



Implications of nest relocation for morphology and locomotor performance of green turtle (*Chelonia mydas*) hatchlings

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ABSTRACT

Sea turtle scute abnormalities are observed in higher proportion in hatchlings compared to adults, suggesting that hatchlings with a non-modal scute pattern (NMSP) have a lower chance of surviving to adulthood. In this study, we collected 732 newly emerged hatchlings from Redang Island, Malaysia, and compared their scute classification, size, and mass to fitness correlates (self-righting ability, crawling speed, and swimming speed). We investigated the proportion of hatchlings from each nest with NMSP to determine if there was a correlation with incubation duration or clutch relocation. We found relocated clutches at Chagar Hutang Turtle Sanctuary had a significantly shorter incubation duration with a higher proportion of NMSP compared to *in situ* clutches. Hatchlings' mass were significantly heavier from *in situ* clutches compared to relocated clutches, although there were no significant differences of hatchling speed based on scute classification or clutch type. The difference of hatchling mass between *in situ* and relocated clutches could affect predation and mortality rates on recently emerged hatchlings. These findings have important conservation implications, suggesting that relocation should only be implemented on clutches with a high potential to be disrupted or with a low chance of survival if left *in situ*. Our findings highlight the need for a standard procedure when clutch relocation is used as a conservation strategy. Relocation should replicate natural nest dimensions by duplicating both nest width and depth, and clutches should be relocated to similar shade conditions as the natural nest.

1. Introduction

There are seven extant species of marine turtles, most of which are classified as Endangered or Critically Endangered by the International Union for the Conservation of Nature (IUCN, 2020). Many marine turtle populations have experienced a decline in the past several decades due to coastal development, habitat loss, plastic entanglement and ingestion, and poaching (Hamann et al., 2007; Lutcavage et al., 1997; Wallace et al., 2011). In addition to these pressures, anthropogenic climate change poses a major threat to marine turtles (Root and Schneider, 2002). Sea turtle clutch relocation is a conservation strategy currently used by many hatcheries to protect eggs in areas where natural hatchling success is low due to human poaching, tidal inundation and erosion threats, or high predation (García et al., 2003; Türkozan and Yılmaz, 2007). There is some evidence that clutch relocation can increase hatchling success (Dutton et al., 2005; García et al., 2003), but there are

also concerns about unintended consequences, including altering the gene pool (Mrosovsky, 2006), decreasing fitness of hatchlings, decreasing hatching success (Limpus et al., 1979; Talbert et al., 2008; Ware and Fuentes, 2018), increasing the frequency of scute abnormalities in hatchlings (Mast and Carr, 1989; Türkozan and Yılmaz, 2007), and disrupting natural sex-ratios (Pintus et al., 2009).

A single nesting beach can have varying microenvironments (*i.e.*, moisture and temperature) around the incubating eggs (Cagle et al., 1993). Thus, relocating clutches can affect the incubation conditions of the eggs, which can in turn influence hatching success, size, and sex (McGehee, 1990; Maulany et al., 2012; Stewart et al., 2019). Temperature affects several aspects of ectotherm development during incubation (Howard et al., 2014), including the incubation duration (Mrosovsky and Yntema, 1980), growth rate (Gillooly et al., 2001), locomotor performance (Maulany et al., 2012), size of hatchlings (Du and Ji, 2003; Sibly and Atkinson, 1994), and sex determination (Mrosovsky

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and Yntema, 1980). While the sex of mammals is determined by sex chromosomes at the time of fertilization, the sex of marine turtles is determined by the nest temperature during the middle third of embryonic development, known as temperature-dependent sex determination (Mrosovsky and Yntema, 1980). Eggs incubated at ~29 °C produce a 50:50 sex ratio, called the pivotal temperature (PT), and temperatures above the PT produce predominantly females and vice versa (Mrosovsky, 1994). For all seven species of marine turtles, there is a thermal range of 25–33 °C in which egg incubation is successful (Howard et al., 2014; Spotila and Standora, 1985), and temperatures towards the higher threshold (prolonged exposure above 33 °C) can result in morphological abnormalities and increased hatchling mortality (Hawkes et al., 2007; Hays et al., 2003; Laloë et al., 2016; Packard et al., 1977).

Rising temperatures due to anthropogenic climate change could have negative impacts on all life stages of sea turtles. Marine turtle development could be adversely affected by increased sand temperature at nesting beaches, as well as other climate change consequences which could lead to nest inundation including increased frequency of storms and sea-level rise (Booth et al., 2004, 2013; Booth and Astill, 2001; Booth and Evans, 2011; Fuentes et al., 2011; Glen and Mrosovsky, 2004; Hawkes et al., 2007; Hays et al., 2003; Lyons et al., 2020). Therefore, marine turtle clutch relocation might be increasingly used as a conservation strategy to cope with these consequences of climate change. Many managed marine turtle nesting beaches use hatcheries that follow a standard procedure regarding clutch relocation techniques, such as ensuring the new egg chamber is the same depth as the natural nest, and choosing a new nest site with the same distance to vegetation and sea (Eckert et al., 1999). With anthropogenic climate change having increasing threats on incubating clutches, it is important to understand the possible consequences of clutch relocation on hatchling fitness and survival if it is to be used by hatcheries as a conservation technique.

