

RESEARCH ARTICLE



Efficacy of artificial nest shading as a climate change adaptation measure for marine turtles at Ascension Island

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Abstract

Successful embryonic development and offspring sex ratios of marine turtles are determined by thermal conditions experienced during incubation, rendering them potentially vulnerable to anthropogenic climate change. With the rate of projected temperature rises likely to outpace the adaptive capacity of long-lived species such as marine turtles, there is growing interest in management interventions aimed at mitigating the effects of climate change at nesting grounds. In this study, we experimentally tested the impacts of artificial nest shading on the incubation temperature, hatching success, and predicted offspring sex ratio of green turtle (*Chelonia mydas*) clutches at Ascension Island. Clutches ($n = 97$) were sampled from 2 nesting beaches with naturally contrasting thermal environments (one hot; one cool) and either left as *in situ* controls or relocated to shaded or unshaded hatcheries on their beach of origin. Compared to unshaded experimental clutches, shading reduced mean incubation temperatures and sex-determining temperatures (i.e., middle third of embryonic development) by 0.5–0.9°C and 0.5–1.2°C respectively, with the reduction being greater on the hotter beach. Shading also differentially

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affected hatchling output across the 2 sites: on the hot beach, shading significantly improved hatching success by ~23% but had minimal effects on offspring sex ratio; whereas on the cooler beach, shading did not impact hatching success but resulted in ~12% more male offspring. Interestingly, mean incubation temperatures of *in situ* controls did not differ significantly from shaded clutches, and were significantly cooler than unshaded experimental clutches, suggesting relocation may have negated some of the benefits of shading. Our results demonstrated that artificial shading may be a viable approach for partially offsetting climate change impacts on nesting marine turtles; however, scalability will be a major challenge in achieving conservation objectives at high-density nesting sites like Ascension Island.

KEYWORDS

artificial shading, Ascension Island, *Chelonia mydas*, climate change, green turtle, hatching success, incubation temperature, marine turtle, nest relocation, sex ratio

Anthropogenic climate change is having profound impacts on the functioning of terrestrial and marine ecosystems globally (Hoegh-Guldberg and Bruno 2010). Species distributions are shifting, species phenologies are changing, and biodiversity is declining (Pacifi et al. 2015, Poloczanska et al. 2016). Relative to 1986–2005, global mean surface temperatures are projected to increase between 0.3–4.8°C by the end of the century (Intergovernmental Panel on Climate Change 2014), posing a serious conservation concern for many ectotherms, such as marine turtles, whose life histories, behaviors, and physiology are intrinsically linked to ambient thermal conditions (Jourdan and Fuentes 2015). Investigations focusing on how future climatic conditions will impact marine turtle populations, and what approaches may effectively mitigate such impacts have increased in recent years (Rees et al. 2016) and have been considered important research priorities (Patrício et al. 2021).

All 7 extant marine turtle species exhibit temperature-dependent sex determination (TSD), whereby offspring sex is determined by incubation temperatures experienced during the middle third of embryonic development (i.e., the thermosensitive period; TSP; Patrício et al. 2021). The incubation temperature during the TSP giving a balanced offspring sex ratio is termed the pivotal temperature and averages ~29°C for marine turtles, but can vary depending on the species and population (Tanabe et al. 2020). Thermosensitive period temperatures above the pivotal temperature produce more female offspring, while lower temperatures produce more males (Booth 2017). Globally, many marine turtle nesting sites already have highly female-biased hatchling production (Broderick et al. 2000, Patino-Martinez et al. 2012, Hays et al. 2014), and this is expected to become further skewed under climate change, with some nesting sites predicted to have near-total hatchling feminization by the end of the century (Tanner et al. 2019, Chatting et al. 2021). Incubation temperature also has a dramatic effect on offspring survival and phenotype. The upper thermal tolerance limit of marine turtle embryos is often reported to range between 33 and 35°C and there is a marked decrease in hatching success as mean incubation temperature approaches this threshold (Howard et al. 2014). Exposure to higher incubation temperatures has also been shown to produce smaller hatchlings, reduce locomotor ability, and increase the prevalence of morphological abnormalities (Booth 2017, Zimm et al. 2017). Projected increases in atmospheric

temperatures thus pose a serious threat to the population dynamics and long-term viability of marine turtle populations globally (Esteban et al. 2018).

