



Short-term gain, long-term loss: How a widely-used conservation tool could further threaten sea turtles

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ABSTRACT

Sea turtles nest on tropical and subtropical beaches, where developmental success of egg clutches depends on nest temperature. Higher nest temperatures increase embryo and hatchling mortalities and produce female hatchlings. Nest shading has been used on some beaches to reduce nest temperatures, and thereby increase number of hatchlings and reduce female-biased sex ratios. We modeled short- and long-term effects of reducing mean nest temperatures on a leatherback turtle (*Dermochelys coriacea*) population for which the effect of temperature on sex ratios and emergence success (# hatchlings emerged/ # eggs) is well-established. We simulated mean nest temperature reductions of -0.5°C , -1°C , -1.5°C and -2°C in relation to current mean (30.4°C) and projected population responses over 100 years. Additionally, we run climate change simulations of $+0.5^{\circ}\text{C}$, $+1.0^{\circ}\text{C}$ and $+2.0^{\circ}\text{C}$ to assess if shading could be needed after passing a certain threshold.

Emergence success increased with reduced nest temperatures. However, lowering nest temperatures ultimately caused long-term declines in number of nesting females and total population size, because the number of female hatchlings was reduced. Because hatcheries are a widely-used conservation tool, caution must be used to avoid reducing the number of female hatchlings by lowering nest temperatures. Nest cooling may only be needed under critically low hatchling production and extremely biased female sex ratios that we only found at $+2.0^{\circ}\text{C}$. If nest shading is to be used, it should be applied strategically to optimize hatchling production with natural sex ratios to achieve both short-term conservation goals and long-term population sustainability.

1. Introduction

Climate change is among the main threats sea turtles are likely to face in the near future (Fish et al., 2005; Hawkes et al., 2007; Jensen et al., 2018). Global air temperatures are projected to increase from 1.5°C to 2°C above pre-industrial levels by the end of the 21st century, with a likely increase in the frequency of high-temperature extreme events (Collins et al., 2013). High nest temperatures increase the rate of embryonic mortality during development and hatchling mortality during emergence (Santidrián Tomillo et al., 2009; Valverde et al., 2012). In sea turtles, typical incubation periods range between 43 and 94 days for

temperatures between 24°C and 33°C , but with differences among species (Booth, 2017). Maximum temperatures that allow development are $\sim 35^{\circ}\text{C}$ (Howard et al., 2014), although eggs from some species (e.g., leatherback (*Dermochelys coriacea*) and olive ridley turtles (*Lepidochelys olivacea*)) are less tolerant to high temperatures than others (e.g., green turtles (*Chelonia mydas*) and loggerhead turtles (*Caretta caretta*)) (Howard et al., 2014; Santidrián Tomillo et al., 2020).

Nest temperatures during the middle third of development determine sex in sea turtles (Morreale et al., 1982; Yntema and Mrosovsky, 1982). During that thermosensitive period, higher temperatures produce a higher proportion of female hatchlings, whereas male gonads

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develop at lower temperatures (Standora and Spotila, 1985), though the range of temperatures within which hatchlings are produced at all is relatively narrow (~ 5 to 8 °C). Female-biased sex ratios have been reported for many nesting sea turtle populations around the world (Binckley et al., 1998; Hawkes et al., 2007; Zbinden et al., 2007, and reviewed in Hays et al., 2014) and extremely female-biased sex ratios ($> 90\%$ female) for a few (Godfrey et al., 1999; Broderick et al., 2000; Jensen et al., 2018).

There has been some speculation about the potentially negative effect of continued warming on sex ratios, but female biased primary sex ratios appear to be natural at most nesting beaches and female-biased sex ratios may also be beneficial as they can increase the size of the nesting population under certain conditions (Laloë et al., 2014), compensating for mortality of early life-stages (Santidrián Tomillo and Spotila, 2020). However, this compensation may not work at extremely high nest temperatures, as hatchling production may reach critically low levels (Santidrián Tomillo et al., 2015; Hays et al., 2017).

As many sea turtle populations around the world are endangered, and there are several threats to developing sea turtle egg clutches, it is a common conservation practice to relocate clutches to safer areas where embryos can complete development and emerge from nests (Wyneken et al., 1988; Tuttle and Rostal, 2010). For example, illegal harvest of eggs is a major threat to sea turtles in many countries, especially in remote areas where beaches extend over many kilometers that are difficult to access and protect (Chacón-Chaverri and Eckert, 2007; Mutalib and Fadzly, 2015), necessitating egg relocation to safe areas that can sometimes include 100% of clutches. Moreover, sea turtles do occasionally nest below the high tide line, where incubating embryos are likely to die from regular tidal inundation and beach erosion. These ‘doomed clutches’ are often relocated. Doomed clutches are most often relocated to beach hatcheries where nests can be monitored and protected from people and predators (Van de Merwe J et al., 2006; Patino-Martinez et al., 2012).

Because there is growing concern on the negative effect of climate warming on hatchling production, measures to reduce nest temperatures, such as shading and watering nests, have been implemented or proposed as climate mitigation strategies in some locations (Maulany et al., 2012; Hill et al., 2015; Jourdan and Fuentes, 2015; Mutalib and Fadzly, 2015). In particular, these widely used interventions are commonly justified by the assumption that production of hatchlings and reduction of the female bias in hatchling sex ratios will promote improved population status. However, there could be important unintended consequences of lowering nest temperatures, and whether reducing female biases actually benefits population dynamics remains an open question. Although Morreale et al. (1982) warned several decades ago about the potential negative effect of clutch relocation on sex ratios, the effectiveness of this very common conservation strategy—particularly when coupled with intentional reductions of nest temperatures—warrants robust examination.