There are difficulties in directly measuring fitness and survival in marine turtles throughout their various life stages (Booth et al., 2004). Due to the difficulty of tagging and tracking hatchlings, assessing the survivability after emergence is problematic. As a consequence, correlates of fitness in hatchling turtles are often used as a proxy, due to the ease of access of hatchlings on nesting beaches (Booth et al., 2004; Freedberg et al., 2004; Ischer et al., 2009; Sim et al., 2014a). Some of these correlates of fitness include body size, self-righting ability, crawling speed, and swimming speed (Booth et al., 2004; Freedberg et al., 2004; Ischer et al., 2009; Sim et al., 2014a). Hatchlings with a larger body size could have increased fitness due to increased swimming and crawling speed (Burgess et al., 2006; Le Gouvello et al., 2020), which would make them less likely to encounter predation (Martins et al., 2020). Hatchlings often experience high rates of predation following nest emergence (Pilcher et al., 2000; Wilson et al., 2019), thus increased locomotor ability could improve their chances of survival. Conversely, smaller hatchlings with shorter incubation times tend to have a larger yolk reserve (Booth et al., 2004) and therefore have the potential to survive longer if food is scarce.

The scute pattern on a hatchling's carapace is a physical attribute that is a proposed indicator of fitness (Sim et al., 2014a, 2014b). The modal scute pattern (MSP) for green turtles (*Chelonia mydas*) is five vertebral scutes and four pairs of costal scutes which are flanked by eleven or twelve pairs of marginal scutes (Özdemir and Türkozan, 2006). The variation in marginal scutes is more common in both adult and hatchling green turtles and typically has little effect on body shape and is considered far less likely to affect fitness of hatchlings compared to the variation in costal and vertebral scutes (Ergene et al., 2011; Margaritoulis and Chiras, 2011; Türkozan et al., 2001). The proportion of hatchlings with non-modal scute patterns (NMSP) is more common than the proportion of adults with scute abnormalities (Limpus, 1971; Mast and Carr, 1989; Türkozan et al., 2001), suggesting that fewer turtles with NMSP survive to adulthood (Mast and Carr, 1989). Abnormalities in scute pattern are likely caused by a variety of factors, including genetics (Velo-Antón et al., 2011), environmental parameters

during incubation (Hewawisenth and Parmenter, 2002), and egg handling during clutch relocation (Sönmez et al., 2011; Türkozan and Yılmaz, 2007).

Since hatchlings' morphology can indicate viability (Booth et al., 2004; Janzen et al., 2000), we assessed if scute patterns and morphology (size and mass) were affected by clutch relocation, and if this, in turn, influenced hatchling locomotor ability at the Chagar Hutang Turtle Sanctuary in Malaysia. We hypothesized that clutch relocation would affect the quality, morphology, and fitness of hatchlings.

2. Material and methods

2.1. Study site

This study was conducted on the northernmost beach of Redang Island (5.812787, 103.008217), located about 23 km off the east coast of Peninsular Malaysia in the South China Sea (Fig. 1). Chagar Hutang Turtle Reserve is a 350 m long beach, only accessible via boat due to surrounding tropical rainforest and hills. Green turtles are the primary species that nest at Chagar Hutang, with an estimated average of 502 clutches laid per year, with the occasional hawksbill nesting, with an estimated average of 9 clutches laid per year (Chan, 2010). Nesting activities have been monitored regularly at Chagar Hutang since 1993 (Chan, 2010). The Sea Turtle Research Unit (SEATRU) volunteer program was introduced at Chagar Hutang in 1998, which conducts yearly monitoring, tagging, and *in situ* egg incubation research from April to September. In 2005, Chagar Hutang was declared as a turtle sanctuary through the Department of Fisheries, and it was closed to the public and thus protected against poaching.

At Chagar Hutang, eggs are relocated as a conservation strategy if the risk of predation or nest inundation are high. In general, clutches are relocated to open areas, and the depth of the relocated clutches are kept the same as the natural nest. This process is completed within 2 h of oviposition. Volunteers and rangers are responsible for nest monitoring; therefore, the decision to relocate and the method of relocation vary. There are certain zones of the beach that have higher water inundation risk, ant predation, and large rocks, thus all clutches laid in these zones are relocated. In addition, clutches laid near the high tide line were relocated to decrease risk of tidal inundation.

2.2. Nest monitoring and hatchling collection

From August 1–19th, 2019, newly emerged hatchlings from 37 green turtle (*Chelonia mydas*) nests were collected. Sampled clutches were incubated both in the shade and sun, *in situ* and *exsitu* (relocated), and at different locations along the beach. The depth of relocated clutches was kept the same as their natural nest, and the relocation procedure was completed within 2 h of oviposition. After 45 days of incubation, a plastic mesh corral was placed above the nest each night at dusk to prevent emerging hatchlings from escaping to the sea. Nests were checked hourly until dawn so the time of emergence could be recorded, and to allow for hatchlings' locomotor performance to be measured soon after emergence. Corral placement was repeated on consecutive nights until hatchling emergence occurred.