Marine turtles have prolonged, migratory life histories characterized by late maturity, long generation times, natal philopatry, and naturally low levels of recruitment (Maurer et al. 2021), which may limit their capacity to adapt to rapid changes in thermal environmental conditions, particularly during their terrestrial reproduction phase. Consequently, there is growing interest in exploring the feasibility of management interventions at nesting beaches that could help to offset the short to medium-term impacts of climate change. Various approaches for manipulating incubation temperatures have been trialled, including irrigation, relocation to cooler sites, and artificial shading (Patino-Martinez et al. 2012, Esteban et al. 2018, Reboul et al. 2021, Gatto et al. 2023). Initial results have been promising; however, more experimental tests across a wider range of nesting environments are needed to fully evaluate the conservation potential of these interventions.

STUDY AREA

In this study, we experimentally investigated the impacts of artificial shading on the temperature, hatching success and offspring sex ratio of green turtle (*Chelonia mydas*) clutches at Ascension Island (14°20'W, 7°55'S), a remote UK Overseas Territory in the central South Atlantic that supports one of the world's largest green turtle nesting aggregations (Weber et al. 2014). Ascension Island has an arid climate and beaches lack any overstory vegetation to provide natural shading. Overall, hatchling sex ratio was estimated to be 75% female (Godley et al. 2002); however, highly variable sand color leads to considerable natural variation in incubation temperatures among the island's 32 nesting beaches, with some approaching the upper thermal tolerance limits for embryonic development (Weber et al. 2012). Ascension Island therefore provides a useful case study for evaluating the efficacy of artificial shading across a range of nesting environments.

METHODS

Shading experiment

An artificial shading trial was carried out during the 2022 nesting season on two of Ascension Island's principal green turtle nesting beaches: Long Beach (LB) and North East Bay (NEB). These beaches support more than 55% of Ascension's total nesting activity (Weber et al. 2014) and differ in sand color and incubation temperature. Long Beach consists of pale biogenic sand and is consistently ~3°C cooler at nest depth (mean = 75 cm) than NEB which primarily comprises of darker, volcanic sand (Weber et al. 2012). Experimental relocation of clutches took place across 20 nights between 8 February and 29 April 2022, spanning the peak in green turtle nesting at Ascension Island. On each night, 3–5 clutches were randomly selected and assigned to 1 of 3 treatment groups. One clutch was left as an *in situ* control and was marked with wooden stakes and a GPS position recorded for later identification. The remaining clutches were relocated to a hatchery (11 × 8 m) that was constructed towards the back of each study beach (Figure 1A). A total of 97 clutches (LB *n* = 50, NEB *n* = 47) were sampled across the two study beaches, 18 clutches were left *in situ* (LB *n* = 10, NEB *n* = 8) and 79 clutches were relocated to the hatcheries (LB *n* = 40, NEB *n* = 39).

Hatcheries were identical and consisted of an unshaded area (4 × 8 m) and a shaded area (7 × 8 m), each divided into twenty 1 × 1 m plots (Figure 1B). The shaded area was covered with 45–55% shade coefficient netting fixed 120 cm above the surface, supported on wooden beams. To minimize potential edge effects, shaded experimental clutches were placed a minimum of 1.5 m from the edge of the shade screen (hence the larger dimensions of shaded enclosure). A protective fence was also placed around each hatchery to safeguard clutches from being disturbed by

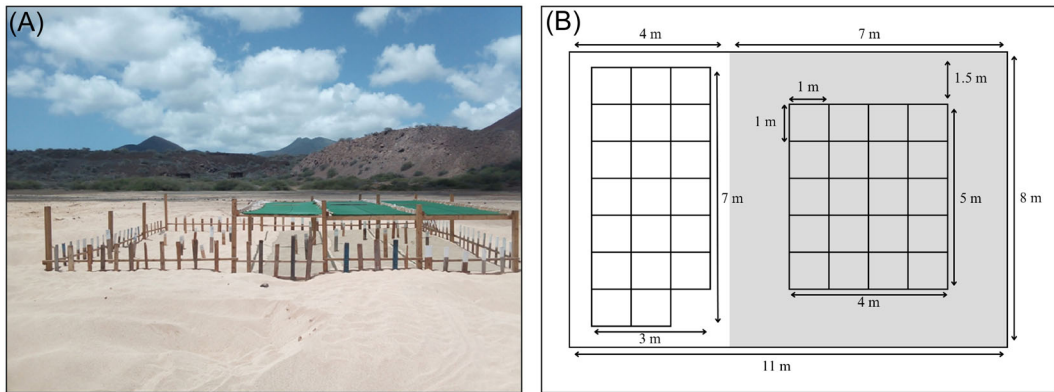


FIGURE 1 Green turtle (*Chelonia mydas*) hatchery design implemented on Long Beach and North East Bay, Ascension Island, UK, during the 2022 nesting season, including A) Hatchery constructed on Long Beach and B) schematic diagram of the hatcheries constructed. Grey and white areas indicate the shaded and unshaded enclosures, respectively.