Sea turtles are long-lived and late-maturing species characterized by high adult survival and low and variable survival of early life-stages (Heppell et al., 2003). Females can mate with multiple males in a season and the occurrence of multiple paternity is common (Crim et al., 2002; Lee et al., 2018). Additionally, although primary sex ratios are female biased at most beaches, the sex ratio of adult reproductive individuals seems to be balanced (Stewart and Dutton, 2011; Wright et al., 2012; Gaos et al., 2018) or male biased (Howe et al., 2018; Lasala et al., 2013; Turkozan et al., 2019). Because males can reproduce more frequently than females (i.e., annually vs semi-annually), and one male could potentially mate with several females, it is likely that population dynamics in sea turtles are largely driven by the number of females (Hays et al., 2017). In fact, altering sex ratios to female biases could increase the size of animal populations in the long-term when the number of eggs limits the population growth (Wedekind, 2002). Therefore, we hypothesize that lowering female biased sex ratios, could have negative impacts on sea turtle populations in the long-term, thus

potentially undermining the stated goals of many conservation projects focused on nesting beaches.

To test this hypothesis and evaluate potentially negative, unintended consequences of measures to cool nest temperatures, we used the known effects of nest temperature on embryo and hatchling mortalities and on sex ratios in a population of sea turtles to examine the potential impacts of shading or irrigating nests in hatcheries. We use the leatherback turtle population that nests in Pacific Costa Rica as an example, because models have been previously used for this population and model parameters have been defined (Santidrián Tomillo et al., 2015; Laúd OPO network, 2020). Specifically, we assessed the effect of reducing nest temperatures, as if nests were artificially shaded or watered, on emergence success, primary sex ratios, number of nesting turtles, number of adult males, total population size, and asymptotic population growth rate (λ_s). To complete the picture, we additionally simulated the effect of increasing mean nest temperatures under climate change scenarios to determine if shading could become needed if temperatures passed a certain threshold. Ultimately, our results will help guide future management actions for sea turtle populations and could inform management of other species with TSD.

2. Methods

To assess the potential negative effect of decreasing nest temperatures when relocating sea turtle clutches, we used data from leatherback turtles nesting at Playa Grande, Costa Rica, which belong to the eastern Pacific (EP) leatherback regional management unit (Wallace et al., 2010). The EP leatherbacks have precipitously declined due to a combination of bycatch and egg harvest (Spotila et al., 2000; Sarti Martínez et al., 2007; Laúd OPO Network, 2020). Pacific Costa Rican leatherbacks have been extensively studied for ~ 30 years, and the effects of nest temperature on egg development, hatchling emergence, and sex ratio have been described (Binckley et al., 1998; Santidrián Tomillo et al., 2015).

We considered current mean beach temperatures of in situ leatherback turtle nests ($T = 30.4$ °C) at Playa Grande (Santidrián Tomillo et al., 2015), as well as those generated by four nest cooling treatments that would reduce mean nest temperatures by 0.5 °C ($T = 29.9$ °C), 1 °C ($T = 29.4$ °C), 1.5 °C ($T = 28.9$ °C) and 2 °C ($T = 28.4$ °C) to simulate what would happen if the Playa Grande beach hatchery was shaded. Mean emergence success and primary sex ratios under current natural conditions at Playa Grande are 41% and 84% respectively (Santidrián Tomillo et al., 2014). To do the simulations, we considered that 100% of clutches laid were shaded every season and therefore, modeled the effect of reducing the mean temperature of nests on the population.

2.1. Population model

To test the effect of shading of nests, we projected sea turtle population dynamics under different thermal conditions. As knowing the number of males in the population may be informative to assess the effects of nest cooling, we built a population model that incorporated males. Our population model followed a pre-breeding census format and considered 12 stages:

- stage 1: females age 1,
- stage 2: juvenile females between year 1 and year 3,
- stage 3: subadult females between ages 3 and 12,
- stage 4: breeding females,
- stage 5: females at sea 2 years after breeding,
- stage 6: females at sea 3 years after breeding,
- stage 7: females at sea 4 or more years after breeding,
- stage 8: females that breed only once,
- stage 9: males age 1,
- stage 10: juvenile males between year 1 and year 3,
- stage 11: subadult males between ages 3 and 12,

– stage 12: adult males

Reproduction in our model was based only on females (Appendix S1) because females control reproductive output, and thus population dynamics are measured by beach-based monitoring systems.

Our population model used previous estimations of dependence of sex ratio and emergence success on nest temperatures (Binckley et al., 1998; Santidrián Tomillo et al., 2015) and of demographic parameters (Laúd OPO Network, 2020) for this leatherback turtle population. In particular, to infer sex ratios, we used the TSD curve defined by Binckley et al. (1998). Following this curve, temperatures in a nest below 29 °C produce 100% male hatchlings and temperatures over 30 °C produce 100% female hatchlings. The percentage of female hatchlings between 29.0 °C and 30.0 °C increases at 0.1 °C increments (Binckley et al., 1998). We used the following equation to estimated emergence success:

$$E = -4.838 + 0.449 * T_{\text{nest}} - 0.009 * (T_{\text{nest}})^2,$$

where T_{nest} is the mean temperature in the nest during the incubation period. This equation was obtained from previous studies that included nine nesting seasons (Santidrián Tomillo et al., 2015). We used emergence success instead of hatching success as emergence success accounts for mortality of (1) embryos during development and (2) hatchlings during emergence from underground nests, and therefore is a more ecologically relevant variable (Wallace et al., 2007).

