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EFFECTIVE HATCHERY MANAGEMENT PRACTICES TO ENHANCE HATCHING SUCCESS AND MALE HATCHLING OUTPUT IN SEA TURTLE NESTS ACROSS SRI LANKA

SANTHUSHYA HEWAPATHIRANAGE[1,2], AND RUPIKA S. RAJAKARUNA[1,3]

[1]Department of Zoology, Faculty of Science, University of Peradeniya, Peradeniya, Sri Lanka
[2]Postgraduate Institute of Science, University of Peradeniya, Peradeniya, Sri Lanka"
[3]Corresponding author, e-mail: rupika.rajakaruna@sci.pdn.ac.lk

Abstract.—**Temperature strongly influences sea turtle embryonic development, affecting incubation duration, hatching success, and sex determination. We investigated whether nest shading moderates incubation temperatures and outcomes for Green Turtles *(Chelonia mydas)* and Olive Ridley Turtles *(Lepidochelys olivacea)* at a hatchery in Sri Lanka. Two incubation pens were used: a tree shaded pen (about 70% canopy cover) and an unshaded pen exposed to direct sunlight. Beach-collected clutches were split evenly and reburied in each pen. Data loggers recorded temperatures at nest centers; in a second phase with Green Turtle clutches, we placed loggers at three depths (10, 35, and 55 cm from the base) to assess within nest stratification. We monitored 14 Green Turtle nests (1,481 eggs) and 13 Olive Ridley nests (1,296 eggs), plus eight Green Turtle clutches for depth profiling. Shaded nests were cooler by a mean of 3.3° C for both species. Hatching success did not differ between treatments: Green Turtles hatched at 82–96% (shaded) and 88–94% (unshaded), and Olive Ridleys at 80–95% (shaded) and 82–96% (unshaded). Incubation duration was shorter in unshaded nests. Sex ratio predictions from middle-third temperatures indicated 100% female production under unshaded conditions, whereas shaded nests produced more balanced ratios. Significant differences in incubation temperatures were observed across the bottom, middle, and top nest levels in both sunny and shaded pens, with stronger stratification in unshaded nests in GLMM analyses. Shading is therefore a practical hatchery tool to reduce thermal extremes and mitigate female-biased sex ratios under climate warming.**

Key Words.—nest temperature; sea turtle conservation; climate change impacts; incubation environment

INTRODUCTION

Five of the seven sea turtle species are classified as Vulnerable: Loggerhead Turtle (*Caretta caretta*), Leatherback Turtle (*Dermochelys coriacea*), and Olive Ridley Turtle (*Lepidochelys olivacea*) or Critically Endangered: Hawksbill Turtle (*Eretmochelys imbricata*) and Kemp's Ridley (*Lepidochelys kempii*) on the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN; 2025) and are safeguarded under Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; https://cites.org/). Sea turtles are globally threatened by multiple stressors, including habitat loss, overexploitation, and climate change, which collectively contribute to their endangered status. A particular vulnerability is their temperature-dependent sex determination (TSD; Mrosovsky and Yntema 1980; Ewert et al. 1994). The temperature of the nest during the middle third of incubation plays a crucial role in influencing the differentiation of the gonads in the developing embryo (Spotila et al. 1987; Georges et al.1994; Mrosovsky 1994). Given the importance of ambient temperature in embryonic development, anthropogenic climate warming poses a significant threat to sea turtle populations, as rising sand temperatures increase the production of female hatchlings and may drive a feminization effect in populations nesting in warmer climates to explain potential future declines of populations and local extinctions of sea turtles (Hawkes et al. 2007; Pike 2014; Jensen et al. 2018; Clarke et al. 2021). Therefore, nest incubation temperatures can have long-term consequences as it can influence hatchling sex ratios, with downstream effects on adult operational sex ratios (Hays et al. 2003) and population dynamics (Santidrián Tomillo et al. 2015). Incubation temperature is also vital for the successful development of hatchlings (Tiwol and Cabanban 2000; Colin Limpus, unpubl. report).

Sea turtle nest temperature is influenced by a complex interplay of physical, chemical, and biological factors, which can vary significantly across and within beaches. Environmental conditions, including rainfall and air temperature (Bustard and

Greenham 1969), as well as physical factors such as shade (Staines et al. 2020), sand moisture, and gas exchange affect nest temperature (Broderick et al. 2000). Deeper nests tend to maintain more stable temperatures, as they are less impacted by solar radiation and fluctuations in air temperature (Mrosovsky 1994; Broderick et al. 2000; van de Merwe et al. 2006).

For all sea turtle species, a thermal range of 25°–33° C is required for successful egg incubation (Standora and Spotila 1985; Howard et al. 2014), and temperatures above this range can result in morphological abnormalities and increased hatchling mortality (Packard et al. 1977; Hays et al. 2003; Hawkes et al. 2007; Laloë et al. 2016). The relationship between incubation temperature and sex ratio follows a logistic model, where the pivotal temperature is the point on the curve corresponding to a 1:1 (50%) sex ratio between male and female hatchlings (Mrosovsky and Pieau 1991). The pivotal temperature varies among species and populations depending on geographical location (Janzen et al. 1991; Pieau et al. 1991; Davenport 1997). The pivotal temperature for Green Turtles (*Chelonia mydas*) varies among geographic regions and populations. For example, recent work on the southern Great Barrier Reef population reports a pivotal temperature of 28.1° C (Smith et al. 2021; Young et al. 2023), which is lower than the 29.1° C reported for Malaysia (Ibrahim et al. 2004; Van De Merwe et al. 2006; Reboul et al. 2021). This lower estimate is consistent with earlier physiological studies that related incubation duration to sexual differentiation in the Green Turtle (Miller and Limpus 1981; Burgess et al. 2006). For Olive Ridley turtles, the pivotal temperature has been reported as 29.5° C for populations in India (Mohanty-Hejmadi et al. 1986). At only 1° C above the pivotal temperature, 80% of hatchlings are female (Limpus et al. 2009). As the global atmospheric temperatures are expected to rise by 0.3°–4.8° C by 2100 (Intergovernmental Panel on Climate Change 2021), there is therefore considerable concern that sea turtle nest temperatures will also rise unless turtles can compensate behaviorally by selecting cooler nest sites. It may push nest incubation temperatures above the sustainable range of 25°–33° C for populations nesting closest to the equator, potentially affecting these populations (Howard et al. 2014).