nesting females, while enabling hatchlings to leave upon emergence. Relocated clutches were randomly split between the shaded or unshaded treatments (Shaded: LB $n = 20$, NEB $n = 19$, Unshaded: LB $n = 20$, NEB $n = 20$) and placed into an artificial egg chamber dug in the center of a hatchery plot. It was not possible to measure the depths of *in situ* nests included in the study until after hatching. Therefore, artificial egg chamber dimensions were standardized to replicate the median dimensions of *in situ* clutches ($n = 40$) excavated on the same beaches during the 2021 nesting season (bottom depth of egg chamber = 90 cm, diameter = 32 cm). All experimental clutches were excavated immediately after the female completed covering her nest, carefully placed into a bucket, and relocated to the hatchery on their beach of origin.

A TinyTag Plus 2 archival temperature logger (Gemini Data Loggers, Chichester, UK) was placed into the approximate center of each *in situ* clutch during the middle of oviposition and into the centre of each experimental clutch during relocation into the hatchery. Temperature loggers were programmed to record nest temperature (accuracy $\pm 0.4^\circ\text{C}$; resolution = 0.01°C) at 1-hour intervals throughout the entire incubation duration. Upon signs of first hatchling emergence, nests were left for an additional 36–72 hours before being excavated to retrieve temperature loggers and determine hatching success based on the number of hatched eggshells and unhatched eggs. For each clutch, we calculated the mean incubation temperature between laying and hatching and the growth-rate-weighted mean temperature during the TSP (hereafter TSP temperature) using the R package *embryogrowth* (Girondot 2022). The latter is considered the most reliable proxy for offspring sex ratio in natural sea turtle nests, where incubation temperature and corresponding rates of embryonic development vary continuously (see Fuentes et al. 2017). The *info.nests* function from *embryogrowth* was then used to predict offspring sex ratio for each clutch based on TSP temperature and an established temperature-sex determination curve for the Ascension Island green turtle, derived from constant temperature laboratory incubation experiments (Tilley et al. 2019).

Statistical analysis

Generalized linear models (GLMs) were used to assess the impact of shading treatment on mean incubation temperature, TSP temperature, hatching success, and predicted offspring sex ratio. Explanatory variables included the two-way interaction between beach (North East Bay, Long Beach) and shading treatment (*in situ*, shaded,

unshaded), along with clutch size and laying date to account for thermal variation due to metabolic heating by embryos and the seasonal temperature gradient, respectively. To test for potential edge effects in the shaded enclosures, separate GLMs were performed on incubation temperatures of shaded experimental clutches, with clutch position in the hatchery (two-level factor: edge or center; Figure 1B) and its two-way interaction with beach, lay date and clutch size included as explanatory variables. Model error distributions were assumed to be Gaussian for incubation temperatures, quasibinomial for hatching success (an over-dispersed binomial proportion), and beta for offspring sex ratio (a continuous proportion). All model fits were assessed using the R package DHARMA (Hartig 2022) and revealed no significant departures from expected residual distributions.

For each model, the significance of explanatory variables was assessed using type III F-tests (Gaussian and quasibinomial errors) or likelihood ratio tests (beta errors) following the deletion of the variable in question from the model, starting with the interaction terms. Models were simplified by stepwise deletion of nonsignificant terms ($P > 0.05$), beginning with the term with the highest P -value. To evaluate the interacting effects of the models, pairwise post-hoc comparisons between groups were performed using the R package emmeans (Lenth 2023). The R function ggpredict from the R package ggeffects (Lüdtke 2023) was also used to extract and plot model-predicted marginal means and associated 95% confidence intervals (CI) for each treatment group. All analyses were performed in R version 4.2.2 (R Core Team 2022).