Recruitment and transient probabilities were estimated specifically for this population by the Laúd OPO Network (2020). First year survival (S_1), was previously estimated by Spotila et al. (1996). Because juvenile survival (S_2), is unknown, we used the S_2 value that kept the population stable. We considered adult and subadult survival rates that maintain population stability, as used in previous models (Saba et al., 2012; Santidrián Tomillo et al., 2015). These were based on the annual survival estimated for adult female leatherback turtles at St. Croix ($S = 0.893$) (Dutton et al., 2005). Subadults were considered to have the same annual survival of adults because of the large size attained at this stage (Jones et al., 2011). Current mean nest temperatures have risen by an estimated 0.5 °C since the beginning of the 20th century based on reconstructed nest temperatures (from 1920 to 2012, Santidrián Tomillo et al., 2015). Because current thermal conditions could already be too warm to keep the population stable due to climate change, we considered two different scenarios of nest temperatures that kept the population initially stable under (1) current mean temperatures of nests ($30.4 \text{ °C} \pm 1.0$) and (2) historical ones ($29.9 \text{ °C} \pm 1.0$). Values of S_2 used in each scenario corresponded to values that kept the population stable under current ($S_2 = 0.445$) and historical ($S_2 = 0.465$) temperature scenarios, respectively (Table 1). As very little is known about male leatherback demography, we assumed the same survival probabilities at each stage for male and female turtles.

We ran one deterministic and five stochastic models under each scenario to project populations that experienced each of the five different mean nest thermal treatments during incubation (without nest cooling and with nest cooling that decreased mean nest temperatures by 0.5 °C, 1 °C, 1.5 °C and 2 °C).

We considered an initial population size of 150 nesting females per year and a total population size (males and females, and all age classes) of 7850 individuals. To account for variability in nest temperature and simulate the natural climatic variability that nests experience in North Pacific Costa Rica, each simulation used a nest temperature value selected randomly within the standard deviation limits of the mean, recreating inter-annual variability in thermal conditions, emergence success and sex ratio. Aside from the stochastic variation on nest temperatures, we did not add uncertainty or covariance on other demographic parameters in order to be conservative. We ran 1000 Monte Carlo simulations for a short and relevant time horizon of 100 years. For each 100-year simulation, we estimated the asymptotic deterministic lambda (λ) and the mean stochastic population growth rate (λ_s), and

Table 1

Mean emergence success, primary sex ratios (% female) and stochastic population growth rate (λ_s) with 95% confidence intervals, resulting from projections of a leatherback turtle population under different temperature regimes. Since it is unknown what temperatures would keep the population stable (current mean temperatures may already be too high), we considered two scenarios: (1) population is stable under current mean temperatures (30.4 °C) and (2) population is stable under historical mean nest temperatures (29.9 °C) based on Santidrián Tomillo et al. (2015).

	Mimic beach temps (30.4 °C)	-0.5 °C	-1.0 °C	-1.5 °C	-2.0 °C
Scenario 1: population stable with current mean temperatures (30.4 °C)					
Emergence success	0.485	0.532	0.574	0.613	0.646
Lower 95% CI	0.273	0.336	0.397	0.452	0.502
Upper 95% CI	0.643	0.674	0.701	0.722	0.738
Hatchling sex ratio	0.812	0.655	0.469	0.288	0.153
Standard deviation	0.320	0.399	0.423	0.385	0.320
Lower 95% CI	0	0	0	0	0
Upper 95% CI	1	1	1	1	1
λ Asymptotic deterministic lambda	1.004	1.001	0.979	0.901	0.901
λ_s Stochastic lambda	0.999	0.992	0.978	0.959	0.941
Lower 95% CI	0.9943	0.985	0.969	0.949	0.932
Upper 95% CI	1.005	0.998	0.985	0.968	0.950
Scenario 2: population stable with historical mean temperatures (29.9 °C)					
Emergence success	0.485	0.532	0.574	0.613	0.646
Lower 95% CI	0.273	0.336	0.396	0.452	0.501
Upper 95% CI	0.645	0.675	0.700	0.722	0.739
Hatchling sex ratio	0.811	0.654	0.469	0.286	0.154
Standard deviation	0.322	0.399	0.424	0.384	0.305
Lower 95% CI	0	0	0	0	0
Upper 95% CI	1	1	1	1	1
λ Asymptotic deterministic lambda	1.012	1.010	0.986	0.902	0.902
λ_s Stochastic lambda	1.007	0.999	0.984	0.964	0.945
Lower 95% CI	1.002	0.991	0.974	0.953	0.935
Upper 95% CI	1.012	1.006	0.992	0.973	0.955

then estimated a mean stochastic growth rate across all 1000 simulated trajectories for each scenario. We also estimated mean emergence success, hatchling sex ratio, adult sex ratio and operational sex ratio (sex ratio of reproductive individuals) under each thermal treatment. We report mean and 95% confidence intervals for these estimates. All projection models were developed and executed in program R (<http://cran.r-project.org>).

2.2. Climate change scenarios

Because nest temperatures could continue rising due to climate change, we ran some additional simulations to assess if shading could be recommended under particular conditions (e.g. if mean nest temperatures surpassed a certain threshold). We tested the effect of increasing temperatures by 0.5 °C, 1.0 °C and 2.0 °C on the emergence success, sex ratios, number of nesting females and total population size of the leatherback population. We selected an initial increase of 0.5 °C because nest temperatures reconstructions showed that mean nest temperatures at Playa Grande could have increased by 0.5 °C from the beginning to the end of the 20th century (Santidrián Tomillo et al., 2015). In addition, we tested the effect of increasing mean nest temperatures to +1.0 °C and +2.0 °C, representing low and moderate climate change scenarios if nest temperatures mirrored the projected increases in global air temperatures by climate change models according to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2013).