Clutch relocation is a common management tool used by sea turtle conservation programs, whereby clutches are moved from a threatened site to a safer location (Glen et al. 2003). This relocation can be to an enclosed hatchery area or simply to another area in the same nesting beach. This conservation tool is known to minimize threats to eggs and hatchlings and thus may help preserve sea turtle populations (Antworth et al. 2006; Mazaris et al. 2009). Clutches from nests in areas known to have a high illegal take, beach erosion or flooding, or high predation risk are usually relocated to safer beaches or to hatcheries, following standard clutch relocation techniques and ensuring that the human-made nest chamber replicates the natural nest in depth and shape (Limpus et al. 1979; Mortimer 1999; Abella et al. 2007). Relocating clutches can still alter egg incubation conditions, affecting hatching success, size, and sex (McGehee 1990; Maulany et al. 2012; Stewart et al. 2018). Shading is one management approach that can be used to reduce sand nest temperatures in hatcheries and offset the harmful impacts of increased temperatures. Natural shade offered from trees covering the nesting grounds has been previously found to minimize temperatures of nests (Maulanyet al. 2012; Wood et al. 2014, Staines et al. 2019). Unshaded hatcheries in hot tropical regions like Malaysia result in nest temperatures near the lethal upper limits for sea turtle development, with poor hatching success and female-skewed sex ratio of hatchlings (Limpus 1993; Shanker et al. 2003; Reboul et al. 2021).

In Sri Lanka, clutch relocation has been undertaken in sea turtle rookeries at Rekawa and Kosgoda as part of the *in situ* conservation programs conducted by the non-governmental organization Turtle Conservation Project (TCP) since 1996 (Ekanayake et al. 2010). Relocations were carried out shortly after nesting was completed, when eggs were at risk or the nesting site chosen by the female was unsuitable. In such cases, the eggs were carefully excavated and moved to a safer location within the same beach area. Clutch relocation has also been a common practice in hatcheries since their establishment in 1956 in Sri Lanka. Currently, all commercial hatcheries obtain eggs collected the previous night from beaches by fishers or local villagers. These eggs are reburied in incubation pens within enclosed hatchery areas and incubated until the hatchlings emerge.

We investigated relocated and hatchery-incubated nests of Green Turtles and Olive Ridley turtles in Sri Lanka. Our specific aims were to: (1) monitor nest temperature profiles under different shading conditions; (2) estimate primary sex ratios based on incubation temperatures; and (3) evaluate hatching and emergence success in relation to incubation

Figure 1. Two egg incubation enclosures at a hatchery along the southwestern coast of Sri Lanka. (A) Incubation pen exposed to direct sunlight. (B) Incubation pen with 70% shade conditions under trees. (Photographed by Santhushya Hewapathiranage).

environment. We evaluated shading as a low-cost management intervention for mitigating female-biased sex ratios and reduced hatchling output in sea turtles, which are increasingly driven by rising incubation temperatures and declining natural beach shading under climate warming. Specifically, we determined the effectiveness of site-specific shading strategies that could be used for conservation of sea turtles.

Materials and Methods

Study site.—We carried out this study at a privately-owned hatchery in Bentota (6.39780°N, 80.00549°E) on the southwestern coast of Sri Lanka from October 2017 to March 2018. After explaining the objectives of the study, we obtained verbal consent from the hatchery owner to collect data. The hatchery was constructed following the IUCN guidelines (IUCN 2005; Rajakaruna et al. 2013) with two egg incubation enclosures located above the high-tide mark. The common practice is that turtle eggs are brought to the hatchery by villagers from the area in the early morning, after being collected from nearby beaches. These eggs are purchased by the hatchery owner and are then reburied inside the hatchery either as whole clutches or divided into two to three secondary clutches, depending on the number of eggs in the clutch and the capacity of each incubation pen (Rajakaruna et al. 2013).

Data collection.—We selected two incubation pens inside the hatchery. One pen was under the shade of a tree (about 70% shading) and the other pen was under direct sunlight in the same hatchery enclosure (Fig. 1). We divided each clutch equally and reburied them in the two pens, maintaining nest depths of 65 ± (standard deviation) 5 cm for Green Turtles and 45 ± 5 cm for Olive Ridley Turtles. We used iButton temperature data loggers (Thermochron™ model DS1921G; OnSolution Pty Ltd, Sydney, Australia) to record nest temperatures (to nearest 0.5° C every 60 min) and placed each logger in thin 40 µm dense plastic food bags to prevent corrosion from ionized coastal vapors. We placed the bags with loggers in the middle of the nest at the time of reburial of the eggs. In a subsequent trial, we divided eight Green Turtle egg clutches equally and reburied them in the two pens. We placed data loggers at the bottom (10 cm from the base), middle (35 cm from the base), and the top (55 cm from the base) of each nest.

