

# Effects of rising temperature on the viability of an important sea turtle rookery

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**A warming world poses challenges for species with temperature-dependent sex determination, including sea turtles, for which warmer incubation temperatures produce female hatchlings. We combined *in situ* sand temperature measurements with air temperature records since 1850 and predicted warming scenarios from the Intergovernmental Panel on Climate Change to derive 250-year time series of incubation temperatures, hatchling sex ratios, and operational sex ratios for one of the largest sea turtles rookeries globally (Cape Verde Islands, Atlantic). We estimate that light-coloured beaches currently produce 70.10% females whereas dark-coloured beaches produce 93.46% females. Despite increasingly female skewed sex ratios, entire feminization of this population is not imminent. Rising temperatures increase the number of breeding females and hence the natural rate of population growth. Predicting climate warming impacts across hatchlings, male-female breeding ratios and nesting numbers provides a holistic approach to assessing the conservation concerns for sea turtles in a warming world.**

It is now widely accepted that climate change is having profound impacts on a range of ecosystems, including shifts in species range, abundance and phenology<sup>1-4</sup>. As evidence accumulates that these impacts continue to increase, there is a growing awareness of the need to go beyond mere descriptions of these changes and instead to understand how species may adapt to changing conditions and if management interventions will be needed<sup>5</sup>. This understanding may help prevent species extinctions and manage emerging threats such as increased disease prevalence and noxious invading species<sup>6-9</sup>. For some taxa the threats to species extinction have been known, in qualitative terms, for decades. For example, for groups that exhibit temperature-dependent sex determination, rising incubation temperatures may induce the production of single-sex populations<sup>10</sup>. However, going beyond these qualitative arguments to more quantitative information on past, present and future offspring sex ratios has proved to be more difficult.

Reptiles are one classic group where species often exhibit temperature-dependent sex determination. For sea turtles, below a certain pivotal incubation temperature (typically near 29 °C) the majority of eggs produce male hatchlings and vice versa (for example, see refs 11-14). For several decades the increasing availability of reliable temperature loggers and dependable temperature-controlled incubators has meant that descriptions of present-day incubation conditions, and hence offspring sex ratios, have become widely available for a number of species<sup>15-17</sup>. More recently, past environmental conditions have been used to assess historic (150-yr) changes in incubation conditions<sup>18</sup> and there is now the potential to blend these past estimates with predictions of climate change made by the Intergovernmental Panel on Climate Change (IPCC; refs 19,20). In this way studies have started to quantify the expected impacts of warming temperatures in terms of increasingly skewed offspring sex ratios.

Here we set out to make an advance in this multi-decadal thread of research by estimating past, present and future offspring sex ratios. We then combine these estimates with emerging information

on operational sex ratios and longevity to identify how offspring sex ratios will translate into operational sex ratios and population size estimates.

## Sand temperatures and metabolic heating

We found a strong relationship between mean monthly sand temperatures and mean monthly air temperatures at Sal, Cape Verde (Figs 1 and 2). No rainfall was recorded during the study. A one-way ANCOVA model showed a significant effect of air temperature ( $p < 0.0001$ ) and of beach colour ( $p < 0.0001$ ) on sand temperature. An F-test for nested models revealed that in fact there was a significant difference between light sand beaches and dark sand beaches ( $F = 21.69$ ,  $p < 0.0001$ ). Hence light sand beaches and dark sand beaches were subsequently treated independently in our analyses. Furthermore, there was no significant interaction between air temperature and beach colour ( $p = 0.989$ ) and therefore the assumption of homogeneity of regression slopes is met. The mean metabolic heating during the middle third of incubation is 0.50 °C ( $\pm 0.11$  °C). Within all the logger pairs, the minimum metabolic heating measured during the middle third of incubation was 0.12 °C ( $\pm 0.05$  °C) and the maximum was 0.86 °C ( $\pm 0.08$  °C). The mean metabolic heating for all the logger pairs is presented in Fig. 3.