3. Results

3.1. Effect of decreasing mean nest temperatures

Relative to mean in situ nest temperatures, both current and historical model scenarios incorporating effects of reducing nest temperatures resulted in increased emergence success and reduction of the female bias in primary sex ratios. The lower the nest temperature, the higher the emergence success in all cases and consequently, the higher the number of hatchlings (Table 1). The increase in emergence success when temperatures were reduced by 2.0 °C would translate into an increase in the number of hatchlings per nest from 30 to 40 hatchlings (for a mean clutch size = 62 eggs), but a decline in the percentage of female hatchlings from 81% female to 15% (Table 1). Thus, the near-term conservation outcomes of reducing nest temperatures would be increases in the overall number of hatchlings and the proportion of male hatchlings.

The sex ratio of adult turtles was about 3 adult females to 1 adult male at current mean nest temperatures (30.4 °C) and became male biased after mean nest temperature declined by 1 °C and extremely male-biased when it declined by 2 °C (1 female to 7.7 male) (Table 2). The estimated operational sex ratio (considering males reproducing twice as often as females) was less female biased at current nest temperatures (2 female to 1 male turtle). Sex ratios were equal when mean nest temperature declined by 0.5 °C and were male-biased when nest temperature declined by 1 °C and 2 °C (Table 2).

Despite the near-term benefits, decreasing nest temperatures resulted in a long-term decline in the number of nesting females and total population size (Fig. 1). Under both current and historical nest temperature scenarios, projections representing different levels of reduced nest temperatures showed lower population viability compared with the ‘no-treatment’ projection (Table 1; Fig. 1). Population sizes declined when nest temperatures were reduced by only 0.5 °C under scenario 1 (population stable under current conditions) and by 1 °C under scenario 2 (population stable under historical conditions). Even if emergence success increased when reducing nest temperature, primary sex ratios became male-biased, ultimately decreasing the stochastic population growth rate (λ_s) at lower nest temperatures. The maximum difference in λ_s was approximately 6% between current nest temperatures ($\lambda_s = 1.007$) and the reduced nest temperature by 2 °C ($\lambda_s = 0.945$) (Table 1; Fig. 1).

The trends in total population size mirrored those of number of nesting females (Fig. 1). The numbers of both declined when nest temperatures were reduced by 0.5 °C and 1 °C under scenarios 1 and 2 respectively. Because females were the limiting sex within the studied thermal range, the number of adult males under reduced nest temperatures first increased, as primary sex ratios shifted to male-bias, but later declined, following the decline in nesting turtles (Fig. 2). The cooler the mean nest temperatures, the lower the long-term number of adult males.

Table 2

Adult sex ratios of leatherback turtles obtained from the population projections after 25, 50, 75, and 100 years. Sex ratios were estimated as the number of females related to one male and operational sex ratios as if males reproduced every other year (twice as often as females). Number of nesting females was zero after year 84 under the -2 °C treatment. Thus, sex ratios were not estimated past that time.

Year	Sex ratio adult turtles (female:male)					Operational sex ratio (female:male)				
	Mimic beach temp	-0.5 °C	-1 °C	-1.5 °C	-2 °C	Mimic beach temp	-0.5 °C	-1 °C	-1.5 °C	-2 °C
Scenario 1: population stable with current mean temperatures (30.4 °C)										
25	2.12	1.27	0.73	0.42	0.27	1.47	0.88	0.50	0.29	0.18
50	3.25	1.37	0.64	0.31	0.15	2.09	0.94	0.45	0.21	0.10
75	3.35	1.37	0.64	0.29	0.13	2.13	0.94	0.45	0.20	0.09
100	3.27	1.41	0.65	0.29	-	2.10	0.96	0.45	0.20	-
Scenario 2: population stable with historical mean temperatures (29.9 °C)										
25	2.22	1.31	0.72	0.41	0.26	1.53	0.91	0.50	0.28	0.17
50	3.18	1.37	0.65	0.30	0.15	2.07	0.95	0.45	0.21	0.10
75	3.28	1.39	0.64	0.29	0.13	2.09	0.96	0.45	0.20	0.09
100	3.36	1.40	0.64	0.29	-	2.14	0.96	0.45	0.20	-

The number of adult males stabilized or increased at the female-producing warmer nest temperatures (Fig. 2).

3.2. Climate change scenarios

Emergence success was reduced from 0.48 at current mean nest temperatures to 0.43, 0.38 and 0.25 when simulated nest temperatures were increased by 0.5 °C, 1 °C and 2 °C respectively. However, female biased sex ratios increased from 81.5% female to 91.4%, 96.8% and 99.8% female when temperatures increased by 0.5 °C, 1.0 °C and 2.0 °C respectively.

The number of nesting females and of total population size did not decline under the +0.5 °C scenario and only slightly decreased when temperatures increased by 1.0 °C under the scenario that was initially stable under current mean temperatures. However, the number of nesting females and total population size clearly declined when temperatures were increased by 2.0 °C (Fig. 3). On the other hand, the number of adult males first declined but later stabilized at lower numbers under scenarios of climate change +0.5 °C and +1.0 °C (but increased again for +0.5 °C under the scenario initially stable with historical temperatures). However, the number of adult males reached close to zero males in approximately 50 years under scenarios +2.0 °C. Adult sex ratio and operational sex ratio were also extremely female biased under scenario +2.0 °C (Fig. 4). The operational sex ratio was about 5 females to 1 male under scenario +0.5 °C, 13 females to 1 male under scenario +1.0 °C and more than 130 females to 1 male under scenario +2.0 °C.