We counted the number of eggs in each clutch brought to the hatchery, assigned a number to each clutch, and reburied the clutch. We excavated the nests 5 d after the first hatchling emergence and counted any live hatchlings that remained in the nest. We removed dead hatchlings, eggshells, and unhatched eggs from the nests at the time of excavation. We noted incubation duration as the number of days between oviposition and the first emergence of hatchlings from the nest, and we counted the number of hatchlings that successfully emerged. We recorded the number of eggs that failed to hatch and dead hatchlings that did not emerge from the nest for each nest and then preserved both unhatched eggs and dead hatchlings in sample jars with 10% formalin.

Data analysis.—We calculated the nest temperature from the beginning to end (overall temperature), middle-third incubation temperature/Thermo Sensitive Period (TSP) temperature, percentage hatching success (Miller, 1997), emergence success (Miller, 1997), incubation duration, and the number of un-hatched eggs/dead hatchlings for all nests buried in the shady and sunny incubation pens for both species. We determined hatching success as:

$$\text{Hatching success} = \frac{\text{Number of hatched eggshells}}{\text{TCC}} \times 100$$

and emergence success as:

$$\text{Emergence success} = \frac{((\text{TCC} - (\text{UH} + \text{L} + \text{D}))}{\text{TCC}} \times 100$$

where UH = unhatched, L = live hatchlings, D = dead hatchlings, and TCC = total clutch count.

We compared nest temperature, hatching success, emergence success, and incubation duration between shady and sunny nests using Paired *t*-tests after checking the normality of the differences (Shapiro–Wilk Test). When differences deviated from normality, we used the Wilcoxon Signed-rank Test. We considered the significance level using $P \leq 0.05$.

We calculated the average recorded hourly temperature for middle-third of incubation temperature (middle third portion of the nest temperature throughout the incubation duration) to estimate the sex ratio of the hatchlings using the logistic function described by Limpus and Fien (2009). Because pivotal temperatures have not been determined for any sea turtle species nesting in Sri Lanka, we used the temperature from the closest geographic locations as the pivotal temperature for even sex ratios: 29.1° C for the Green Turtle in Malaysia (Ibrahim et al. 2004; Van De Merwe et al. 2006) and 29.5° C for the Olive Ridley Turtle in India (Mohanty and Dimond 1986).

According to the logistic model of pivotal temperature (Blechschmidt et al., 2020), we defined the sex ratio of hatchlings as a function of nest temperature (Limpus, 2009). The proportion of females f(t), is determined using the following equation:

$$\text{f}(\text{t}) = \frac{\text{a}}{1 + \text{e}^{\frac{-(\text{t}-\text{tpiv})}{\text{b}}}}$$

where t is the mean middle-third incubation temperature, tpiv = 29.1° C (the pivotal temperature for Green Turtles), or is 29.5° C (the pivotal temperature for Olive Ridley Turtles), a = 1, and b = 0.4424779. This function predicts 99%, 88%, 44%, 8%, and 1% male hatchlings at incubation temperatures of 27°, 28°, 29°, 30°, and 31° C, respectively, for Green Turtles and 97%, 76%, 24%, 3%, and 0% male hatchlings at incubation temperatures of 27°, 28°, 29°, 30°, and 31° C, for Olive Ridley Turtles.

For the second experiment (temperatures at various levels in the nest), we compared temperatures within the nest using a Generalized Linear Mixed Model to determine if there was a significant difference in the incubation temperatures of the nest at different depths. Nest level (top, middle, bottom) and pen type (shady or sunny) were treated as fixed factors. Clutch identity was included as a random factor to account for repeated measurements within nests. Models were fitted with a Gaussian error structure and an identity link function, as the response variable (temperature) was continuous and normally distributed. We used R version 4.3.2 (R Core Team 2023) and the lme4 package (Bates et al. 2015) for all analyses.

Results

We collected data from 14 Green Turtle nests containing 1,481 eggs and 13 Olive Ridley Turtle nests with 1,296 eggs, all of which were equally divided into two incubation pens. In the second phase, which involved recording temperature variations across the depth of the nests, we obtained data from eight Green Turtle clutches. No evidence of external mortality factors such as ant or ghost crab predation, root intrusion, or fungal/bacterial infection was observed in any of the nests.

Nest temperature.—The mean nest temperature during middle third incubation duration for Green Turtles varied from 32.5° to 34.0° C in the sunny pen and 29.0° to 32.5° C in the shady pen, and for Olive Ridley Turtles, it varied from 32.0° to 33.0° C in the sunny pen and 28.5° to 31.5° C in the shady pen (Table 1). Overall, nest temperatures differed significantly between the shady and sunny incubation pens for both species (Green: $t = 9.91$, df = 13, $P < 0.001$; Olive Ridley: W = 0, $P < 0.001$). The mean middle third nest temperatures of the Green Turtles between the shady (mean = 29.9° ± 0.89° C) and sunny pens (mean = 33.3° ± 0.37° C) differed significantly ($t = 12.92$, df = 13, $P < 0.001$) and that of the Olive Ridley

Table 1. Mean (± standard deviation) nest temperatures in sunny and shady incubation pens with 14 Green Turtles (*Chelonia mydas*) nests and 13 Olive Ridley Turtles (*Lepidochelys olivacea*) nests relocated in a hatchery in southwestern coast of Sri Lanka. Minium and maximum nest temperatures are in parentheses.

