

Projected response of an endangered marine turtle population to climate change

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Assessing the potential impacts of climate change on individual species and populations is essential for the stewardship of ecosystems and biodiversity. Critically endangered leatherback turtles in the eastern Pacific Ocean are excellent candidates for such an assessment because their sensitivity to contemporary climate variability has been substantially studied^{1–4}. If incidental fisheries mortality is eliminated, this population still faces the challenge of recovery in a rapidly changing climate. Here we combined an Earth system model⁵, climate model projections assessed by the Intergovernmental Panel on Climate Change⁶ and a population dynamics model to estimate a 7% per decade decline in the Costa Rica nesting population over the twenty-first century. Whereas changes in ocean conditions had a small effect on the population, the ~2.5 °C warming of the nesting beach was the primary driver of the decline through reduced hatching success and hatchling emergence rate. Hatchling sex ratio did not substantially change. Adjusting nesting phenology or changing nesting sites may not entirely prevent the decline, but could offset the decline rate. However, if future observations show a long-term decline in hatching success and emergence rate, anthropogenic climate mitigation of nests (for example, shading, irrigation)^{7,8} may be able to preserve the nesting population.

Climate change can affect both the marine and terrestrial habitat of marine turtles⁹. The population of eastern Pacific leatherback turtles (*Dermochelys coriacea*) nesting on the northwest coast of Costa Rica has been studied in terms of its sensitivity to contemporary climate variability in the nesting beach^{1,2} and ocean^{3,4}. Leatherbacks forage almost exclusively on gelatinous zooplankton and the preferred foraging hotspots are typically waters with high primary productivity of large phytoplankton (that is, upwelling and coastal zones)⁴. Foraging success and reproductive frequency of mature females are enhanced after periods (~one year) of high primary productivity in the eastern equatorial Pacific³. In northwestern Costa Rica, hatching success, hatchling emergence rates and the proportion of male hatchlings all increase during cool and wet conditions^{1,2}. Variability in both foraging success of mature females in the ocean and in the local climate in the nesting beach are primarily associated with the El Niño/Southern Oscillation^{2,3} (ENSO). The La Niña phase of ENSO is associated with higher primary productivity of large phytoplankton/cooler sea surface temperature (SST) in the eastern equatorial Pacific¹⁰ and enhanced precipitation/cooler air temperature in northwestern Costa Rica².

Nesting seasons that follow La Niña events thus result in peaks in the number of nesting females³, higher than average hatching success and emergence rate² and a larger proportion of male hatchlings¹, whereas the opposite holds true for El Niño events. Leatherback hatchling sex ratios in Costa Rica are typically female biased (88%; ref. 11) and La Niña events are essential for producing pulses of male recruitment (>50%; ref. 1) into the population.

Historic egg poaching¹² and incidental fisheries mortality¹³ have rendered the eastern Pacific leatherback population critically endangered¹⁴. Although some steps have been taken to reduce these losses (for example, beach protection), the sensitivity of eastern Pacific leatherbacks to contemporary climate variability makes it essential for recovery plans to consider the impacts of anthropogenic climate change. Climate projections assessed by the fourth assessment of the Intergovernmental Panel on Climate Change (IPCC AR4) show relatively strong agreement that much of Central America is very likely to (>90%) become warmer and is likely to (>66%) become drier over the twenty-first century¹⁵. Projections also suggest possible changes in the strength and frequency of El Niño and La Niña events, though there is less agreement on the sign and magnitude of these changes¹⁶. Here we describe the response of a population dynamics model for eastern Pacific leatherback turtles to changes in environmental forcing from an ensemble of climate model projections that were assessed in the IPCC AR4. We used a series of sensitivity simulations to identify the source of any climate-change-driven trends and then assessed the implications of adaptation through plastic responses.

We developed a climate-forced population dynamics model (CLIMPOP) based on existing nesting beach and ocean models^{1–4} (Methods and Supplementary Methods). We assumed that future ENSO-linked SST anomalies would remain robust indicators of productivity changes over the twenty-first century. This assumption was examined within the Geophysical Fluid Dynamics Laboratory's Earth System Model (GFDL-ESM2.1; ref. 5), which included both physical climate and ocean biogeochemical dynamics. The SST anomaly remained highly correlated with large phytoplankton productivity throughout the 100-year projection to the year 2100 ($r = -0.84$, Fig. 1a). Reliance on SST as an indicator of large phytoplankton productivity allowed us to compare bias-corrected output¹⁷ from 14 global climate models⁶ that were assessed in the IPCC AR4 and select only those that captured observed covariance between SST anomalies in the eastern equatorial Pacific and air temperature/precipitation in northwestern Costa Rica to force