4. Discussion

The ostensible goal of cooling sea turtle nests is to produce more hatchlings. Our results confirmed that lowering nest temperature increased hatching and emergence successes, as found in operating hatcheries in Indonesia and Malaysia where shading has been implemented (Maulany et al., 2012; Mutalib and Fadzly, 2015). This apparently positive outcome from reductions in nest temperature can, however, negatively affect sea turtle populations causing long-term abundance declines, if nest temperatures are maintained consistently lower. Our results also confirmed that altering sex ratios by producing more males in hatcheries could be detrimental for sea turtle conservation, as previously suggested (Mrosovsky and Yntema, 1980; Morreale et al., 1982). Fewer female hatchlings translate into fewer nesting turtles laying eggs in the future, reducing the population reproductive output and causing population declines. These results also support the notion that concerns about increased nest temperatures creating single-sex populations and population extinctions are likely unfounded except at the most extreme climate warming scenarios (Hays et al., 2017; Booth et al., 2020).

Over the range of nest temperatures studied, trends in total

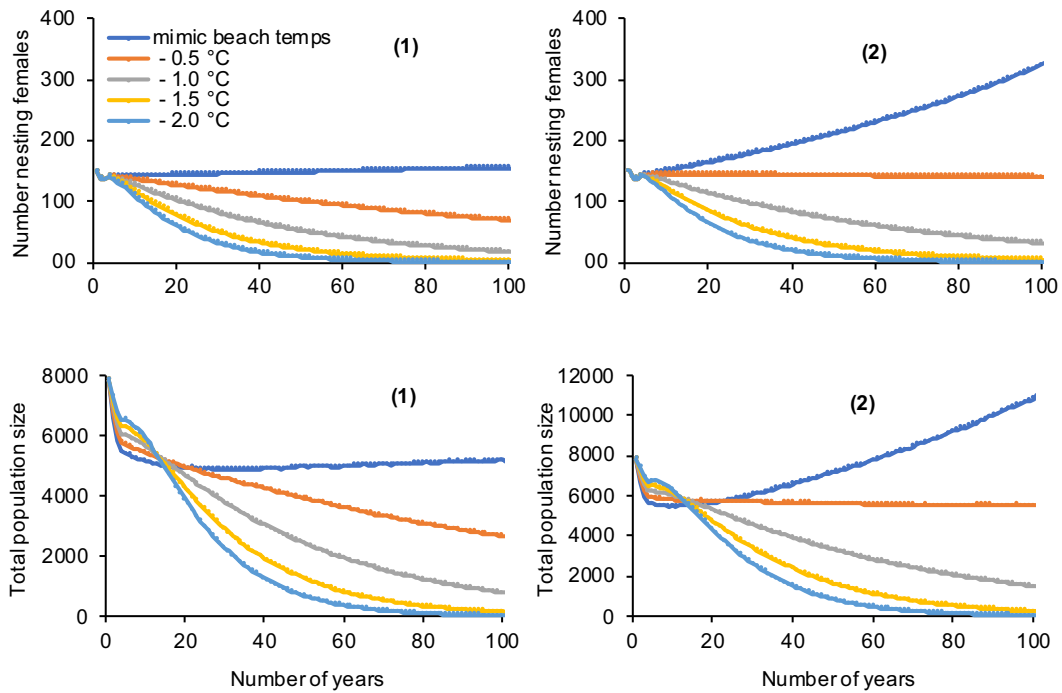


Fig. 1. Stochastic population projections of number of nesting female leatherback turtles and total population size over 100 years under different mean nest temperatures, as if 100% of nests were temperature-controlled with nest shading. We simulated the effect of maintaining mean temperatures as in natural nests (30.4 °C) and lowering mean temperatures by 0.5 °C, 1 °C, 1.5 °C and 2 °C. (1) and (2) correspond to the scenarios that kept the initial population stable under current mean temperatures (30.4 °C) and under historical mean temperatures (29.9 °C) respectively.