	Sunny	Shade
	Green Turtle	
Overall Nest	33.4 ± 0.5 (32,5, 34.5)	31.2 ± 0.8 (30.0, 32.5)
Middle-third incubation	33.3 ± 0.4 (32.5, 34.0)	29.9 ± 0.9 (29.0, 32.5)
	Olive Ridley Turtle	
Overall Nest	33.3 ± 0.5 (33.0, 34.0)	31.1 ± 0.5 (30.5, 32.0)
Middle-third incubation	32.5 ± 0.5 (32.0–33.0)	30.0 ± 0.8 (28.5, 31.5)

Turtles between the shady (mean 30.0° ±0.80° C) and sunny pens (mean 32.5° ± 0.48° C; $t = 10.41$, df = 12, $P < 0.001$).

The results suggest a possibility of 100% female-biased hatchling populations based on TSP temperature for clutches incubated in the sunny incubation pen for both Green and Olive Ridley Turtles (Fig. 2). Whereas the mean hatchling sex ratio estimated for Green Turtle clutches in the shaded pen was 80% female (range of values, 56–100% female), while the mean hatchling sex ratio estimated for Olive Ridley clutches in shaded incubation pen was 70% (range of values, 9–99% female; Fig. 2).

The vertical thermal regimes within the nests of Green Turtles in relation to mean incubation temperatures between shady and sunny incubation pens, showed differences among the top, middle, and bottom regions in both incubation pens (Fig. 3). The mean vertical thermal gradient along the clutches incubated in the shady incubation pen ranged from 33° to 29.5° C from top to bottom with a 2.5° to 3.0° C difference, while clutches incubated in the sunny incubation pen ranged from 36° to 30° C obtaining much higher thermal variation of 4.5° to 5.5° C within the nests. Nests in the sunny incubation pen displayed pronounced temperature differences across depths, resulting in much greater thermal variation within the nests. Mean bottom temperatures at a depth of 55 cm ranged from 29.5° to 30.0° C in the shady incubation pen and 30° to 31.5° C in the sunny incubation pen. In the middle of the nests at a depth of 35 cm, mean temperatures ranged from 30.0° to 32.0° C in the shady incubation pen and 33° to 34.5° C in the sunny incubation pen. In the topmost regions at a depth of 10 cm, mean temperatures ranged from 32.0° to 33.0° C in the shady incubation pen and 35.5° to 36.0° C in the sunny incubation pen. The upper limits of mean bottom temperatures were about 1.5° C, mean middle temperatures about 2.5° C, and the mean top temperatures were about 3.0° C higher in the sunny incubation pen than in the shady incubation pen.

The incubation temperatures in the shady pen differed significantly among the top, middle, and bottom nest levels ($F_{2,28} = 11.02$, $P < 0.001$). The top and middle levels (L.Ratio = 10.97, $P = 0.001$) and the top and bottom levels (L.Ratio = 11.23, $P < 0.001$) were significantly different, whereas the middle and bottom levels (L.Ratio = 0.02, $P = 0.887$) did not differ significantly. In the sunny area, incubation temperatures also varied significantly across all three nest levels ($F_{2,28} = 28.59$, $P < 0.001$). The top differed significantly from both the middle (L.Ratio = 26.85, $P < 0.001$) and bottom levels (L.Ratio = 38.25, $P < 0.001$), and the middle and bottom levels also differed significantly (L.Ratio = 5.25, $P = 0.022$). Both the shady and sunny incubation pens showed significant variation in temperatures across the three nest levels (top, middle, and bottom). The magnitude of this variation, however, was considerably greater in the sunny nests ($F_{2,28} = 28.59$, $P < 0.001$) compared with the nests in the shady pen ($F_{2,28} = 11.02$, $P < 0.001$).

Hatching success and incubation duration.—The hatching success rate for Green Turtles was 89.5 ± 6.47% in the shady pen and 90.1 ± 5.72 in the sunny pen, while for Olive Ridley Turtles, it was 86.6 ± 6.55% in the shady pen and 87.1 ± 4.89 in the sunny pen (Fig. 4, Table 2). There was no significant difference in the hatching success of Green Turtle eggs between the sunny and shady pens ($t = -0.81$, df = 13, $P = 0.435$) or in the hatching success of Olive Ridley Turtle eggs between the sunny and shady pens ($t = -1.22$, df = 12, $P = 0.244$). The emergence success rate for Green Turtles was 89.1 ± 6.36% in the shady pen and 89.5 ± 5.85% in the sunny pen, while for Olive Ridley Turtles, it was 86.2 ± 6.76% in the shady pen and 86.5 ± 4.41 in the sunny pen (Fig. 4, Table 2).

There was no significant difference in the emergence success of Green Turtle eggs between the sunny and shady pens ($t = -0.52$, df = 13, $P = 0.615$) or in the emergence success of Olive Ridley Turtle eggs between the sunny and shady pens ($t = -0.36$, df = 12, $P = 0.724$). The incubation durations were shorter in the sunny pens compared to the shady incubation pens for both species (Fig. 4, Table 2). For Green Turtles, the average incubation duration of clutches in sunny pens was 47.9 ± 1.61 d, which was significantly shorter ($t = 7.26$, df = 13, $P < 0.001$) than the average duration in shady pens (52.9 ± 1.98 d). Similarly, for Olive Ridley Turtles, clutches in sunny pens had a mean incubation duration of 48.5 ± 1.94 d, which was significantly shorter ($t = 4.46$, df = 12, $P < 0.001$) than the duration observed in shady pens (51.6 ± 1.71 d).