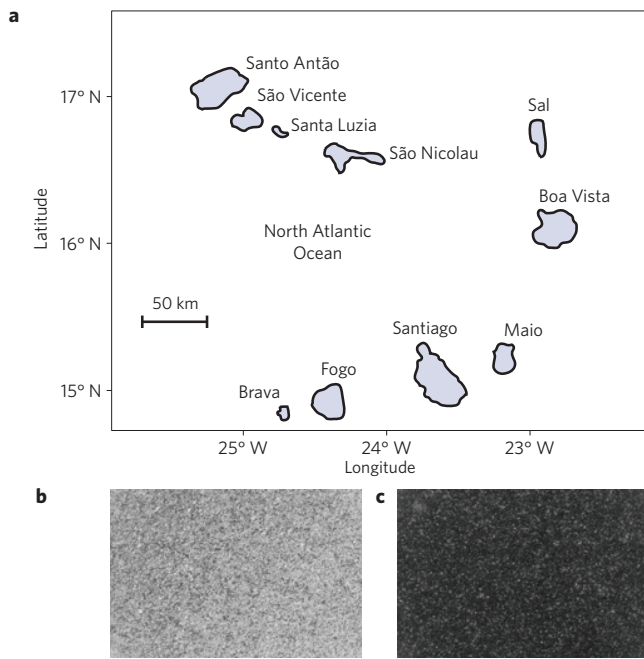
## Incubation temperatures and hatchling sex ratios

Using the equations describing the relationship between air temperature and sand temperature, incubation temperature reconstructions and predictions were made for both light sand beaches and dark sand beaches (Fig. 4). The conversion from sand temperature to incubation temperature was completed by adding the observed mean value for metabolic heating during the middle third of incubation to the sand temperatures. The majority of beaches on Sal have light coloured sand. Only 10.65% of clutches on Sal are laid on dark coloured beaches (Cozens, unpublished data spanning five years). We used the proportion of clutches laid on each type of beach to estimate the overall sex ratio of hatchlings.

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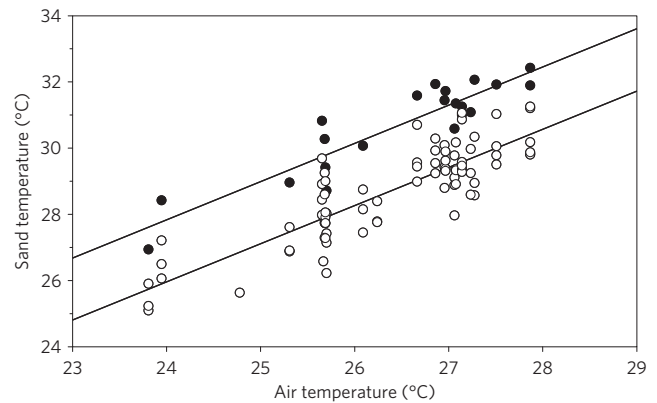
**Figure 1** | Cape Verde is a very important loggerhead rookery with an estimated 10,000–15,000 nests laid annually across the archipelago<sup>49,50</sup>.

**a**, Nesting takes place on all ten islands in the archipelago and on more than 20 beaches. Our work focussed on nesting beaches on the island of Sal, which lies in the northeast of the archipelago. Sand colour varies across the nesting beaches. **b**, The majority of nesting beaches are light in colour (high albedo). **c**, 10.65% of nests occur on beaches with dark sand (low albedo; Cozens, unpublished data spanning five years).

Assuming a pivotal temperature of 29 °C, the Hill equation and parameters suggested by the program TSD (see ref. 21) that describes the relationship between incubation temperature ( $t$ ) and hatchling sex ratios ( $sr$ ) are:

$$sr(t) = \frac{1}{1 + e^{(1/S)(\ln(P+K) - \ln(t+K))}} \quad (1)$$

where  $sr(t)$  is sex ratio at a specific temperature  $t$ ,  $S = -0.0336281$ ,  $P = 28.95065$  and  $K = 0.1$ . Using this equation we can estimate hatchling sex ratios based on incubation temperatures. From 1854 to 2013, estimated hatchling sex ratios were 55.60% female ( $\pm 12.72\%$ ) for light beaches and 87.90% female ( $\pm 5.49\%$ ) for dark beaches (Fig. 5). Although there was considerable inter-annual variability, for neither the light nor dark coloured beaches was there any clear long-term trend in historic sex ratios. However, this situation changes when projecting sex ratios into the future. According to the Special Report on Emissions Scenarios (SRES) A2 scenario the percentage of female hatchlings produced on the light and dark coloured beaches rises monotonically between 2013 and 2100, from 70.10% to 97.80% and from 93.46% to 99.54%, respectively. If we repeat these calculations assuming pivotal temperatures of 28.8 °C and 29.2 °C, the key conclusions remain the same, albeit the specific percentage of female hatchlings being produced is higher with a lower pivotal temperature (Supplementary Figs 1 and 2). For example, with a pivotal temperature of 28.8 °C, between 2013 and 2100 the percentage of female hatchlings from the light and dark beaches increases from 74.07% to 98.15% and from 94.51% to 99.99% respectively; with a pivotal temperature of 29.2 °C these values are 65.77–97.38% and 92.22–99.29% respectively. If we consider the SRES A1B, female production is projected to increase to 95.79% on light coloured beaches and to 99.17% on dark