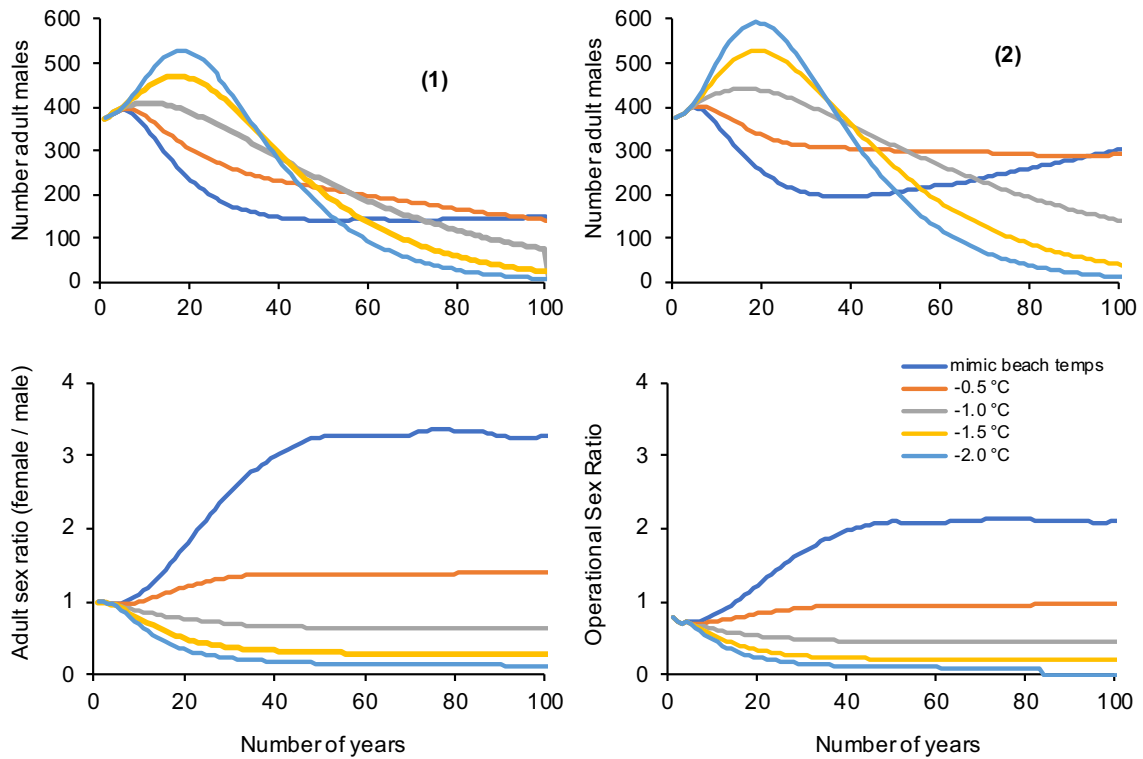


Fig. 2. Stochastic population projections of number of adult male leatherback turtles, adult sex ratios and operational sex ratios over 100 years under different mean nest temperatures as if 100% of nests were temperature-controlled with nest shading. Temperatures tested included current mean temperatures in natural nests (30.4 °C) and temperatures that were lower by 0.5 °C, 1 °C, 1.5 °C and 2 °C. (1) and (2) correspond to the scenarios that kept the initial population stable under current mean temperatures (30.4 °C) and under historical mean temperatures (29.9 °C) respectively. Adult sex ratio includes not only nesting cohorts but all reproductive and non-reproductive individuals. Operational Sex Ratio includes reproductive individuals only. We are only representing sex ratios for one scenario as they were nearly identical.

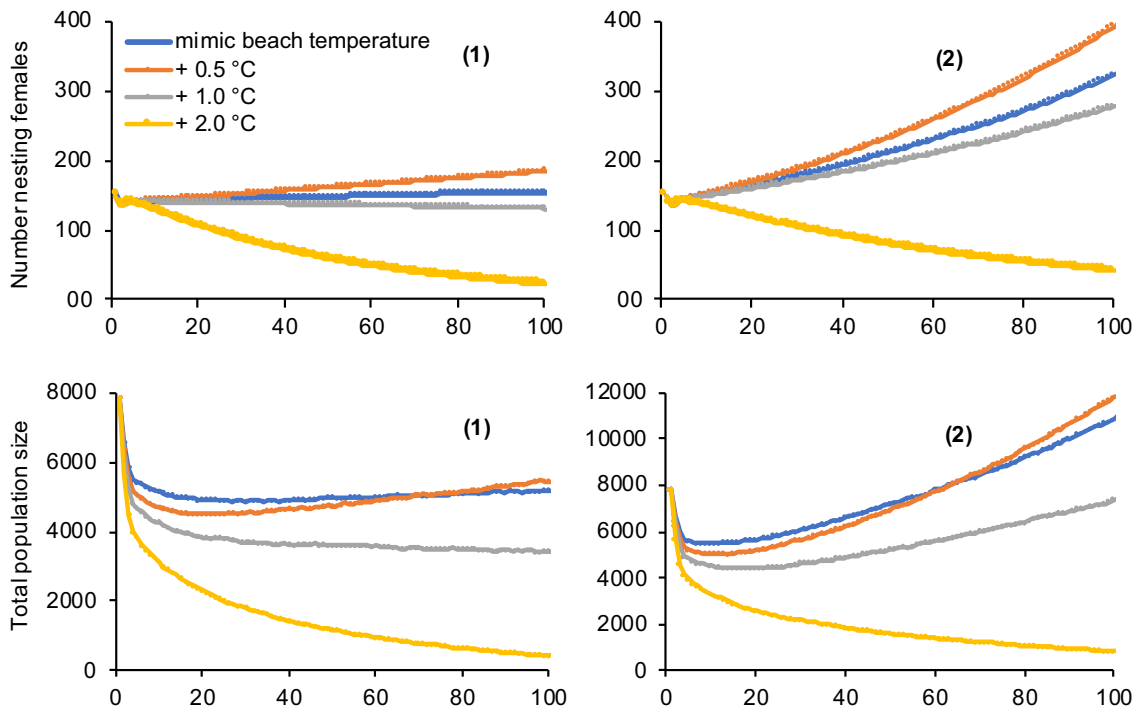


Fig. 3. Stochastic population projections of number of nesting female leatherback turtles and total population size over 100 years under climate change scenarios. We simulated the effect of maintaining mean temperatures as in natural nests (30.4 °C) and increasing mean temperatures by 0.5 °C, 1 °C and 2 °C. (1) and (2) correspond to the scenarios that kept the initial population stable under current mean temperatures (30.4 °C) and under historical mean temperatures (29.9 °C) respectively.

