher proportion of hatchlings with the major non-modal scute patterns at Mon Repos. Similarly, there is some evidence that non-modal scute patterns are more common in relocated nests (Mast and Carr, 1989), which could explain the difference we observed. Additional research needs to be done on how non-modal scute patterns affect long-term fitness and survival of hatchlings.

Conclusion.—Despite differences in hatchling size between the two ESUs, we did not observe any differences in terrestrial locomotor performance. This suggests that hatchlings from each ESU deal with terrestrial locomotion differently. The difference in the proportion of hatchlings with major non-modal scute patterns is also an interesting finding, although more research is needed into the causes. Because of these differences it is important to study several ESUs of a species before implementing large-scale conservation efforts.

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