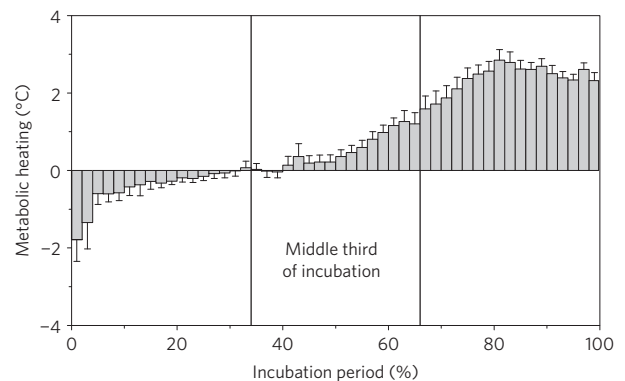


**Figure 2** | Mean sand temperature versus mean air temperature for nesting beaches on the island of Sal. A single point represents the monthly mean sand temperature recorded for August, September or October of 2009, 2010, 2011 or 2012. Light sand beaches (open circles) are differentiated from dark sand beaches (filled circles). The least squares fit regression equations are: mean sand temperature of light beaches =  $1.15 \times$  air temperature  $- 1.70$  ( $r^2 = 0.73$ ); mean sand temperature of dark beaches =  $1.15 \times$  air temperature  $+ 0.12$  ( $r^2 = 0.84$ ).

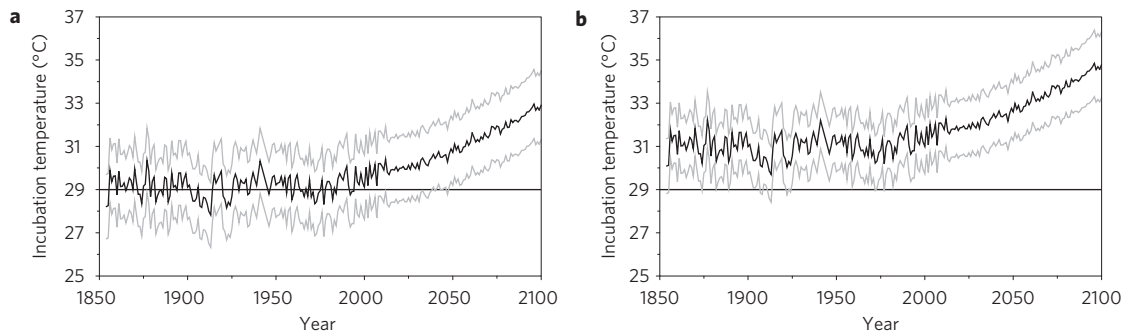
coloured beaches by the year 2100. Considering SRES B1, projected female production will increase less dramatically to 90.01% on light beaches and to 97.99% on dark beaches by the year 2100 (Supplementary Fig. 3).

### Operational sex ratios and female recruitment

Working under the assumption that male loggerheads breed twice as often as females<sup>22</sup>, we translated hatchling sex ratios to operational sex ratios, introducing a 45-year age-at-maturity time lag<sup>23</sup> (Fig. 6). The mean percentage of female hatchling production from 1854 to 2013 of 59.04% ( $\pm 11.94\%$ ) for all beaches translates to a female operational sex ratio of 42.93% ( $\pm 11.93\%$ ) for the years 1899 to 2058. In effect, despite highly female-biased primary sex ratios, the percentage of breeding females is closer to, and even below, the 50:50 male-to-female sex ratio. However, with warming air temperatures, the operational sex ratios will depart further from balanced sex ratios and with the SRES A2 scenario the female operational sex



**Figure 3** | Mean metabolic heating of loggerhead eggs on the island of Sal, Cape Verde. At first metabolic heating seems to be negative because the temperature recorders were placed inside the nest at the time of nesting, whereas the control recorder was buried before nesting and therefore had adjusted to the surrounding sand temperature. The x-axis shows the time during incubation so the vertical lines define the middle third of incubation, which is the temperature sensitive period of sex determination for sea turtles. The error bars indicate the standard deviation for each percentile group.