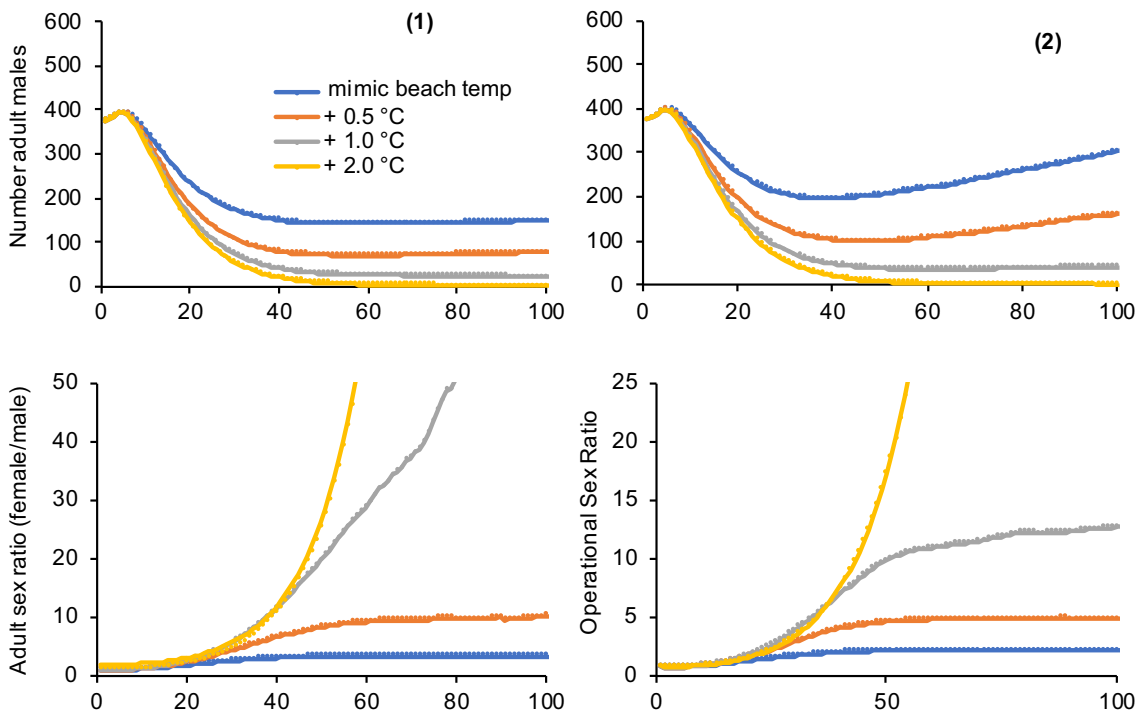


Fig. 4. Stochastic population projections of number of adult male leatherback turtles, adult sex ratios and operational sex ratios over 100 years under climate change scenarios. Temperatures tested included current mean temperatures in natural nests (30.4 °C) and temperatures that were increased by 0.5 °C, 1 °C and 2 °C. (1) and (2) correspond to the scenarios that kept the initial population stable under current mean temperatures (30.4 °C) and under historical mean temperatures (29.9 °C) respectively. Adult sex ratio includes not only nesting cohorts but all reproductive and non-reproductive individuals. Operational Sex Ratio includes reproductive individuals only. We are only representing sex ratios for one scenario as they were nearly identical.

population size (including juveniles, subadults, and adults) closely followed that of nesting females, indicating that the number of nesting females was the critical demographic factor in determining the fate of this sea turtle population. Consistently and significantly increasing the percentage of male hatchlings resulted in population declines, even under relatively small changes in nest temperature (0.5 °C or 1 °C depending on the scenario). On the other hand, increasingly warmer conditions could drive the number of males too low for all clutches to be fertilized, or, more importantly, would reduce hatchling production to critically low levels through worsened hatching and emergence success (Santidrián Tomillo et al., 2015; Hays et al., 2017). Although intentional cooling of nests could produce seemingly beneficial outcomes in the short-term (i.e., increased hatching success, increased production of males), such practices should be implemented to optimize increased hatchling production and sex ratios that promote population stability or recovery.

Female-biased primary sex ratios in sea turtles translate into balanced operational sex ratios in adults (Stewart and Dutton, 2011; Wright et al., 2012; Gaos et al., 2018; Howe et al., 2018; Lasala et al., 2013) because males can migrate to the nesting beaches twice as often as females (Hays et al., 2010). In addition, sea turtles have multiple paternity (Crim et al., 2002; Lee et al., 2018) with one male turtle potentially mating with several females. Therefore, female-biased primary sex ratios may only be of concern if they reached extreme levels (Hays et al., 2017; Patrício et al., 2021), as we found only in the climate change scenario in which mean temperatures were increased by 2 °C. Warm nest temperatures, like those currently registered at Playa Grande, produce female-biased sex ratios—81% female in our simulations, similar to that estimated in nature (79%–85%, Santidrián Tomillo et al., 2014), which translated into ‘normal’ adult (3 female to 1 male) and operational (2 female to 1 male) sex ratios.

Our results from the climate change scenarios do not call for immediate intervention. Instead, it seems that some sea turtle populations can handle increases in mean nest temperature of even several degrees before declining. The decline in emergence success at +0.5 °C and +1 °C was compensated by an increase in female biased sex ratio. However, this compensation was insufficient when mean nest temperature was increased by 2 °C, confirming the occurrence of temperature thresholds as previously shown (Santidrián Tomillo et al., 2015). Although our model did not consider changes in fertility rates depending on the number of adult males, it seems highly unlikely that an operational sex ratio of 130 female: 1 male (found at +2.0 °C) could maintain the same percentage of fertilized eggs in the population. Thus, if temperatures were increased by two or more degrees, sea turtle populations would suffer from both a decline in the nesting population and a scarcity of adult male turtles. However, as mentioned before, more worrisome than female-biased sex ratios (except in extreme conditions), are the male-biased primary sex ratios that can result from shading of nests. This is not because male-biased sex ratios translate into a high number of adult male turtles, but because they reduce the number of female hatchlings and thus the size of the future nesting population, causing population declines, including in the number of adult male turtles.