2.3. Locomotor performance and morphology of hatchlings

After emergence, the number of vertebral and costal scutes of all hatchlings was recorded. Twenty hatchlings were collected from each nest, 10 MSP and 10 NMSP, but if there were less than 10 NMSP hatchlings, the balance was made up of MSP hatchlings. We did not count the number of marginal scutes, as variations in the number of marginal scutes have been found to have little effect on hatchlings (Sim et al., 2014a). Hatchlings selected from each nest were labeled on their plastron with a marking pen. Within 2 h of hatchling emergence, the self-righting locomotor performance test was started. Each hatchling

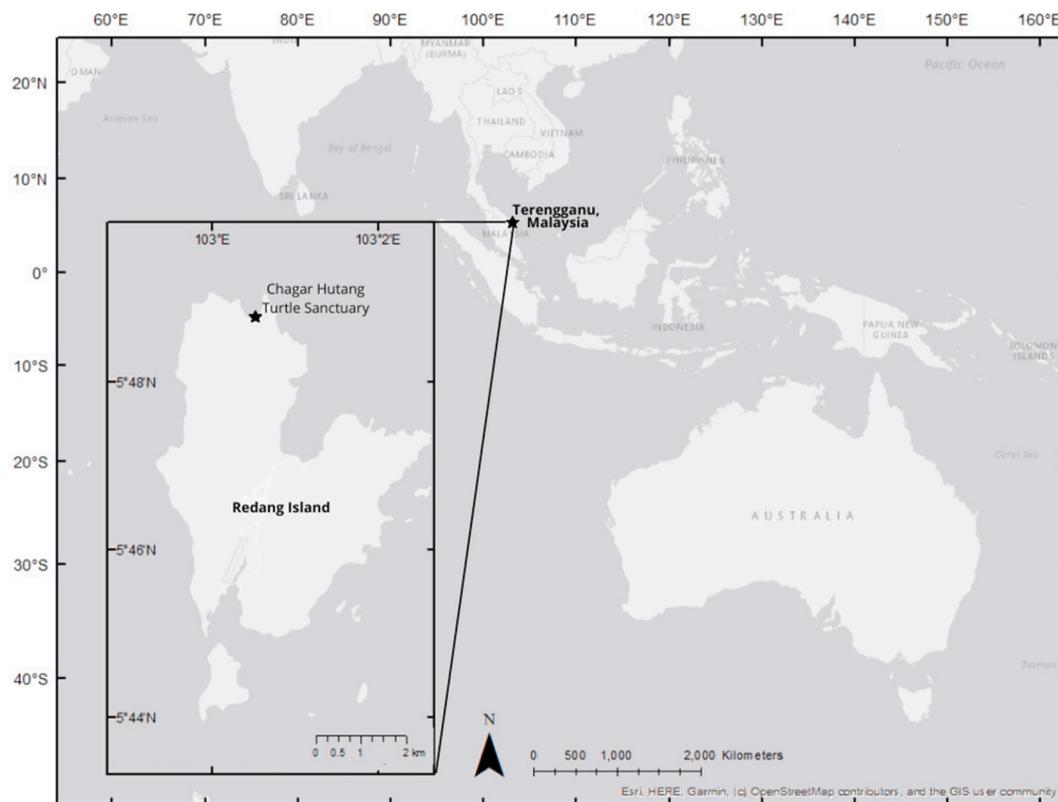


Fig. 1. Chagar Hutang Turtle Sanctuary located on the northern tip of Redang Island, approximately 23 km east of Peninsular Malaysia.

was placed upside down on its carapace in a flat-bottomed plastic tub and the time it took it to self-right was measured. If the hatchling failed to self-right within 30 s it was placed upright for 10 s before being trialed again. Between each trial, the hatchling was given 10 s of rest, for a total of three self-righting tests. Immediately following the self-righting experiment, the crawling test was conducted.

For the crawling and swimming experiments, a 2.9 m length of black plastic guttering was used. The raceway was placed on a sea-ward facing slope, which we lined with fresh sand each night. A light was attached to the seaward-facing end of the gutter, and hatchlings were released at the opposite end. Crawl speed was calculated as the time it took for hatchlings to crawl the 2.9 m, and the trial was ended if the time exceeded 2 min. Swimming speed was measured in the same method as above, but the raceway was moved to a flat surface, and fresh seawater was used to fill the gutter each night.

Immediately following the swimming tests, the hatchlings' carapace length and width was measured at the widest point using a 150 mm digital caliper (± 0.1 mm). A hatchling size index (carapace length \times carapace width) was calculated for each hatchling. Hatchlings were weighed using an electronic balance (Electronic Compact Scale, SF-400C, 500 ± 0.01 g) and then released to crawl to the sea.

All experimental procedures were approved by the University of Malaysia Terengganu animals ethics committee (approval no. UMT/RMIC/2-2/1/23).

2.4. Statistical analyses

Three different statistical approaches were used to examine the effect of clutch relocation on incubation duration and scute pattern of hatchlings. First, after testing for normality and equal variance with Shapiro-Wilk and Levene tests, a *t*-test was conducted to compare incubation duration between relocated and *in situ* clutches. Next, to assess the relationship between incubation duration and proportion of NMSP hatchlings, a Kendall rank correlation coefficient was used. A

comparison of the proportion of hatchlings with NMSP between *in situ* and relocated clutches was conducted with a Mann-Whitney *U* test.