**Figure 4 | A 250-year incubation temperature time series for the beaches of Sal according to the SRES A2 scenario with the 95% prediction intervals (grey lines). a, Data for the light sand beaches. b, Data for the dark sand beaches.**

ratio is predicted to increase to 96.05% by the middle of the twenty-second century.

We divided the predicted future percentage of female hatchlings being produced across different beaches by the historic long-term mean percentage of female hatchlings. All else being equal (for example, there is no long-term decline or increase of population size) this calculation essentially produces a relative index of the number of female hatchlings being produced. If we assume 45 years to sexual maturity, this gives us an index of the relative number of females recruiting to the adult population. This calculation shows that accompanying the progressive skew of the operational sex ratio towards more females, by 2150 there will also be an increase of approximately 60% in the number of females recruiting to the adult population (Fig. 6). Altering the age-at-maturity simply displaces the operational sex ratio curves and relative number of females to one side, with the absolute values remaining unchanged. For example, if the age at maturity is a decade lower than we have assumed (35 years versus 45 years), then the translation of hatchling sex ratios into operational sex ratios and relative number of adult females happens ten years sooner.

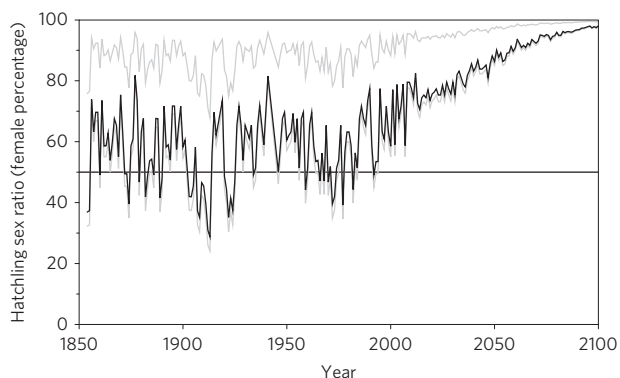
### Discussion and conclusion

Our results highlight the future extent of warming-induced feminization of hatchling sex ratios for a globally important sea turtle rookery. Although our specific conclusions apply to the Cape Verde rookery, which is a major rookery for loggerhead turtles, the model development is generic and can be applied to other turtle breeding sites globally. Importantly we make the conceptual advance of not only assessing warming impacts on hatchling sex ratios but also the impact for operational sex ratios and the number of breeding females recruiting to the adult population. This holistic consideration of different life history stages suggests that despite expected future warming leading to more female-biased hatchling sex ratios, the implication for the size of the adult population is unlikely to be dire in the next 150 years. Interestingly, we predict that the increasing skew towards more female hatchlings will actually lead to increased recruitment of females to the adult population and so an increase in nesting numbers. Hence warming temperature may actually have some conservation benefit, with more females and a greater number of clutches increasing the natural rate of population growth.

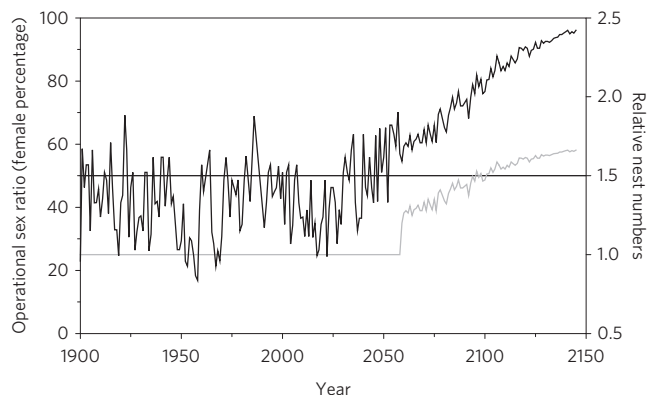
Our results suggest that by the middle of the twenty-second century we expect operational sex ratios at the Cape Verde rookery to include only 3.95–16.74% adult males on the breeding grounds, which may potentially impact clutch fertility. It is well known that a few male sea turtles can probably go a long way in terms of breeding with females, and female sea turtles are known to store sperm to fertilize multiple clutches<sup>24–26</sup>. The breeding season precedes the start of the nesting season by several weeks<sup>27,28</sup> and then, before the onset of nesting, most males depart from the breeding grounds<sup>22,29</sup>.