All sea turtles have the same physiological characteristics (i.e. sex is determined by temperature and successful embryonic development has thermal limits), but these relationships vary among species, populations and individuals, which is not accounted for in population models. For example, some species and populations are more tolerant to high nest temperatures than others (Howard et al., 2014; Weber et al., 2011) and individual variability in TSD curves likely exists and may change through time (Santidrián Tomillo and Spotila, 2020). Sex and egg/hatchling mortality could also depend on particular thermal experiences (e.g. stage of development, constant versus fluctuating temperatures or mean versus extreme temperatures). Likewise, individuals exhibit variability in nest-site and beach selection that could ultimately affect thermal conditions in the nest and consequently egg and hatchling mortalities and sex ratios (Reneker and Kamel, 2016; Patrício et al.,

2018). Additionally, our model was based on mean temperatures, but minimum or maximum temperatures could also have important effects on egg and hatchling mortalities. Finally, there are some uncertainties in the mechanism of sex determination that could also affect the outcome of population models if these were better known. For example, the thermosensitive period for sex determination (middle third of incubation) can shift under fluctuating temperatures (Girondot et al., 2018), TSD curves could result from sampling imperfections to determine sex (Mrosovsky and Provancha, 1991) and moisture may also play a role in sex determination (Lolavar and Wyneken, 2017). Thus, we recommend future research into how these factors and patterns affect sex determination and egg/hatchling survival to support optimized management of sea turtle nests.

Climatic effects at the population level are also more complex than what we have considered here. For instance, remigration intervals in sea turtles depend on oceanic conditions in years before the nesting season (Limpus and Nicholls, 2000; Solow et al., 2002; Saba et al., 2007; Ramírez et al., 2021) also affecting populations dynamics. For these reasons, we note that while our results show the potentially negative, unintended consequences of techniques to intentionally cool sea turtle nests, they do not provide explicit guidance about the specific nest temperatures and other conditions that conservation practices should target to optimize hatchling production and viable sex ratios that promote long-term population stability. Nonetheless, in small and/or declining threatened populations, the production of female hatchlings could be desirable to increase the size of the population (Wedekind 2002).

Due to several factors, particularly the high levels of egg harvest that threaten several sea turtle populations around the world (Chacón-Chaverri and Eckert, 2007; Mutalib and Fadzly, 2015), it may not always be feasible to protect nests in situ. In such cases, relocating clutches can prevent egg loss. However, once in the hatchery, nest temperatures should ideally reflect those encountered on the beach, as long as those nest temperatures are favorable for hatchling production. If shading was to be used, different type of shading material such as palm leaves or fabric could create distinct conditions (Esteban et al., 2018). For instance, a recent study on the effect of nest shading on green turtle nests showed that natural tree shading reduced temperatures over 2.5 °C, whereas artificial shading in hatcheries had a lower impact on nest temperatures (Reboul et al., 2021).

Applying the precautionary principle, we recommend minimally invasive manipulation of clutches, as well as adaptive management in hatcheries that could minimize the negative impacts of climate change and improve the outcomes (Fuentes et al., 2016). Further, we recommend that conservation priorities should focus on nest protection under natural conditions, when possible, rather than shading clutches in hatcheries.

5. Implications for nest management under climate warming

Our results indicate that nest shading may only be needed to conserve sea turtles under extreme female biases that could result in non-fertilized eggs and that are accompanied by high embryo and hatchling mortality, as we found in the highest future mean nest temperature increases, but not in the scenarios of low and intermediate temperature increases. Some populations such as the green turtles that nest in the northern beaches of the Great Barrier Reef are already extremely female biased (> 99% female in juveniles) (Jensen et al., 2018; Booth et al., 2020). Despite being one of the largest populations in the world, their future could eventually be compromised if no males were produced to fertilize eggs and there was no mixing with males from other rookeries (Jensen et al., 2018).

As climate gets warmer, it is likely that the negative impact of high nest temperatures on hatching and emergence success will increase, severely reducing the reproductive output of some populations (Saba et al., 2012; Santidrián Tomillo et al., 2020). Nest shading, as shown

here and found in previous studies (Maulany et al., 2012; Mutalib and Fadzly, 2015), could be an effective way to increase the number of hatchlings produced, but it must be used with caution. For example, future managers could shade nests after the thermosensitive period had passed (i.e., during the last third of the incubation period). In this way, high nest temperatures could potentially be mitigated, reducing at least mortality occurring in late developmental stages, without altering sex ratios. Before such refined interventions are implemented, however, the effects of nest temperatures on different embryonic stages should be assessed. An alternative would be to shade nests at any time during development as long as the resulting nest temperatures were maintained over male-producing temperatures. This approach would require that the TSD-curve had been determined for the target population. This would be especially important in small or declining populations as female-biased sex ratios can potentially increase the size of a population (Wedekind 2002; Laloë et al., 2014). For example, targeting nest temperatures in the future that are similar to the current or historical ones would be a good management strategy for our study population (Fig. 1).

Finally, climate change may affect sea turtle populations and species differently, with thermal variability even occurring among nearby nesting beaches (Weber et al., 2011). Thus, it is essential to first assess the effect of nest temperatures on the particular population that it is the focus of conservation efforts, and then to consider the ecological risks before intervening (Patrício et al., 2021). As climate gets warmer, climate mitigation strategies to protect sea turtle nests will likely be more used. Analyzing the impact of any conservation actions involving human intervention, as well as that of climate change on sea turtles on the long-term will be critical for adequately conserving them into the future.

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CRedit authorship contribution statement

Pilar Santidrián Tomillo: Conceptualization, methodology, writing-original draft, supervision; **Bryan P Wallace:** Conceptualization, methodology, writing-reviewing editing; **Frank V Paladino:** writing-reviewing editing, supervision; **James R Spotila:** writing-reviewing editing, supervision; **Meritxell Genovart:** methodology, population model development, writing-reviewing editing.

Declaration of competing interest

The authors have no competing interests to declare.

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