RESULTS

Effects of shading on incubation temperature

After controlling for clutch size and laying date, artificial shading significantly reduced the mean incubation temperature of green turtle clutches compared to unshaded experimental clutches on both beaches (GLM, beach $\times$ treatment interaction: $F_{2,79} = 7.04$, $P = 0.002$; Table 1), although the effects were more pronounced on the hotter beach. Shading achieved a mean reduction of $0.5 \pm 0.1^\circ\text{C}$ on Long Beach and $0.9 \pm 0.10^\circ\text{C}$ on North East Bay compared to unshaded experimental clutches (post hoc tests, $P < 0.001$; Figure 2). However, the mean incubation temperature of shaded clutches did not significantly differ from those of *in situ* controls on either beach (post hoc tests, $P > 0.9$).

Similar results were found for mean incubation temperatures during the sex-determining TSP. Compared to unshaded experimental clutches, shaded clutches were significantly cooler during the TSP at both study sites (GLM, beach $\times$ treatment interaction: $F_{2,79} = 11.80$, $P < 0.001$; Table 1); shaded clutches were $0.5 \pm 0.1^\circ\text{C}$ and $1.2 \pm 0.1^\circ\text{C}$ cooler during the TSP than unshaded clutches on Long Beach and North East Bay, respectively (post hoc tests,

TABLE 1 Summary of GLMs fit to incubation temperatures, hatching success, and predicted sex ratios of green turtle (*Chelonia mydas*) clutches on Long Beach and North East Bay of Ascension Island, UK, during the 2022 nesting season. Results are presented as test statistics and associated degrees of freedom (d.f.) from F-tests or likelihood ratio tests comparing a more saturated model with a reduced model minus the term of interest. Note that clutch size was excluded from the hatching success model as it forms the binomial denominator in the response.

Model	Beach $\times$ shade treatment		Clutch size		Laying date	
	Test statistic _{d.f.}	P	Test statistic _{d.f.}	P	Test statistic _{d.f.}	P
Mean temp.	$F_{2,79} = 7.04$	0.002	$F_{1,79} = 48.24$	<0.001	$F_{1,79} = 6.92$	0.010
TSP temp.	$F_{2,79} = 11.80$	<0.001	$F_{1,79} = 20.97$	<0.001	$F_{1,79} = 11.41$	0.001
Sex ratio	$\chi^2_2 = 8.59$	0.014	$\chi^2_2 = 30.51$	<0.001	$\chi^2_2 = 17.76$	<0.001
Hatch success	$F_{2,87} = 3.88$	0.024	-	-	$F_{1,86} = 0.57$	0.454