Factorial Analysis of Variance (ANOVA) tests were used to assess if there were differences in size (mass and size index) between NMSP and MSP hatchlings and between hatchlings from relocated and *in situ* clutches, with clutch ID as the random factor. A Kendall rank correlation coefficient was used to determine the relationship between incubation duration and size and mass of the hatchlings. Factorial ANOVAs were also used to evaluate the crawling, swimming, and self-righting speeds between NMSP and MSP hatchlings and hatchlings from relocated and *in situ* clutches. For the swimming and crawling speeds, we deemed the speed trial a failure if the hatchling took longer than 2 min to finish, and we excluded them from the analysis. Thus, we had swim speeds from 294 relocated hatchlings and 401 *in situ* hatchlings, and crawl speed from 306 relocated hatchlings and 404 *in situ* hatchlings. Self-righting attempts were deemed a failed attempt if they took longer than 30 s.

In order to assess the relationship between size and locomotor performance, we first checked for normality and equal variance. If the data was normal and equal variance was achieved, we assessed the correlation with a Pearson's product correlation. If the data was not normal or there was not equal variance, a Kendall rank coefficient was calculated. All statistical analyses were performed using RStudio V1.2.5001 (R Development Core Team, 2019), and statistical significance was assumed as $P < 0.05$.

3. Results

A total of 2133 newly emerged hatchlings from 37 nests were examined during the course of this study (Table 1). A Mann-Whitney *U* test showed that relocated clutches had a significantly higher proportion of NMSP hatchlings ($M = 25.38$, $SD = 21.22$) compared to *in situ* clutches ($M = 8.55$, $SD = 8.73$), $W = 79.5$, $P = 0.009$ (Fig. 2).

A Student's *T*-Test showed that relocated clutches had significantly shorter incubation durations ($M = 49.0$, $SD = 1.93$), compared to *in situ*

Table 1

Descriptive statistics comparison between relocated and *in situ* green turtle clutches. Incubation duration was defined as the number of days before the eggs were laid and the day of first emergence. Hatching success was defined as the proportion of the entire clutch that hatched to produce live hatchlings. Percentage of hatchlings demonstrating non-modal scute pattern (NMSP) was calculated. Distance from vegetation was measured in meters from the nest to the closest major region of vegetation.

	Relocated	<i>In situ</i>
Nest Count	15	22
Hatchling Count	760	1313
Incubation Duration \pm SD	49 \pm 1.93	52 \pm 2.87
Hatching Success \pm SD	71.39 \pm 16.33	85.96 \pm 9.61
% NMSP \pm SD	25.38 \pm 21.22	8.55 \pm 8.73
Distance from Vegetation (m) \pm SD	6.17 \pm 2.84	5.11 \pm 3.32

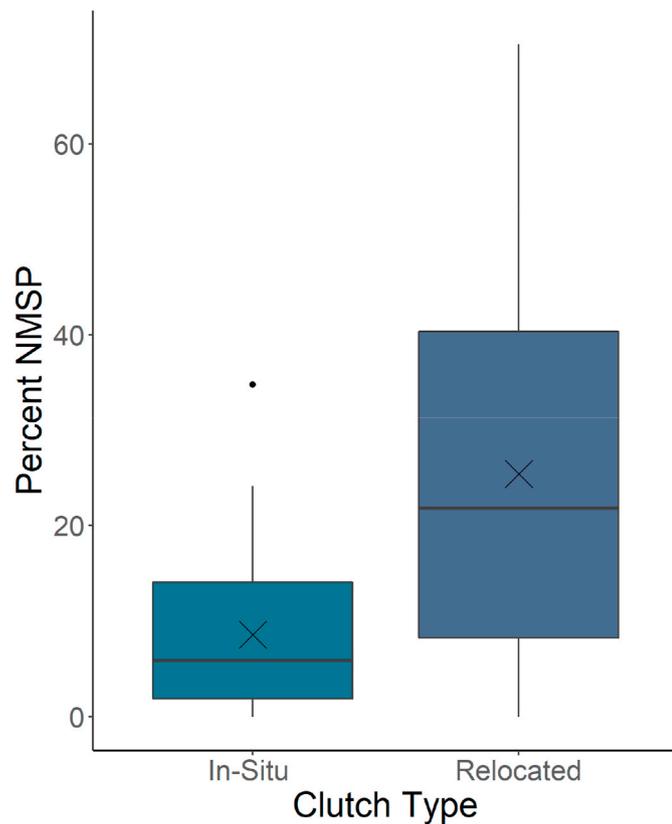


Fig. 2. Comparison of the percent of hatchlings with non-modal scute patterns (NMSP) between relocated and *in situ* nests. Relocated clutches had a significantly higher proportion of mutated hatchlings compared to *in situ* nests ($P = 0.009$). Mean values are represented by an X, the center line of each boxplot denotes the median, the boxes contain the inner quartiles of the sampled values, the whiskers extend to the most extreme data point which is within 1.5 times above the 75th percentile or below the 25th percentile, and the black dots denote outliers that are >1.5 times the interquartile range above the 75th percentile and below the 25th percentile.

clutches ($M = 52.05$, $SD = 2.87$), $t_{35} = 3.86$, $P = 0.0005$ (Fig. 3). A Kendall's tau correlation was run to determine the relationship between incubation duration and proportion of NMSP hatchlings within the 37 nests. There was a strong, negative correlation between incubation duration and proportion of NMSP hatchlings, which was statistically significant ($\tau_b = -0.283$, $P = 0.018$) (Fig. 3). This means that nests with shorter incubation durations (presumed due to higher temperatures) had a higher prevalence of hatchlings with NMSP.