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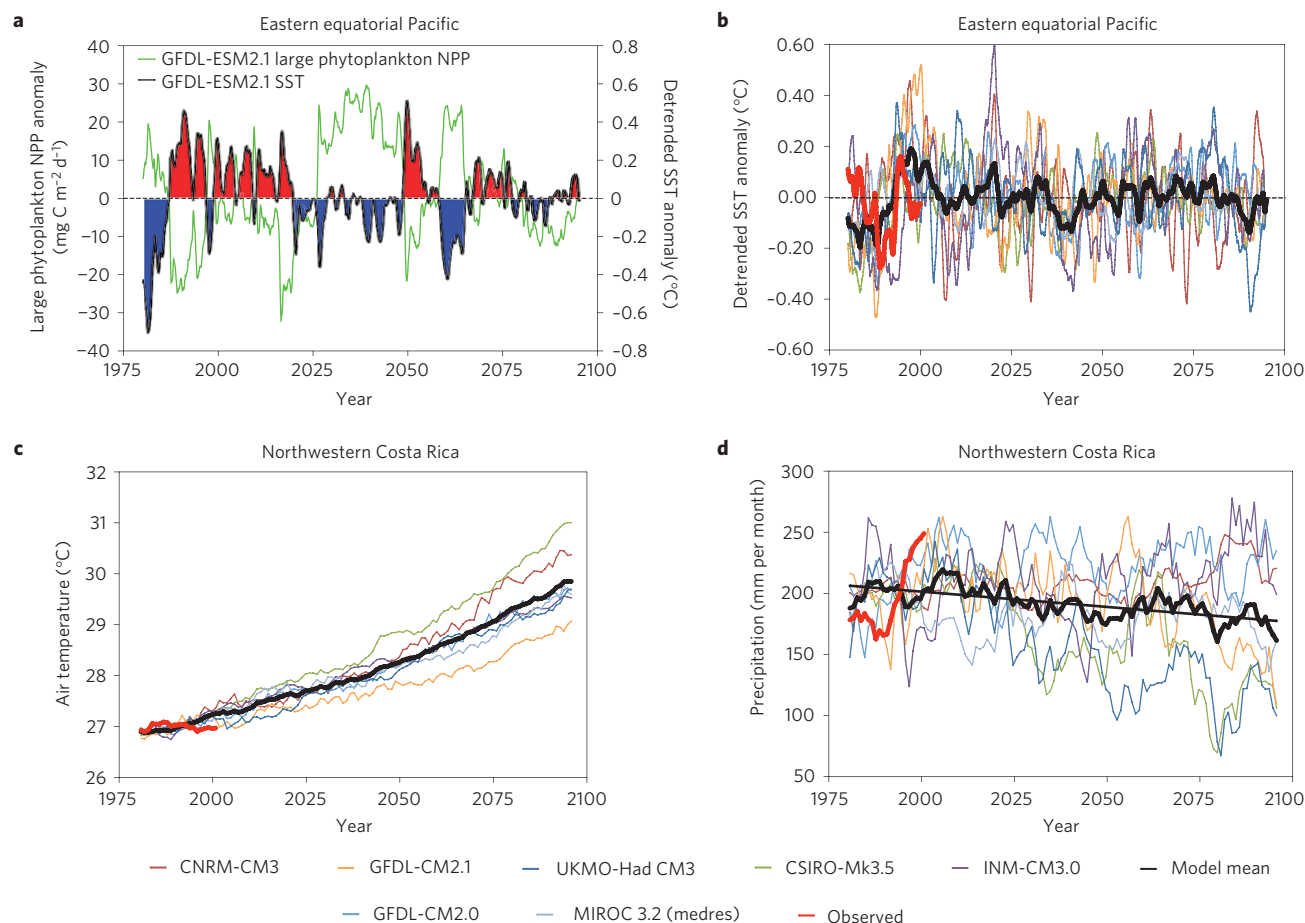


Figure 1 | Biological and climatic projections under the IPCC SRES A2 in the eastern equatorial Pacific and in northwestern Costa Rica. **a**, GFDL-ESM2.1 (ref. 5) historical estimates (1975–1999) and IPCC SRES A2 projections (2000–2100) of SST variability (detrended) and large phytoplankton net primary productivity (NPP) in the eastern equatorial Pacific (2.5° N–2.5° S, 85° W–125° W). Detrending SST isolates ENSO-linked variability. The inverse relationship between SST variability and large phytoplankton NPP variability remains consistent over the next century of climate change (correlation coefficient = -0.84 , $P < 0.005$). **b–d**, Seven climate model bias-corrected historical estimates and SRES A2 projections of eastern equatorial Pacific SST variability (**b**) northwestern Costa Rica (10° N–11° N, 85° W–86° W) mean surface air temperature during the nesting season's egg incubation months (October–February) (**c**) and mean monthly precipitation at the end of the rainy season (August–December) (**d**). Observed data in **b–d** are shown for the historical period from 1975 to 1999 (from local airport; Supplementary Methods). All time series in **a–d** are a ten-year moving average.