Discussion

The findings demonstrate that the middle-third incubation temperatures in the shady pen were significantly cooler than those in the sunny pen, with an average difference of 3.3° C. This aligns with studies such as Reboul et al. (2021), which showed

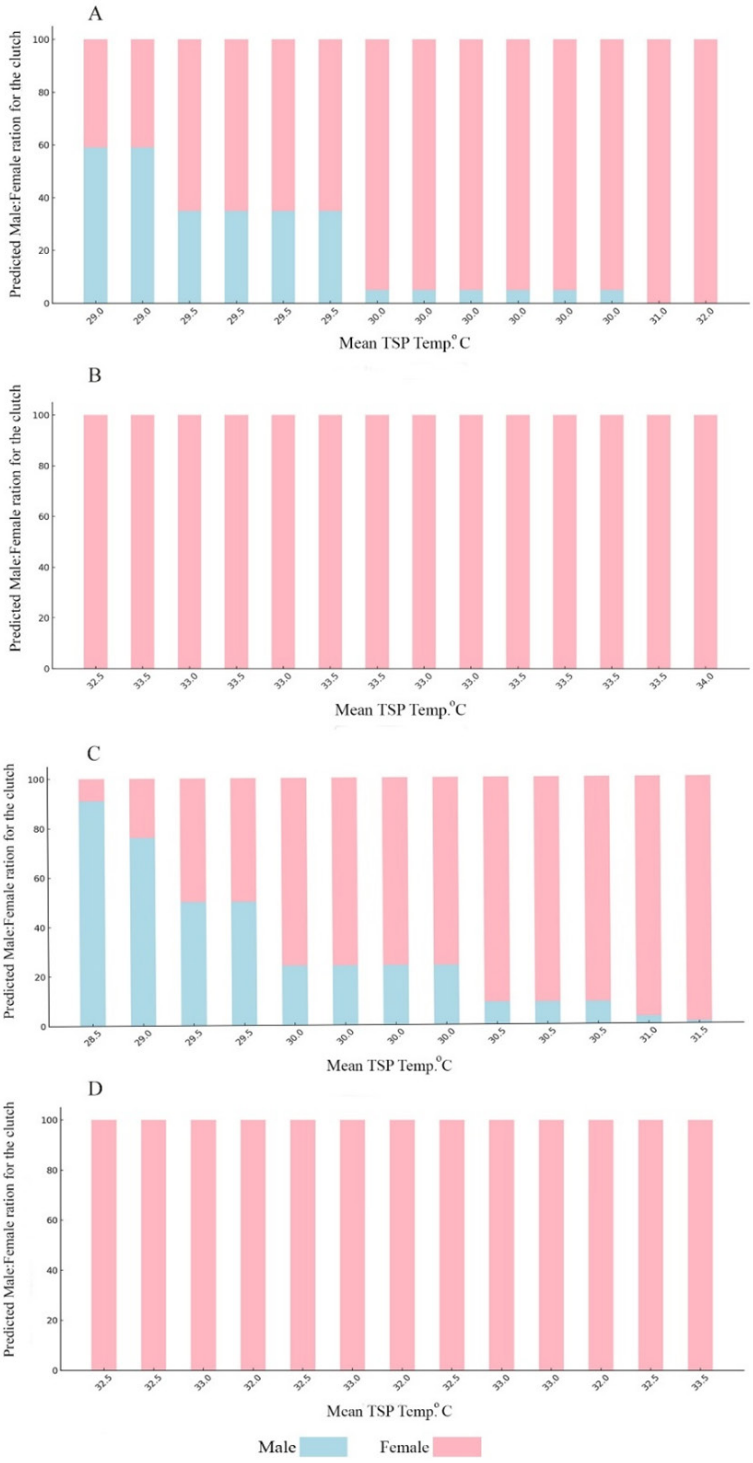

FIGURE 2. Mean middle-third incubation (TSP) temperatures and calculated sex ratios for (A) Green Turtle (*Chelonia mydas*) clutch incubated in the shady incubation pen, (B) *C. mydas* incubated in the sunny incubation pen, (C) Olive Ridley Turtle (*Lepidochelys olivacea*) clutch incubated in shady incubation pen, and (D) *L. olivacea* incubated in sunny incubation pen.

Table 2. Mean (± standard deviation) and minimum (Min) and maximum (Max) hatching success, emergence success, incubation duration, and clutch size data collected for Green Turtles (*Chelonia mydas*) in sunny and shady incubation pens with 14 nests and 13 Olive Ridley Turtles (*Lepidochelys olivacea*) nests relocated in a hatchery in the southwestern coast of Sri Lanka. Minimum and maximum nest temperatures are in parentheses.

	Sunny	Shade
	Green Turtle	
Hatching success (%)	90.07 ± 5.72 (76, 95)	89.50 ± 6.47 (76, 96)
Emergence success (%)	89.50 ± 5.85 (76, 95)	89.14 ± 6.36 (76, 96)
Incubation duration (days)	47.86 ± 1.61 (46, 51)	52.93 ± 1.98 (49.56)
Clutch size	55.18 ± 10.52 (36, 81)	55.18 ± 10.52 (36, 81)
	Olive Ridley Turtle	
Hatching success (%)	87.08 ± 4.89 (80, 97)	86.62 ± 6.55 (79, 96)
Emergence success (%)	86.54 ± 4.41 (80, 95)	86.15 ± 6.76 (78, 96)
Incubation duration (days)	48.54 ± 1.94 (46, 52)	51.62 ± 1.71 (48, 53)
Clutch size	64.04 ±17.64 (38, 94)	64.04 ±17.64 (38, 94)

that nests shaded by trees were considerably cooler than those under shade cloth in an open beach setting, and Rajakaruna and Ekanayake (2015), who reported extreme temperature ranges in unshaded hatcheries on the southwestern coast of Sri Lanka. Similar results were observed in Indonesian Olive Ridley hatcheries (Maulany et al. 2012), highlighting elevated temperatures during early development stages that could be lethal to embryos (Miller 1997). Embryos become increasingly tolerant of higher temperatures later in incubation, however, as shown by successful nest emergence even at temperatures exceeding 34° C during the final incubation weeks (Bustard 1971; Chu et al. 2008).