A Kendall's tau correlation was run to determine the relationship between incubation duration and hatchling size. There was a negative

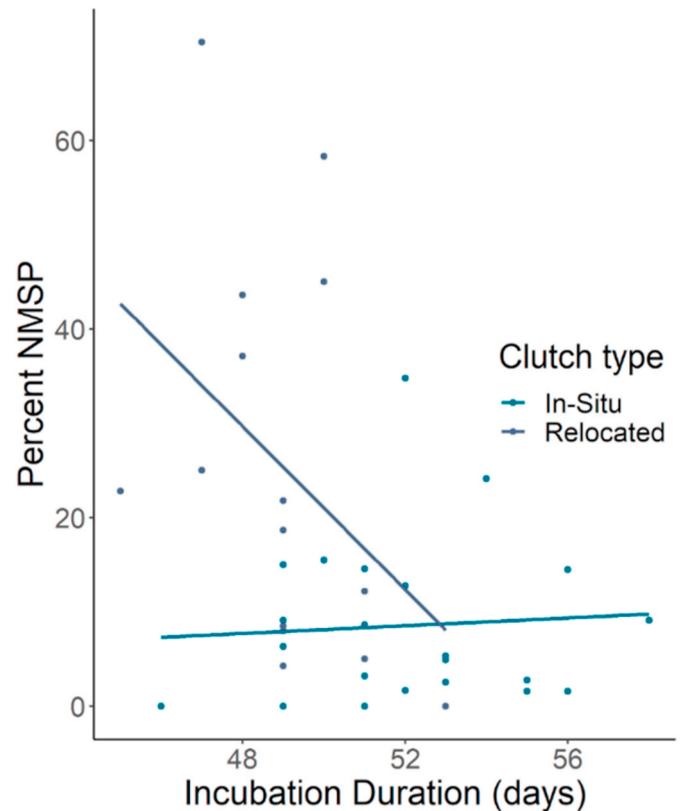


Fig. 3. The relationship between incubation duration (days) and percent of hatchlings with non-modal scute patterns (NMSP) between *in situ* ($n = 15$) and relocated ($n = 22$) nests. There was a negative correlation between incubation duration and proportion of NMSP hatchlings ($P = 0.018$). Relocated clutches had significantly shorter incubation durations compared to *in situ* nests ($P = 0.0005$).

correlation between incubation duration and size indices of hatchlings ($\tau_b = 0.324$, $P < 0.0001$). Similarly, there was a negative correlation between incubation duration and mass of hatchlings ($\tau_b = 0.213$, $P < 0.0001$). Nests with shorter incubation durations (presumed due to higher temperatures) had lighter and smaller hatchlings.

Next, morphological differences in mass and size indices were assessed by scute classification and clutch type. A factorial ANOVA was used to test the interaction effects of clutch type and scute classification on the hatchlings' mass. Clutch type included two levels (*in situ*, relocated), scute mutation consisted of two levels (MSP, NMSP), and the clutch ID was added as a random factor. There was no significant interaction between scute classification and clutch type on the hatchlings' mass, $F_{1,724} = 0.278$, $P = 0.598$ (Fig. 4). There was also no significant difference between MSP and NMSP hatchlings' mass, $F_{1,724} = 3.828$, $P = 0.051$. Although we did find a significant difference between relocated ($M = 19.41$, $SD = 1.59$), and *in situ* hatchlings' mass ($M = 19.87$, $SD = 1.59$), $F_{1,724} = 20.708$, $P < 0.0001$. To summarize, hatchlings from relocated clutches were lighter compared to hatchlings from *in situ* clutches, but there was no difference in mass between hatchlings with and without MSP scute patterns.

A factorial ANOVA was also conducted to test the interaction effects of clutch relocation and scute classification on hatchling size, with clutch ID added as a random factor. There was no significant interaction between scute classification and clutch type on the size index of hatchlings, $F_{1,724} = 0.058$, $P = 0.810$ (Fig. 4). The main effect for relocation yielded an F ratio of $F_{1,724} = 1.853$, $P = 0.174$, indicating no significant difference in size between hatchlings from relocated ($M = 1514$, $SD = 104.87$), and *in situ* clutches ($M = 1592$, $SD = 111.87$). The main effect for scute classification produced an F ratio of $F_{1,724} =$