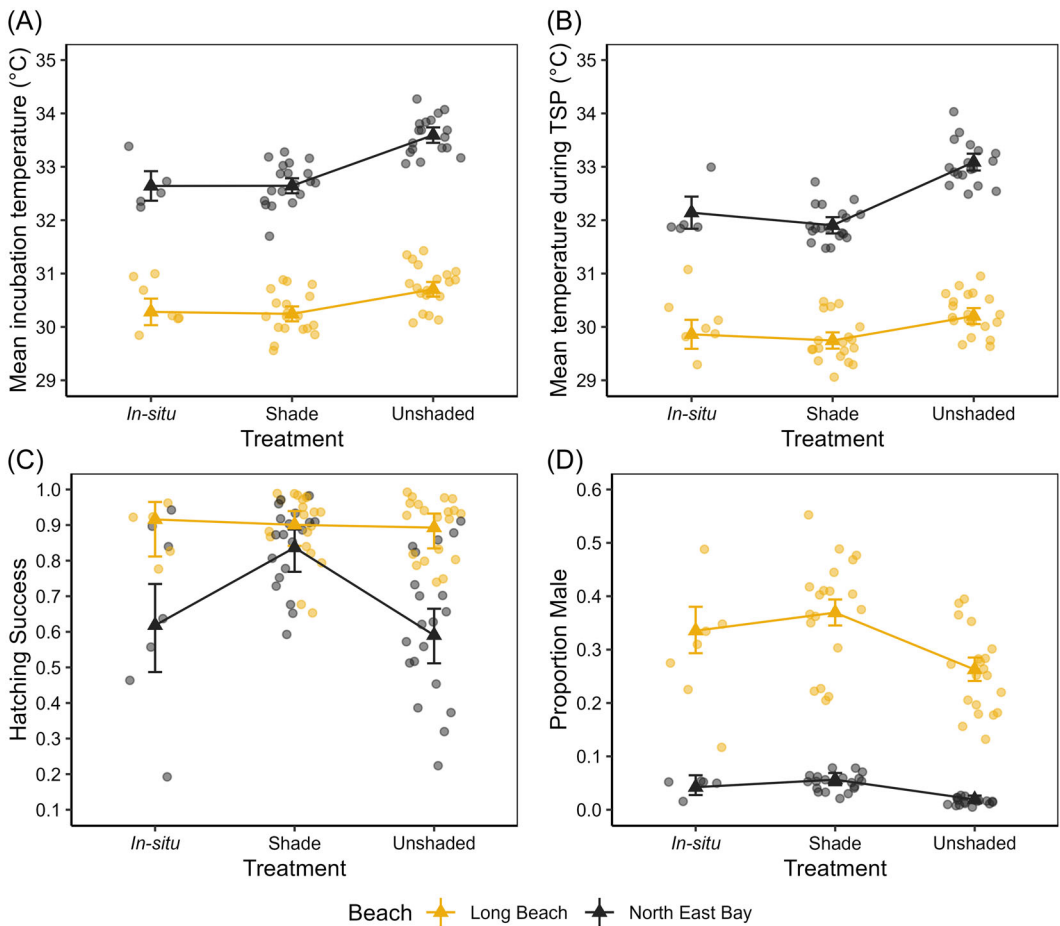


FIGURE 2 Effect of shading treatment on (A) mean incubation temperature, (B) mean temperature during the thermosensitive period (TSP), (C) hatching success, and (D) sex ratio (proportion of males produced) of green turtle (*Chelonia mydas*) clutches on Long Beach and North East Bay, Ascension Island, UK, during the 2022 nesting season. Triangle points indicate estimated marginal means, and error bars depict 95% confidence interval. Solid circles indicate observed values for each treatment and study site.

$P < 0.001$; Figure 2). Again, the mean TSP temperature of shaded and *in situ* clutches were not significantly different at either study site (post hoc tests, $P > 0.3$).

When considering only experimentally shaded clutches, mean incubation temperature and TSP temperature were not significantly affected by clutch position within the hatchery (GLM, mean incubation temperature: $F_{1,33} = 0.12$, $P = 0.74$; TSP temperature: $F_{1,33} < 0.001$, $P = 0.99$) or its interaction with beach (GLM, mean incubation temperature: $F_{1,32} = 0.67$, $P = 0.42$; TSP temperature: $F_{1,32} = 0.37$, $P = 0.55$), indicating a lack of edge effects of the shade treatment.

Effects of shading on hatching success and predicted offspring sex ratio

Effects of shading on hatching success and predicted offspring sex ratio of green turtle clutches also differed between beaches (GLMs, beach $\times$ treatment interaction, $P < 0.03$; Table 1). On the cooler beach, mean hatching

TABLE 2 Summary of observed mean incubation temperatures, the thermosensitive period (TSP) temperatures, hatching success, and predicted sex ratios of *in situ*, shaded, and unshaded green turtle (*Chelonia mydas*) clutches on Long Beach and North East Bay of Ascension Island, UK, during the 2022 nesting season.

Nesting beach and treatment	Incubation temperature (°C) mean ± SE (range)	TSP temperature (°C) mean ± SE (range)	Hatching success (%) mean ± SE (range)	Sex ratio (% male) mean ± SE (range)
Long Beach				
<i>In situ</i>	30.4 ± 0.2 (29.8–31.0)	30.1 ± 0.2 (29.3–31.1)	91.6 ± 3.2 (78–100)	30.0 ± 4.3 (11.7–48.8)
<i>Shaded</i>	30.2 ± 0.1 (29.6–30.9)	29.7 ± 0.1 (29.1–30.5)	89.7 ± 2.2 (65–99)	37.4 ± 2.3 (20.5–55.2)
<i>Unshaded</i>	30.8 ± 0.1 (30.1–31.4)	30.2 ± 0.1 (29.6–31.0)	89.5 ± 1.9 (74–99)	25.7 ± 1.7 (13.2–39.5)
North East Bay				
<i>In situ</i>	32.6 ± 0.2 (32.2–33.4)	32.1 ± 0.2 (31.8–33.0)	64.7 ± 10.2 (19–94)	4.5 ± 0.7 (1.6–5.3)
<i>Shaded</i>	32.7 ± 0.1 (31.7–33.3)	31.9 ± 0.1 (31.5–32.7)	83.9 ± 2.6 (59–98)	5.1 ± 0.4 (2.1–7.8)
<i>Unshaded</i>	33.6 ± 0.1 (33.1–34.3)	33.1 ± 0.1 (32.5–34.0)	61.3 ± 4.4 (22–91)	1.6 ± 0.1 (0.5–2.7)