Females then remain and produce several clutches using their stored sperm<sup>24</sup>. Although there is relatively little information on the free-living ecology of male turtles, there is also some evidence that they move around breeding areas more than females<sup>30</sup>. In other words, males produced from light coloured beaches may still fertilize eggs of females that originate and have fidelity to nearby dark coloured beaches. For example, at Ascension Island, a major rookery for green turtles in the equatorial Atlantic, it is estimated that one major nesting beach where the sand is dark, North East Bay, has only produced female hatchlings for the past 150 years. Yet females still produce fertile eggs on this beach and this seems to be mediated by mating with male turtles that are produced at lighter coloured beaches a few kilometres away<sup>18</sup>. Hence, even with a few males it is likely that females will be mated with and produce fertile offspring. However, the issue of how many males are required is central to the conservation implications of progressive warming and feminization. Eventually a point will be reached when there are insufficient males to fertilize all eggs. Assessing that point should be a key conservation priority and might be achieved, for example, by long-term records of clutch fertility at rookeries while also recording operational sex ratios. Ultimately if males are so scarce that egg fertility is compromised, management intervention will be needed. Translocating nests from dark beaches to light beaches could be a strategy to produce more male hatchlings. Another strategy would be to shade nests (for example, with beach vegetation) to lower incubation temperatures<sup>31</sup>. Furthermore, at very high incubation temperatures (>33 °C) mortality of developing embryos occurs<sup>10</sup>, which will provide a further reason to artificially cool nests.

Clearly our estimates of long-term changes in operational sex ratios can be fine-tuned as more refined data emerges on all the steps in this calculation. We can examine each of these steps in turn along with the outcomes of sensitivity analysis of model parameterization to identify the most important knowledge gaps. Estimates of metabolic heating are now routinely made. Although our results stem from only a few pairs of loggers inside and outside clutches, our results align with previously published research with larger sample sizes: metabolic heating rates of loggerhead sea turtles were measured to be 0.2 °C in Cyprus<sup>32</sup>, 0.2 °C in Greece<sup>33</sup> and 0.5 °C in the USA (ref. 34). Metabolic heating is also generally assumed to be constant within any one nest. This is a simplification, as it may be that eggs in the middle of the clutch heat more than eggs at the edge of the clutch because the rate of heat loss to the surrounding sand is less<sup>35</sup>. So although the effect of metabolic heating is fairly minimal, it is nonetheless important to include this term in models of hatchling sex ratios and to continue refining these warming estimates<sup>36</sup>. Links between sand temperature at nests depths and environmental proxies such as air temperature also seem to be fairly robust<sup>18,19,37,38</sup>. For many rookeries, as we found in our study, rainfall is minimal during the incubation season and



**Figure 5** | A 250-year hatchling sex ratio time series for the light sand beaches (lower grey line), dark sand beaches (upper grey line) and all beaches combined (black line) of Sal according to the SRES A2 scenario. The female percentages were calculated by converting incubation temperatures into sex ratios using equation (1). The mean for all beaches was calculated by multiplying the sex ratio for each beach by its respective nesting ratio, summing all the ratios and dividing the result by 100. The horizontal line is the 50% male-to-female ratio.



**Figure 6** | A 250-year operational sex ratio time series (upper line) and expected change in nesting numbers (lower line) for Sal according to the SRES A2 scenario. We assumed that male loggerheads breed twice as often as females and an age-at-maturity of 45 years. The horizontal line is the 50% male-to-female ratio. The change in nesting numbers was calculated by dividing the primary sex ratios by the mean primary sex ratio from 1854 until 2012 and then introducing a 45-year lag (time-to-maturity).

so does not compromise these strong relationships between sand and air temperatures. But at some sites rainfall is important in influencing incubation temperatures<sup>39</sup>. In a warming world it is not just temperature that may change but also other components of the climate<sup>40</sup> (for example, rainfall and wind) and so there needs to be continued consideration of the suite of environmental conditions that may ultimately drive sand temperatures.