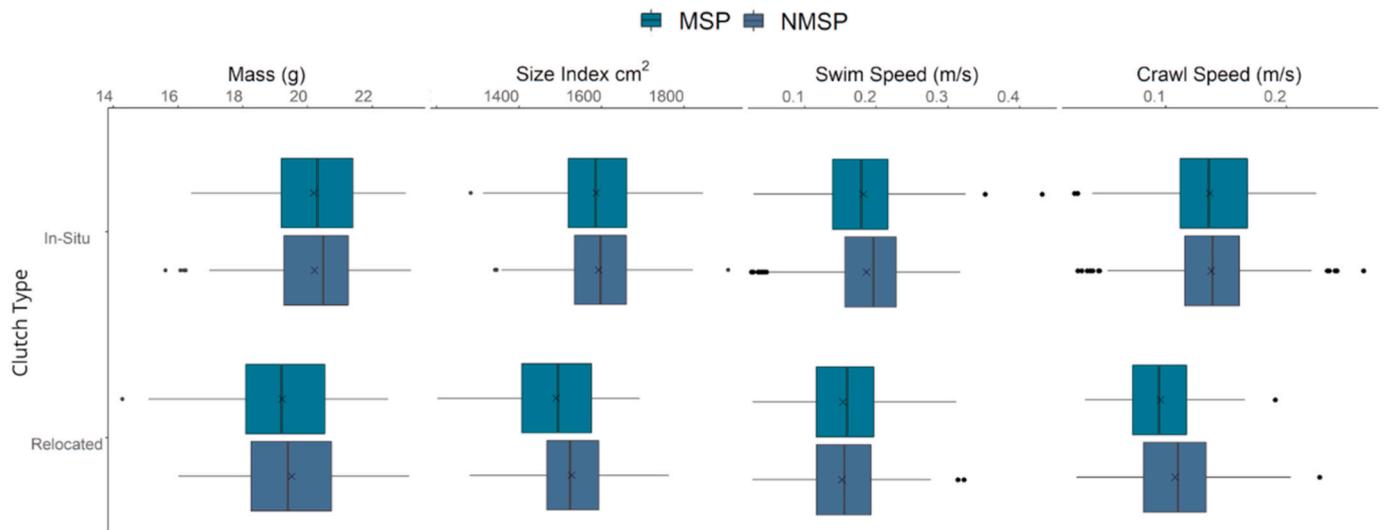


Fig. 4. Box plot showing the effects of clutch type and scute pattern (modal scute pattern in green and non-modal scute pattern in blue) on morphology and fitness of hatchling turtles. Clutch type is defined as relocated or *in situ* clutches. Scute pattern is defined as modal scute pattern (MSP) or non-modal scute pattern (NMSP). Morphology was assessed through measuring mass (g) and size index (carapace length (cm) x carapace width (cm) measurements) of 320 hatchlings from relocated clutches and 413 hatchlings from *in situ* clutches. Fitness was assessed through swim and crawling speed trials and the time was cut off at 2 min, thus this analysis includes swim speeds from 294 relocated hatchlings and 401 *in situ* hatchlings and crawl speed from 306 relocated hatchlings and 404 *in situ* hatchlings. Mean values are represented by an X, the center line of each boxplot denotes the median, the boxes contain the inner quartiles of the sampled values, the whiskers extend to the most extreme data point which is within 1.5 times above the 75th percentile or below the 25th percentile, and the black dots denote outliers that are >1.5 times the interquartile range above the 75th percentile and below the 25th percentile. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

11.133, $P = 0.0009$, indicating a significant difference between MSP ($M = 1567$, $SD = 103.96$) and NMSP hatchlings' size indices ($M = 1536$, $SD = 125.91$). Thus, hatchlings with NMSP were smaller than those with MSP, but there was no difference in size between hatchlings from relocated clutches compared to hatchlings from *in situ* clutches.

Next, the locomotor performance of 734 hatchlings from 37 nests was evaluated using swimming and crawling trials. We assessed how swimming and crawling speed were influenced by clutch type and scute classification. Clutch type included two levels (*in situ*, relocated) and scute mutation consisted of two levels (MSP, NMSP), and the clutch ID was added as a random factor. First, the data was filtered to only compare hatchlings that completed crawling the length of the raceway in <2 min, as time trials exceeding 2 min were considered failed attempts.

A factorial ANOVA was used to test the interaction effects of clutch type and scute classification on swimming speed. There was no significant interaction between scute classification and relocation on the crawl speed of the hatchlings, $F_{1,687} = 1.341$, $P = 0.247$ (Fig. 4). There was also no significant difference between MSP and NMSP hatchlings' swimming speed, $F_{1,687} = 0.033$, $P = 0.856$. We also did not find a significant difference of swimming speed between hatchlings from relocated ($M = 0.155$, $SD = 0.062$), and *in situ* clutches ($M = 0.186$, $SD = 0.061$), $F_{1,687} = 2.363$, $P = 0.125$.

We also conducted a factorial ANOVA to test the interaction effects of clutch type and scute classification on crawl speed. There was no significant interaction between scute classification and clutch type on the crawl speed of the hatchlings, $F_{1,702} = 0.975$, $P = 0.324$. There was also no significant difference between MSP and NMSP hatchlings' crawl speed, $F_{1,702} = 1.469$, $P = 0.246$. We also did not find a significant difference of crawling speed between hatchlings from relocated ($M = 0.105$, $SD = 0.036$), and *in situ* clutches ($M = 0.135$, $SD = 0.038$), $F_{1,702} = 0.572$, $P = 0.450$ (Fig. 4).