success was high (ca. 90%) across all treatment groups and was not significantly improved by shading compared to unshaded clutches or *in situ* controls (post-hoc tests, $P > 0.9$; Figure 2). On the hotter beach, however, shading resulted in a significant ~19–23% increase in mean hatching success relative to other treatment groups (post hoc tests, $P < 0.01$; Table 2, Figure 2), yielding a mean success (84%) that approached that of clutches laid on the cooler beach (Table 2, Figure 2). There was no evidence that clutch relocation negatively impacted hatching success, with unshaded hatchery nests performing as well as *in situ* controls at both beaches (post hoc tests, $P > 0.8$; Figure 2).

Across both study sites, shading had a non-significant effect on the proportion of male hatchlings predicted relative to *in situ* controls (post hoc tests, $P > 0.3$; Figure 2). However, compared to unshaded experimental clutches shading significantly increased predicted male hatchling production by 4% and 12% on North East Bay and Long Beach, respectively (post hoc tests, $P < 0.001$; Table 2, Figure 2).

DISCUSSION

The efficacy of artificial nest shading as a climate change mitigation strategy for marine turtles has attracted increasing interest in recent years, with a small but growing number of experimental trials (Patino-Martinez et al. 2012, Jourdan and Fuentes 2015, Esteban et al. 2018, Vindas-Picado et al. 2020, Reboul et al. 2021). In this study, artificial shading successfully reduced incubation temperatures compared to unshaded experimental clutches by 0.5–1.2°C, which is comparable to results reported in previous studies. For example, Esteban et al. (2018) reported that both natural and artificial shading materials (i.e., white sand, white cotton sheet, and palm leaves) reduced sand temperatures at nesting sites in St. Eustatius by an average of 0.6°C. Similarly, Vindas-Picado et al. (2020) found that artificial shading treatments (i.e., 50%, 80% and 90% shade mesh) reduced sand temperatures at Playa Grande, Costa Rica, by up to 0.4°C and 0.8°C at depths of 75 cm and 45 cm, respectively, and Reboul et al. (2021) reported that compared to unshaded clutches artificial shading (90% shade cloth) reduced incubation temperatures of green turtle clutches at Chagar Hutang beach, Malaysia, by an average of 1.3°C.

However, the effectiveness of shading at reducing sand temperatures can be impacted by other factors such as, but not limited to, precipitation, depth, and artificial irrigation (Hill et al. 2015, Jourdan and Fuentes 2015, Staines et al. 2020). In this study, the magnitude of the effect of shading depended on beach sand color. This finding can be explained by the interplay between shading and sand albedo (the proportion of incident solar radiation reflected).

On hotter, dark sand beaches with lower albedo, removing a fixed proportion of incident solar radiation via shading will result in a larger absolute reduction in solar energy absorbed and hence a larger reduction in incubation temperature. The effects of shading and associated temperature reductions on hatching success and predicted offspring sex ratio also differed between sites, depending on where they lie on the thermal reaction norms for these traits. On the cooler beach, hatching success was naturally high and not thermally limited, meaning shading had no significant impact. Similar results were reported by Wood et al. (2014) at Mon Repos in Australia, where hatching success of *in situ* loggerhead (*Caretta caretta*) clutches are also naturally high and where natural nest temperatures also fall well within the thermal tolerance limits for successful embryonic development. In contrast, mean incubation temperatures on the hotter beach are approaching the maximal thermal tolerance limit for embryonic development (33–35°C, Howard et al. 2014) and artificial shading significantly increased hatching success to rates like those previously reported by Patino-Martinez et al. (2012). For predicted offspring sex ratio, the opposite pattern was found. Although shading significantly increased the estimated proportion of male offspring produced at both sites, the absolute change was much greater on the cooler beach where TSP temperatures naturally lie closer to the pivotal temperature. These results demonstrate that the impacts of artificial shading are highly dependent on the thermal environmental conditions of the nesting beach.