Experimental work further confirms that late-stage embryos can survive brief exposure to 34°–36° C without significant reductions in hatching success, although some impacts on hatchling condition may occur (Tedeschi 2015). Particularly, incubation temperatures in this study remained below critical thresholds during the thermosensitive period (TSP). The results also suggest a potential for 100% female-biased hatchling populations based on TSP temperatures in sunny pens for both Green and Olive Ridley Turtles. Natural shading may mitigate the influence of direct sunlight on relocated nests and reduce female-biased sex ratios; however, in natural nests these ratios could vary based on locality-specific factors such as beach orientation, beach vegetation, and sand temperatures (Booth and Freeman 2006). The nest shape and depth are key determinants of the temperature gradient, with studies by Kochet al. (2007) and Najwa-Sawawi et al. (2021) indicating Green Turtle nests have distinctive oval shapes that are difficult to replicate in hatcheries.

While our study estimated primary sex ratios of hatchlings, it is important to consider how these translate into operational sex ratios (OSRs) in breeding populations. OSRs are often more balanced than hatchling sex ratios because of differential survival, maturation rates, and remigration intervals between males and females. For example, females typically have longer remigration intervals (2–4 y) than males, which may breed more frequently and therefore contribute disproportionately to the OSR (Wright et al. 2012; Hays et al. 2014; 2022). This means that even strongly female-biased hatchling outputs do not necessarily translate into equivalent biases in adult breeding populations; however, persistent production of overwhelmingly female-biased primary sex ratios could reduce the number of males recruited into populations over time, ultimately constraining effective population size and limiting genetic diversity (Wright et al. 2012; Hays et al. 2014; Santidrián Tomillo et al. 2015). Such skewed OSRs could impact mating opportunities and threaten long-term population viability, especially under climate warming scenarios that further feminize sex ratios.

Our findings therefore highlight the need to link hatchery management practices and nest temperature regulation with demographic models that consider OSRs and their consequences for future population resilience as even slight temperature variations (1°–2° C) can significantly impact hatchling sex ratios due to the narrow transitional range in temperature (TRT) of 1.5°–2.0° C (Mrosovsky and Yntema 1980; Georges et al. 1994). Climate change is already influencing sea turtle populations, with studies showing extreme feminization of hatchlings (over 99% females at Raine Island; Jensen et al, 2018) and elevated egg mortality associated with hotter nest conditions (Booth et al. 2020; Blechschmidt et al. 2020). Temperature profiles within the nests revealed marked differences among the top, middle, and bottom sections in both sunny and shady incubation pens. In shaded pens, temperatures were relatively uniform across nest depths, whereas in sunny pens,

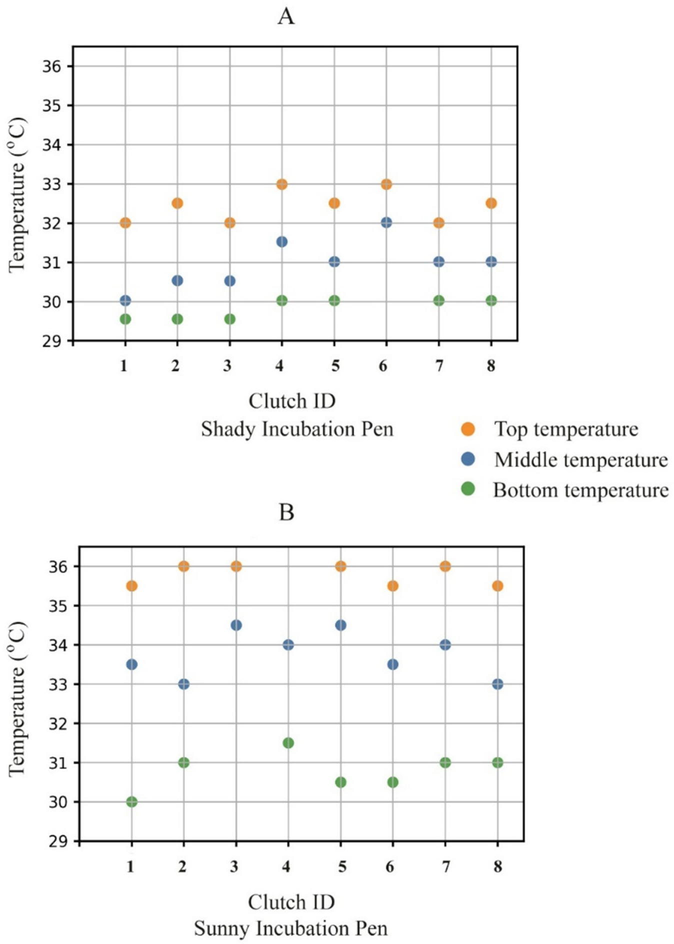

Figure 3. Vertical thermal profiles within Green Turtle (*Chelonia mydas*) nests incubated in (A) a shady pen and (B) a sunny pen. Points show mean incubation temperatures recorded at three nest levels (top, middle, bottom) for each clutch (Clutch ID 1–8). Temperatures were measured using data loggers placed at the bottom (10 cm from the base), middle (35 cm from the base), and top (55 cm from the base) of nests (nest depth 65 ± 5 cm).

distinct temperature gradients were observed with mean temperatures increasing by about 1.5° C at the bottom, about 2.5° C in the middle, and about 3.0° C at the top compared to shady pens. This pattern suggests a relatively shallow vertical temperature gradient in shaded nests. In contrast, the sunny pen exhibited significant differences among all three levels, with the top being the warmest and the bottom the coolest. This demonstrates a pronounced and consistent vertical gradient in sunny nests, where each depth level maintained distinctly different temperatures. This highlights the cooling effect of shading in maintaining favorable nest temperatures. Studies on regional temperature differences within nests reveal that nest depth and clutch size contribute to thermal variations between the top and bottom of nests (Limpus et al. 1984). Eggs at the top are typically warmer (about 1.4° C higher) compared to the bottom, affecting sex ratios (Kaska et al. 1998).