Next, the relationship between the size of hatchlings (size index and mass) and locomotor performance (crawl and swim speed) was assessed. A significant but weak correlation was detected between size index and crawling speed $r_{562} = 0.16$, $P = 0.0001$. A Kendall rank correlation

coefficient was used to find a weak but significant correlation between mass and crawling speed $\tau_{562} = 0.09$, $P = 0.001$, size index and swim speed $\tau_{562} = 0.066$, $P = 0.019$, and mass and swim speed $\tau_{562} = 0.072$, $P = 0.011$. Therefore, larger and heavier hatchlings have slightly faster swimming and crawling speeds.

Additionally, the average self-righting time was compared by clutch type and scute classification using a factorial ANOVA, and hatchlings with 3 failed self-righting attempts were omitted. Clutch type included two levels (*in situ*, relocated), scute classification consisted of two levels (MSP, NMSP), and the clutch ID was added as a random factor. There was no significant interaction between scute classification and clutch type on the self-righting of the hatchlings, $F_{1,644} = 0.013$, $P = 0.909$. There was also no significant difference between MSP and NMSP hatchlings' self-righting speed, $F_{1,644} = 1.980$, $P = 0.160$. We also did not find a significant difference between hatchlings from relocated ($M = 3.027$, $SD = 3.062$), and *in situ* clutches self-righting speed ($M = 2.514$, $SD = 2.400$), $F_{1,644} = 0.458$, $P = 0.499$. We also compared the proportion of hatchlings with failed self-righting attempts between clutch type and scute classification. Failed self-righting attempts were defined as taking longer than 30 s, and each hatchling was given three attempts to self-right. We found that NMSP hatchlings from relocated clutches had the highest proportion (23%) of failed self-righting attempts (Fig. 5). Interestingly, MSP hatchlings from relocated clutches had a lower proportion of hatchlings with failed attempts compared to hatchlings from *in situ* clutches. Despite a lower proportion of failed attempts, 3.6% of all MSP hatchlings from relocated clutches failed at self-righting in all three of their self-righting attempts.

4. Discussion

Clutch relocation is used as a conservation strategy to protect turtle populations around the world, but we found that the turtles produced from these nests could be smaller, less fit, and have a higher proportion of hatchlings with NMSP compared to clutches left *in situ*. The relocated green turtle clutches at Chagar Hutang were found to have significantly shorter incubation duration compared to *in situ* clutches. Incubation

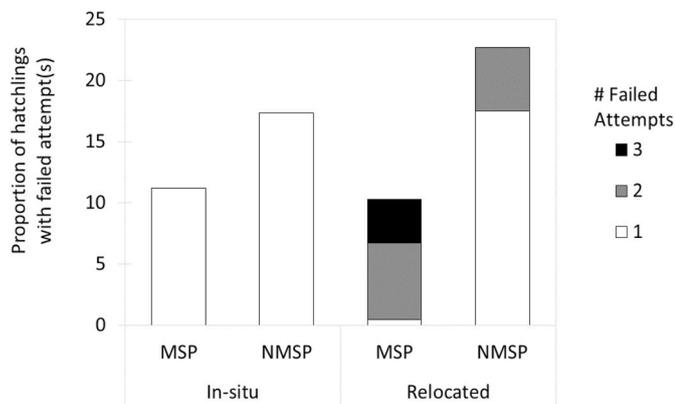


Fig. 5. Comparison of clutch type and scute classification on the proportion of hatchlings with failed self-righting attempts, with each hatchling allowed three attempts. If time was >30 s, it was deemed a failed attempt. Nest type is defined as relocated or *in situ* nests. Scute pattern was defined as modal scute pattern (MSP) or non-modal scute pattern (NMSP).

duration has a direct relationship with incubation temperature of the nest, with increased temperatures having shorter incubation durations. Higher temperatures speed up physiological processes during incubation, including growth and development (Schmidt-Nielsen, 1997). Thus, it is possible that relocated clutches were warmer due to either shallower nest depths or relocation to open areas which receive more direct sun. Similar results were found in a study comparing relocated and *in situ* loggerhead clutches, where relocated clutches had a shorter incubation duration and warmer temperatures compared to *in situ* clutches (DeGregorio and Williard, 2011).

We found that incubation duration was correlated with hatchling size, mass, and even the proportion of hatchlings with NMSP. Nests with longer incubation durations (presumed lower temperatures) produced hatchlings with larger sizes and masses. Researchers have speculated that larger hatchlings may have reduced predation pressure in the neritic zone (Hirth, 1980). Further, MSP hatchlings were significantly larger (size index) compared to NMSP hatchlings. In addition, hatchlings from relocated clutches had a larger proportion of hatchlings with NMSP. NMSP may reflect underlying internal abnormalities that are the ultimate cause of lower hatchling locomotor performance (Mast and Carr, 1989).

Hydric conditions have been shown to affect mass (Packard, 1991), and temperature determines sex and can affect post-hatchling growth rate. Both of these nest environment factors can influence hatchling morphology and fitness, and thus play a crucial role in hatchling survival. Hatchling size can have an impact on survivorship since larger animals might have less predation pressure due to its superior locomotor abilities as well as being too large for some predators (Gyuris, 2000; Limpus, 1973). In addition, a negative correlation between hatchling size and nest temperature has been recorded for sea turtles (Reece et al., 2002). It is thought that with lower temperatures and longer incubation durations, more yolk is converted to hatchling material (Ischer et al., 2009).