Table 1 | Seven selected climate models assessed in the IPCC AR4 that resolved the contemporary relationship between SST variability in the eastern equatorial Pacific and air temperature/precipitation in northwestern Costa Rica.

Climate model	SRES A2 projections			
	Precipitation trend (annual) (mm yr ⁻¹ per decade)	Precipitation trend (end of rainy season; mm per month per decade)	Air temperature trend (°C per nesting season per decade)	Amplitude of ENSO variability
CNRM-CM3	No change	+3.46	+0.31	Increases
CSIRO-Mk3.5	–59.44	–10.12	+0.36	Decreases
GFDL-CM2.0	No change	No change	+0.25	Increases
GFDL-CM2.1	–26.57	No change	+0.18	Decreases
INM-CM3.0	No change	No change	+0.24	Decreases
MIROC 3.2 (medres)	–39.09	No change	+0.24	Decreases
UKMO-Had CM3	–55.93	–11.04	+0.24	Increases
Mean	–25.37	–2.83	+0.26	Decreases

Trends are calculated from 1975 to 2100 (historical and SRES A2) and only statistically significant ($P < 0.05$) trends are shown for precipitation and air temperature. Changes in the amplitude of ENSO variability are based on the amplitude of SST variability trends in the eastern equatorial Pacific from 1975 to 2100. CNRM-CM3, Center for National Weather Research Climate Model 3; CSIRO-Mk3.5, Commonwealth Scientific and Industrial Research Organization Mk3.5; GFDL-CM2.0, Geophysical Fluid Dynamics Laboratory Climate Model 2.0; GFDL-CM2.1, Geophysical Fluid Dynamics Laboratory Climate Model 2.1; INM-CM3.0, Institute for Numerical Mathematics Climate Model 3.0; MIROC 3.2, Model for Interdisciplinary Research On Climate 3.2 (medium resolution); UKMO-Had CM3, Hadley Centre for Climate Prediction UK, Met Office Climate Model 3.