Relocation of clutches to a hatchery was a necessary part of the current study design, as *in situ* shade structures applied to individual nests (c.f. Esteban et al. 2018) would have been quickly disturbed by other females at this high-density nesting site. Contrary to the findings of previous studies (e.g., Pintus et al. 2009), relocation did not compromise hatching success. However, unshaded hatchery clutches were significantly warmer than *in situ* controls, suggesting that relocation resulted in increased incubation temperatures that offset some of the benefits of shading. Hatchery location is the most plausible explanation for this. Previous research has shown that turtle nesting beaches are thermally heterogeneous, with clutches located further from the sea tending to have higher mean incubation temperatures (Rees and Margaritoulis 2004, Türkozan et al. 2023). In the current study, hatcheries were deliberately placed towards the rear of beaches to reduce the risk of seawater inundation during high swells and may therefore have been hotter than an average *in situ* nest. Future artificial shading schemes should carefully consider hatchery location or apply *in situ* shading where possible to maximize potential benefits.

Climate change forecasts project mean near-surface air temperature will increase between 1.1–2.5°C in the equatorial Atlantic Ocean by 2060 depending on the socioeconomic pathway achieved (Gutiérrez et al. 2021). If these projections are reflected in incubation temperatures, the impact of artificial shading reported in the present study may offset or at least partially offset near to medium term impacts of climate change. However, the major challenge of nest shading at Ascension Island does not lie in its efficacy, but in its scalability. The 79 clutches experimentally relocated in this trial represent approximately 0.3% of the estimated ca. 24,000 clutches laid on the island annually (Weber et al. 2014). Shading a sufficiently large proportion of these clutches to effect meaningful change at a population level could be achievable, but would require the erection of large, shaded structures that would be financially costly to construct and maintain long-term. Additionally, construction of such structures may elicit public opposition due to their aesthetic impact on the natural environment and have unintended ecological impacts on other species, such as seabirds that predate on sea turtle hatchlings. For these reasons, artificial shading may be best considered as a last resort rather than as a proactive strategy for maintaining the status quo at high density nesting sites.

At many sea turtle nesting sites, beach overstory vegetation provides natural shading (Wood et al. 2014) and has shown to significantly reduce incubation temperatures (Reboul et al. 2021) and could be substituted at treeless sites like Ascension Island through mass plantings of already naturalized, nonnative species (e.g., *Casuarina* spp.). However, given the reported negative impacts of invasive trees on sea turtle nesting habitat (Awale and Phillott 2014), such an initiative would carry high risk and is again best considered as a last resort. More tractable approaches that could contribute to enhanced climate change resilience of large marine turtle rookeries include improved coastal development planning to alleviate coastal squeeze from future sea level rise (Varela et al. 2019) and addressing other sources of nesting habitat degradation (Fuentes et al. 2012). The ability of marine turtles to

adapt to climate change may depend on their natural dispersal potential and phenological plasticity (Dalleau et al. 2012, Rees et al. 2016). Some populations have already been observed to alter their nesting phenology in response to increasing temperatures (Weishampel et al. 2010). However, whether such plasticity would be effective at offsetting the impacts of long-term climate change, and whether such adaptability is universal across all populations remains uncertain (Monsinjon et al. 2019).

CONSERVATION IMPLICATIONS

Assessing the efficacy of climate change adaptation measures is fundamental for developing management strategies to mitigate the impacts of climate change. The results of our study demonstrate that artificial nest shading could be a viable approach for conservation practitioners to partially alleviate the impacts of climate change on nesting marine turtles by reducing incubation temperatures, increasing hatching success, and balancing offspring sex ratios. However, the magnitude of these effects is highly contingent on the natural thermal conditions of the nesting beach and therefore can vary significantly between nesting sites. Additionally, implementing artificial nest shading at a scale that would achieve meaningful impacts at the population level for large high-density nesting sites such as Ascension Island would pose significant challenges and financial costs. Therefore, leaving eggs to incubate *in situ* is currently the most suitable management strategy for green turtle clutches at Ascension Island, as overall hatching success is naturally high and incubation temperatures allow for the production of both male and female offspring. Artificial nest shading may be a more appropriate climate change adaptation measure for smaller low-density nesting sites, yet, whether such measures could be a potentially viable long-term solution should be evaluated on a case-by-case basis.

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CONFLICT OF INTERESTS STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This research was ethically approved by the University of Exeter, CLES ethics committee (Ref. 491773).

DATA AVAILABILITY STATEMENT

The data and R code used in the study is available on Zenodo at <https://doi.org/10.5281/zenodo.7945081>.

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