Understanding differences in temperature between relocated versus *in situ* clutches has significant conservation implications, as relocation to warmer sand could lead to all female production. The thermal regime of sand can differ on a single beach based on the microenvironment, so the beach zone that clutches are relocated to can influence hatchling outcomes. This highlights the need for a standard procedure for clutch relocation. For example, many hatcheries keep distance from vegetation and nest depth comparable to the natural nests, but the artificial nest dimensions can be overlooked. By failing to recreate the natural nest shape, eggs might be closer to the surface, which can cause an increased temperature regime for these incubating hatchlings, though to test this hypothesis it would be necessary to deploy temperature loggers in both

in situ and relocated clutches. Additionally, the location of clutch relocation could influence the temperature regime of the nests. At Chagar Hutang, many of the clutches are relocated to open areas of the beach that may receive more sun exposure compared to *in situ* clutches that are laid near vegetation or in the shade (Fig. 6). These higher temperatures can lead to a higher proportion of females (Jensen et al., 2018), morphological abnormalities (Du and Ji, 2003), decreased fitness (Booth et al., 2004), and mortality (Matsuzawa et al., 2002).

It is important to note that the goal of establishing a standard procedure of clutch relocation is not to standardize the exact size, shape, and location of every nest, but to replicate the same dimension and microenvironment of the nest from which the clutch came from. Furthermore, we found that in addition to relocation causing shorter incubation durations, hatchlings from relocated clutches had a significantly higher proportion of hatchlings with NMSP compared to *in situ* clutches. A study conducted on Kemp's ridley turtles (*Lepidochelys kempi*) compared egg-handling methods during clutch relocation and found that the least handled eggs produced turtles with the lowest levels of variability in scute patterns, and the roughly handled eggs produced the highest levels of scute pattern variability (Mast and Carr, 1989). In addition, a 1994 study found that the scute deviation rate was higher for relocated hatchlings compared to *in situ* hatchlings (Suganuma et al., 1994). The exact implications of scute variation for sea turtles are unclear, although since there are fewer adults with NMSP, it is believed that hatchlings with NMSP have reduced survivorship (Mast and Carr, 1989). Thus, clutch relocation and artificial incubation should be only used in "doomed nests", where natural survival would otherwise be very low. In order to separate the effects of egg handling from the placement (and thermal regime) of relocated clutches, future studies could include relocating eggs back into the natural nest and compare hatchling morphology and fitness.

5. Conclusion

Our results suggest that clutch relocation at Chagar Hutang Turtle Sanctuary can result in smaller hatchlings with a higher proportion of NMSP. Although there are potential benefits of relocation on clutches for nests that would otherwise have a low chance of survival if left *in situ*, there do appear to be some adverse consequences of clutch relocation on hatchlings. Relocated clutches had a lower hatching rate than clutches

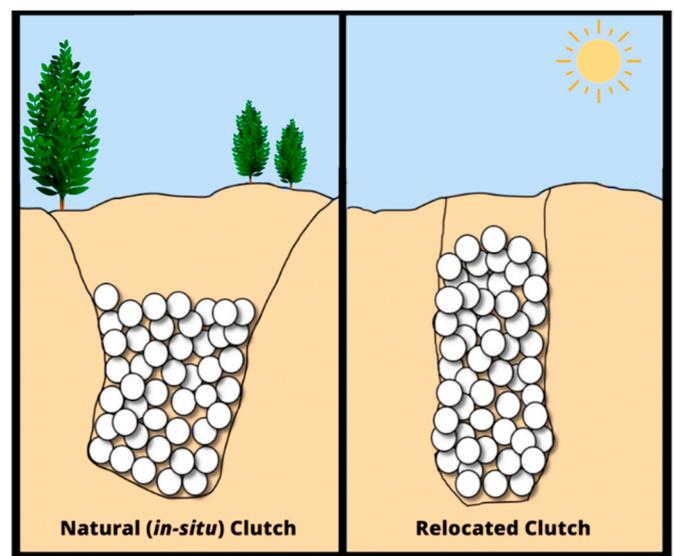


Fig. 6. We found relocated clutches had a shorter incubation duration which suggests they could have a warmer thermal regime compared to the clutches left *in situ*. These relocated clutches can have hatchlings with morphological abnormalities, smaller sizes, and lower fitness.

left *in situ*, but it is important to note that relocation was only implemented on clutches that faced a higher threat of predation or inundation, so success was likely higher than if they were left *in situ*. The highest mortality rate of turtles is believed to be during the early stages of life, between incubation and swimming out to the open ocean after emergence (Crouse et al., 1987). With mortality rates of 40–60% within the first 2 h in the sea (Pilcher et al., 2000), it is crucial that hatchery management strategies work to decrease the likelihood of predation during this critical time. If clutch relocation is used, then it is important to minimize handling and ensure that the artificial nest dimensions, particularly the egg chamber diameter, carefully replicates the natural nest from which the clutch came from. If the natural clutch was laid in the shade, the relocated clutch should also be placed under the shade, to try to reproduce the natural nest conditions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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