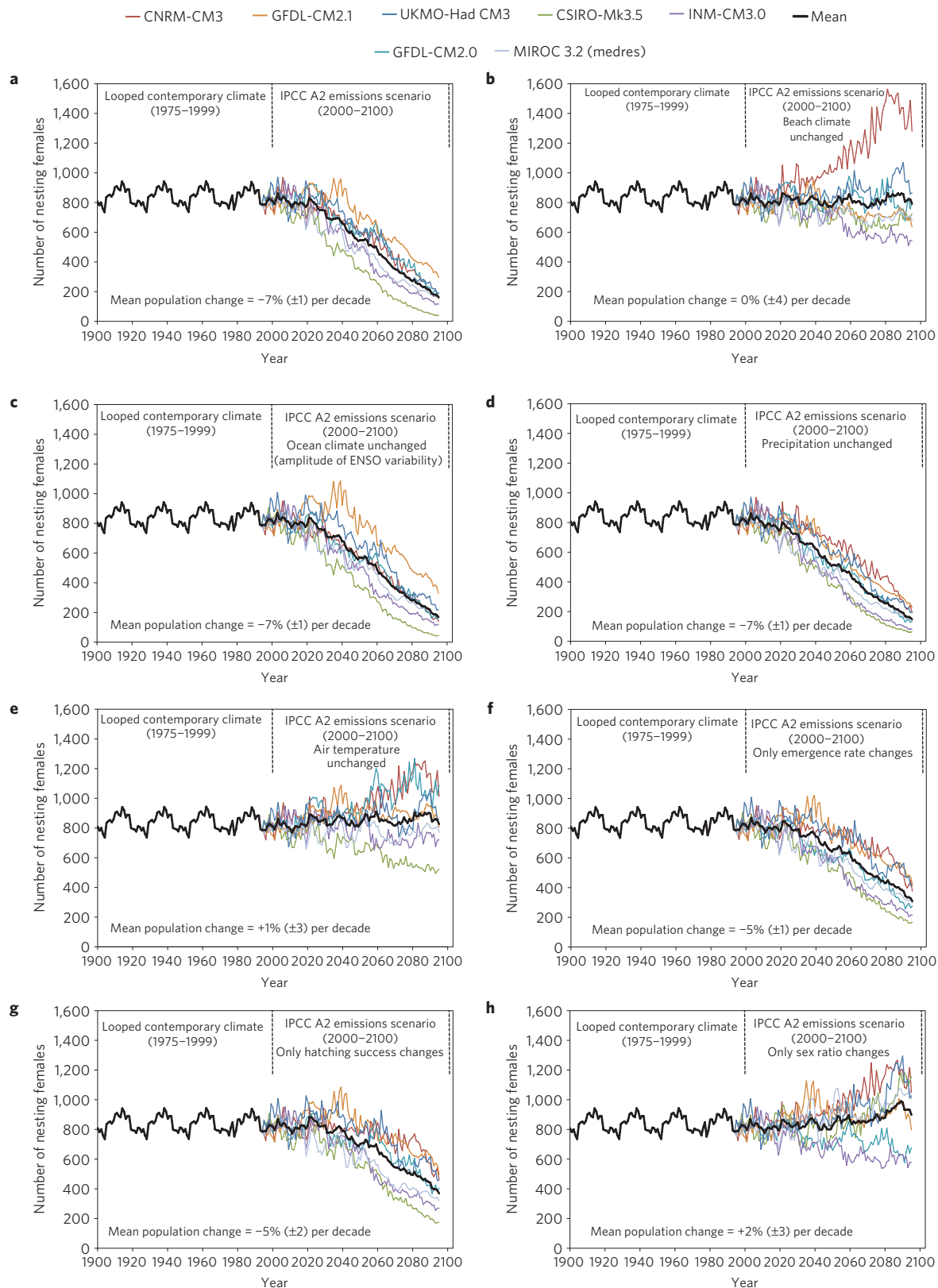


Figure 2 | Nesting population projections under the IPCC SRES A2. a–h, CLIMPOP projections of annual numbers of nesting female leatherbacks at Playa Grande, Costa Rica, during SRES A2 (among seven climate models) when considering eight different scenarios of the impacts of beach versus ocean climate change. The looped observed contemporary climate (1976–1999) forces the population model before the year 2000 when the SRES A2 scenario begins. The nesting population is initialized with 1,000 nesting females (Supplementary Methods). Change in the ocean climate (detrended SST anomalies) is a function of the amplitude of ENSO variability. Change in the beach climate (air temperature and precipitation) is a function of both the mean and variability. All time series are a ten-year moving average.