Furthermore, it should be noted that an increase of incubation temperatures is not the only effect of global warming with regards to sea turtle conservation. Global warming is also threatening the nesting beaches through sea level rise<sup>41</sup>. Rising sea levels resulting in the loss of nesting beaches could push local turtle populations over the brink unless new suitable nesting beaches are found. Turtles can adapt to the loss of their nesting beaches by moving to other beaches and such migrations have already been observed, but it could be that sea level rise coupled with beachfront development on nesting beaches will eliminate the remaining suitable nesting beaches for sea turtles.

Probably the weakest links in the calculation of future operational sex ratios are the predicted changes in air temperature and the

relative breeding periodicity of males and females. The former is encompassed in the various predictions of the IPCC. As in other studies we took the medium predicted air temperatures changes, but these predictions will continue to be refined by the IPCC so that in future years we will have a more informed estimate of which IPCC future trajectory is likely to materialize. However, estimating breeding intervals for males and females is something that can be addressed by turtle researchers. Researchers tend to focus on females because they come ashore to nest and hence are easy to observe and equip. It is far more problematic working with adult male turtles, but some researchers have perfected in-water capture which allows identification and attachment of data-loggers and tracking equipment<sup>42</sup>. More work in this vein is needed to establish if the increased male breeding rates that have been recorded in Greece<sup>22</sup>, Cyprus<sup>43</sup> and Australia<sup>44</sup> also apply to other species and populations and will hopefully prompt researchers to narrow down the uncertainties in climate change prediction both for sea turtles and other groups showing temperature-dependent sex determination.

Our findings re-iterate previous work showing how sand albedo has profound impacts for incubation conditions, with darker beaches being warmer and so expected to produce more female hatchlings<sup>18</sup>. The thermal difference at nest depths between beaches can be quite profound (several °C). In conservation terms, this importance of sand albedo shows that in a warming world the light coloured beaches are a conservation priority because they will become those producing the only male hatchlings<sup>18</sup>.

Elsewhere globally, researchers should be aware that, all else being equal, feminization of hatchling production through rising incubation temperatures will lead to more females being recruited to the adult population and hence increases in nesting numbers. Indeed, increases in nesting numbers have been widely noted, although this 'feminization effect' has not been considered. Our evidence suggests that although management intervention is not needed now to prevent feminization of the Cape Verde population, sand temperatures (and hence hatchling sex ratios) should continue to be monitored. In short, a holistic approach is needed in examining the impacts of warming temperatures for sea turtles, considering not only hatchling sex ratios but also operational sex ratios, nesting numbers and clutch fertility.

## Methods

**Sand temperature.** Sand temperature data were collected during the 2009, 2010, 2011 and 2012 nesting seasons using Tinytag Plus 2 loggers (model TGP-4017, Gemini Data Loggers, UK). The loggers are originally calibrated to United Kingdom Accreditation Service (UKAS) standards. Further trials have shown that Tinytag loggers of this type give readings that are, on average, identical to National Measurement Accreditation Service (NAMAS) standards with a standard deviation of  $\pm 0.1$  °C (ref. 45).

The loggers were buried during the breeding season at a depth of 35 cm, which is the mean depth at which the middle of a clutch of eggs is found for this population of loggerheads (Cozens, unpublished data spanning five years). Temperature was recorded every hour. Five loggers were buried during the 2009, 2010 and 2011 nesting seasons and nine loggers were buried during the 2012 nesting season. Loggers were deployed at different sites on six of the major nesting beaches of the island of Sal. Both dark sand and light sand nesting beaches were selected.

**Air temperature.** We obtained air temperature data in the vicinity of Sal (14°–18° N and 22°–26° W) from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) through the National Center for Atmospheric Research (NCAR) (<http://rda.ucar.edu/datasets/ds540.1/>). The ICOADS is a comprehensive weather data set that extends as far back as the early nineteenth century. We used the Enhanced ICOADS Monthly Summary Release 2.5 at 2-degree spatial resolution and restricted the dataset to months with at least 30 observations. We did not interpolate observations to fill data voids, so some gaps in the dataset remain. The 4-degree square region used in this study encompasses all of the islands of Cape Verde, which enables us to expand our predictions to the whole of Cape Verde. Air temperature predictions for the region containing the archipelago of Cape Verde were obtained from the United