Additionally, metabolic heat generated during late-stage embryonic development raises egg temperatures above surrounding sand levels (Bustard 1971; Spotila et al. 1987; Mrosovsky 1994). Because our study protocol required halving clutches for relocation, however, the amount of metabolic heating in these artificial nests was likely reduced compared with natural full clutches, where the greater number of embryos produces more substantial heat. Further research is needed on the combined effects of nest depth and metabolic heat on incubation temperatures. Metabolic heat can elevate nest temperatures by about 2.5° C during late incubation, sometimes contributing to female-biased sex ratios and higher mortality when sand is already warm (Gammon et al. 2020).

Incorporating metabolic heat and nest depth into mechanistic models would improve predictions of

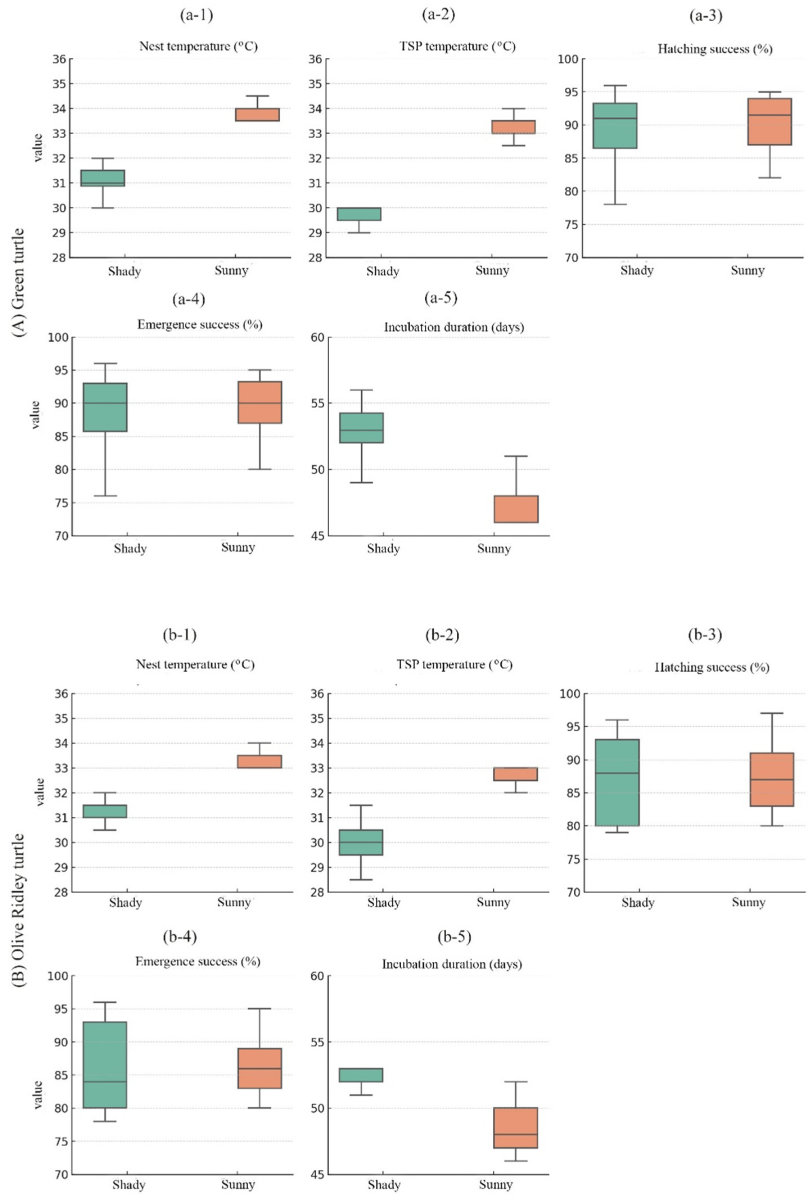

Figure 4. Median differences between shaded and unshaded hatchery pens in (a-1,b-1) whole incubation nest temperature (°C), (a-2,b-2) thermo-sensitive period (TSP) nest temperature (°C), (a-3,b-3) hatching success (%), (a-4,b-4) emergence success (%), (a-5,b-5) and incubation duration (days). The top two rows of panels (a-1)-(a-5) depict results for Green Turtles (*Chelonia mydas*) nests and the bottom two rows of panels (b-1)-(b-5) depict results for Olive Ridley Turtles (*Lepidochelys olivacea*) nests. In each plot, the box represents the interquartile range (IQR; 25th–75th percentiles), the horizontal line within the box indicates the median, and the whiskers extend to the minimum and maximum values that fall within 1.5 × IQ.

sex ratios and hatching success, and such insights are directly relevant for hatchery management strategies such as shading, adjusting nest depth, or splitting clutches. Global studies on TSP determination have been limited by the historical reliance on destructive methods to identify hatchling gonads. New research on blood hormone analyses (Anti-Müllerian hormone) from loggerhead hatchlings, however, show some promise for non-lethal sexing methods for neonate turtles (Tezak et al. 2020).