Nations Development Programme (UNDP). The projected values come from an analysis of 15 climate models used by the Intergovernmental Panel on Climate Change (IPCC) for their Fourth Assessment Report published in 2007 (ref. 46). Yearly air temperature means were available, as well as quarterly temperature means. The projections used are the Special Report on Emissions Scenarios (SRES) developed by IPCC in 2000. The different scenarios make different projections based on different greenhouse gas emission scenarios. Three different SRES scenarios have been examined in our research: scenarios A2, A1B and B1. For the purpose of succinctness, only SRES scenario A2 analyses are presented in the main text but the Supplementary Information includes the analyses for the different scenarios (Supplementary Figs 1–5). The UNDP data is freely available online (<http://www.geog.ox.ac.uk/research/climate/projects/undp-cp/>). We used the mean air temperatures for the months of August, September and October for the purpose of temperature reconstruction and temperature projections in our analysis, as this is the peak incubation time for loggerhead turtles in the Cape Verde islands (Cozens, unpublished data spanning five years).

**Metabolic heating.** A further three loggers were placed inside three different clutches to measure metabolic heating during the 2012 nesting season. Two of these clutches were hatchery nests and the last clutch was an *in situ* nest. These loggers were also buried at a depth of 35 cm. The clutch loggers were paired to respective control loggers buried on the same beach. Metabolic heating was measured throughout the incubation period by subtracting the temperature measured by the control logger from the temperature measured by the clutch logger. The baseline difference between clutch loggers and control loggers was removed using the method described in 2006 (ref. 33). We defined the incubation period as the time between laying and the first emergence of hatchlings. This is a definition commonly used in this type of research and it does not require manipulation of the nest to see the eggs hatch.

**Sex ratios.** We created a model curve for the percentage of male and female hatchlings produced at different incubation temperatures using the program TSD (ref. 21; Supplementary Fig. 6). A pivotal temperature of 29 °C was used as it aligns with pivotal temperatures measured in geographically close loggerhead populations<sup>14,47</sup>. However, in addition we ran sensitivity analyses assuming pivotal temperatures of 28.8 °C and 29.2 °C to assess the importance of this value to the model predictions (Supplementary Figs 1 and 2). Before converting incubation temperatures to sex ratios a final adjustment was made: as for a given nesting season, incubation temperatures are normally distributed around the mean incubation temperature, using the standard deviation of the normal distribution we created 'temperature bins' in which nests would fall into. To calculate the overall sex ratio, the sex ratios of each bin are multiplied by their respective bin sizes and then summed together (Supplementary Fig. 7). The mathematical equation to calculate the hatchling sex ratio  $sr$  at a mean temperature  $T$  is  $sr(T) = \sum sr(t_i) \times d_i$  where  $sr$  is the sex ratio,  $t_i$  is the median temperature of bin  $i$ , and  $d_i$  is the size of bin  $i$ .

**Operational sex ratios.** There is evidence that male loggerhead sea turtles visit breeding sites two to three times more often than their female counterparts<sup>22</sup>. As males can fertilize the eggs of many females, this means that hatchling sex ratios do not reflect a breeding population's sex ratios: whereas females breed every other year or every third year, males breed every year. By considering an age-at-maturity of 45 years for loggerhead turtles<sup>23</sup>, we can translate hatchling sex ratios to operational sex ratios with a 45-year lag by using the formula  $OSR(t_{i+45})_{\text{females}} = (100 \times sr(t_i)_{\text{females}}) / (sr(t_i)_{\text{females}} + 2 \times sr(t_i)_{\text{males}})$ , where  $OSR_{\text{females}}$  is the operational sex ratio of females and  $sr(t_i)$  is the primary sex ratio at time  $t_i$  given in years. We also consider the sensitivity to this parameterization given that sea turtles may mature at different ages elsewhere<sup>48</sup>.

**Statistical analysis.** Statistical analyses were performed using R (R version 2.15.1, R Core Team (2012)). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>. Throughout mean values are reported  $\pm 1$  s.d.

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### Author contributions

J.C. initiated the project and completed all the field work. J.C., B.R., and A.T. compiled the data. G.C.H. conceived the manuscript. J-O.L. led the data analysis. J-O.L. and G.C.H. wrote the manuscript with contributions from all authors.

### Additional information

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### Competing financial interests

The authors declare no competing financial interests.