Despite the temperature differences between shady and sunny pens, no notable variation in hatching success was observed in the present study. Green Turtle hatching success rates were 89.5% and 90.0% in shady and sunny pens, respectively, while Olive Ridley Turtles recorded 86.6% and 87.0%.

These values exceed previous reports from Sri Lankan hatcheries (0–80%; Wickremasinghe 1982; Amarasooriya et al. 1997) and also surpass natural nest success at major rookeries. For Green Turtles at Kosgoda, the mean natural hatching success was 77.3% ± 22.2 with emergence success of 74.3% with a range of threats including predation, erosion, and environmental variability (Ekanayake et al. 2016), while at Rekawa the average was reported at about 82% (Ekanayake and Kapurusinghe 2000). These findings greatly support the use of hatcheries into sea turtle conservation programs in Sri Lanka, as there were substantial increases to hatching success rates when compared to those *in situ* on nearby beaches.

Incubation durations were significantly shorter in sunny pens compared to shady pens for both species, consistent with prior findings on relocated eggs and natural nests (Reboul et al. 2021; Morreale et al. 1982; Patino-Martinez et al. 2014; Wood et al. 2014; Staines et al. 2019). Elevated temperatures accelerate physiological processes, resulting in shorter incubation durations (Schmidt-Nielsen 1997). Sunny pen clutches were 2.75 d shorter, while shady pen clutches were 2.32 d longer than those at the Kosgoda rookery. Shady pens may offer additional biological benefits, such as larger hatchling carapace sizes due to extended incubation periods allowing for better yolk conversion (Booth and Freeman 2006); however, smaller hatchlings from sunny nests may be more vulnerable to predation (Rebelo et al. 2012; Fisher et al. 2014).

Elevated incubation temperatures not only skew sex ratios but also influence hatchling phenotype and performance traits such as size, morphology, locomotor speed, and swimming endurance (Booth and Freeman 2006; Burgess et al. 2006; Fisher et al. 2014; Maulany et al. 2012). Research has shown that hatchlings from cooler nests are generally larger and display faster crawl speeds and stronger swimming performance compared with those from warmer nests (Booth and Evans 2011; Santidrián Tomillo et al. 2015). These traits are critical for survival during what is called the frenzy period immediately after emergence, when hatchlings must rapidly cross the beach and reach the sea. In Sri Lanka, where ghost crabs (*Ocypodinae* sp.), domestic dogs (*Canis familiaris*), and birds are common predators on nesting beaches (Kapurusinghe and Ekanayake 2002), faster crawling hatchlings produced in cooler nests would likely have higher survival probabilities because they are less exposed to predation during this vulnerable terrestrial phase.

Conclusions.—We demonstrated that shading exerts a strong influence on incubation environments in Sri Lankan turtle hatcheries, producing significantly cooler nest temperatures compared with unshaded pens. Although hatching and emergence success were consistently high and did not differ significantly between treatments, incubation duration was shorter in sunny pens, and temperature-dependent sex ratio estimates indicated extreme feminization under unshaded conditions. In contrast, shaded pens produced more mixed-sex cohorts, highlighting shading as a practical management tool to mitigate the risk of producing exclusively female hatchlings under warm conditions. Hatcheries can secure high hatching success, while shading offers a means to balance sex ratios and avoid excessive feminization under climate warming scenarios. Future conservation efforts should integrate shading, nest-depth regulation, and temperature monitoring into hatchery practices, and link hatchery outputs to broader demographic models that consider how primary sex ratios translate into operational sex ratios in breeding populations. Such approaches will strengthen the role of hatcheries in sustaining viable sea turtle populations in the region.

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Santhushya Hewapathiranage is a research professional with over a decade of hands-on experience in wildlife ecology, conservation biology, and interdisciplinary public health studies. She earned her Bachelor of Science (Specializing in Zoology) and Master of Philosophy in Conservation Biology from the University of Peradeniya, Sri Lanka. Her M.Phil. thesis focused on the hatching success, nest temperature, and embryonic development of hatchery-relocated Green and Olive Ridley sea turtle eggs. Santhushya has contributed to collaborative international research, notably with Stanford University and the University of Connecticut, USA, addressing chronic kidney disease of unknown etiology (CKDu) in Sri Lanka through a multidisciplinary approach. She has co-authored multiple peer-reviewed articles and presented her research at global conferences, including the World Congress of Nephrology and the International Sea Turtle Symposium. Her academic interests span herpetology, marine conservation, public health, and the One Health framework. (Photographed by Dilan Chathuranaga).

Rupika S. Rajakaruna is Senior Professor and Chair of Applied Zoology in the Department of Zoology, Faculty of Science, University of Peradeniya, Sri Lanka. She earned her B.Sc. (Hons) in Zoology and M.Phil. in Molecular Parasitology from the University of Peradeniya, and completed her Ph.D. in Marine Biology at Memorial University of Newfoundland, Canada. With an academic career spanning more than three decades, she has published over 100 peer-reviewed articles on diverse topics, including sea turtle conservation, parasitology, amphibian malformations, and vector-borne zoonoses. She is a Fellow of the National Academy of Sciences, Sri Lanka, and the recipient of numerous honors, including Fulbright, Commonwealth and Endeavour Fellowships. An active participant in national and international scientific symposia, her research bridges conservation biology and infectious disease ecology, with significant implications for public health. (Photographed by Harshana).