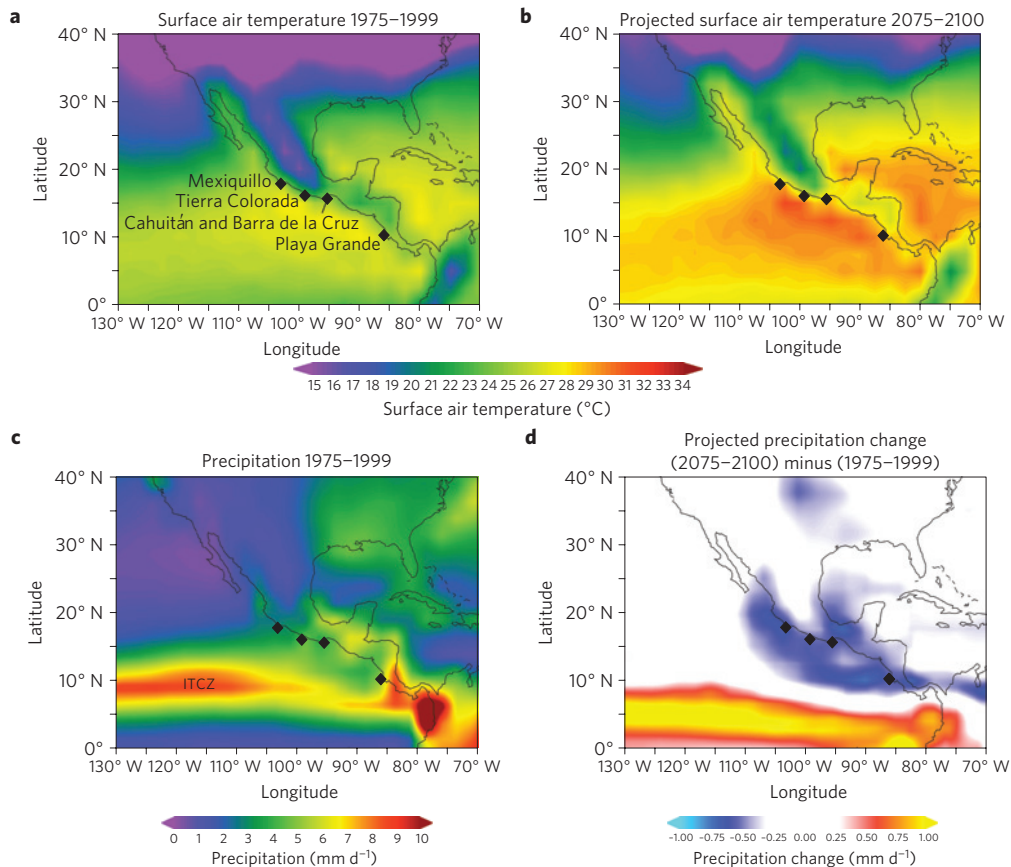


Figure 3 | Surface air temperature and precipitation projections under the IPCC SRES A2 in the area encompassing the four main leatherback nesting sites in the eastern Pacific. **a**, Mean surface air temperature from 1975 to 1999 from the National Centers for Environmental Prediction (NCEP)/National Center for Atmospheric Research (NCAR) reanalysis 1 (uses assimilated observed data; ref. 29). **b**, Projected surface air temperature from 2075–2100 based on the ensemble mean projected change applied to the NCEP/NCAR reanalysis. **c**, Mean precipitation from 1975 to 1999 from the Global Precipitation Climatology Project (GPCP) version 2.2 (combines land observations and satellite data; ref. 30). **d**, Mean precipitation change between the GPCP data from 1975 to 1999 (in **c**) and the seven climate model projections from 2075 to 2100 under IPCC SRES A2. Projections of air temperature and precipitation are based on the seven climate models used to force CLIMPOP (Table 1). The four nesting sites are indicated with black diamonds.

CLIMPOP (Table 1; Fig. 1b–d; Supplementary Fig. S1). These seven models provided a range of projections of the trend and amplitude of ENSO variability over the twenty-first century (Table 1 and Fig. 1b). All seven models projected an increase in air temperature during the nesting season and six projected either a decrease or no change in precipitation in the second half of the rainy season (August–December; Table 1 and Fig. 1c,d).

Relative to the stable nesting population forced by the looped contemporary climate up to the year 1999, we estimated that the nesting population at Playa Grande will decline at rate of 7% per decade over the next century of climate change under the *Special Report on Emissions Scenarios* (SRES) A2 scenario (Fig. 2a). This decline rate was based on the ensemble mean, but similar declines also occurred for each ensemble member. The nesting population remains stable up until ~2030 but is reduced 75% by the year 2100. Comparison of projections after removing climate change trends in beach conditions (that is, constant mean and variability of air temperature and precipitation; Fig. 2b) against those without climate change trends in ocean conditions (that is, constant amplitude of ENSO variability; Fig. 2c) identified beach conditions as the primary driver of the population decline. Sensitivity to projected changes in ENSO was relatively small, though an increase/decrease in the amplitude of ENSO variability did augment the population by ~+3%/–1% per decade (Supplementary Fig. S2). Within the nesting beach, comparison of projections after removing climate change trends in

precipitation (Fig. 2d) against those without climate change trends in air temperature (Fig. 2e) identified increasing air temperature as the primary driver of the population decline. Comparison of projections including climate change trends in only emergence rate (Fig. 2f) against those with climate change trends in only hatching success (Fig. 2g) or sex ratios (Fig. 2h) revealed that increasing air temperature drives the decline in the nesting population through its negative influence on both emergence rate and hatching success. Long-term trends in sex ratio towards a higher proportion of female hatchlings (mean increases ~2%, from 91% to 93%) in slightly drier annual conditions (Table 1) tended to increase the nesting population by a very small amount (Fig. 2h), but not enough to offset declines in hatching success and emergence rate.

Synergistic effects of reduced hatching success and emergence rate and the small increase in female bias among hatchlings caused a decline in male hatchling recruitment rate that was twice the decline rate of female recruitment (Supplementary Fig. S3a,b). Consequently, the decline in adult male turtles was also higher than the decline of adult females (Supplementary Fig. S3c,d). Males from other species of sea turtle return to waters adjacent to nesting beaches (to breed) nearly three times more often than females¹⁸. It is uncertain whether the propensity of males for more frequent returns to nesting beaches is enough to maintain breeding rates despite a reduced male population.

Results of our analysis suggest a potential marked decline in the eastern Pacific leatherback population that nests in Costa Rica,

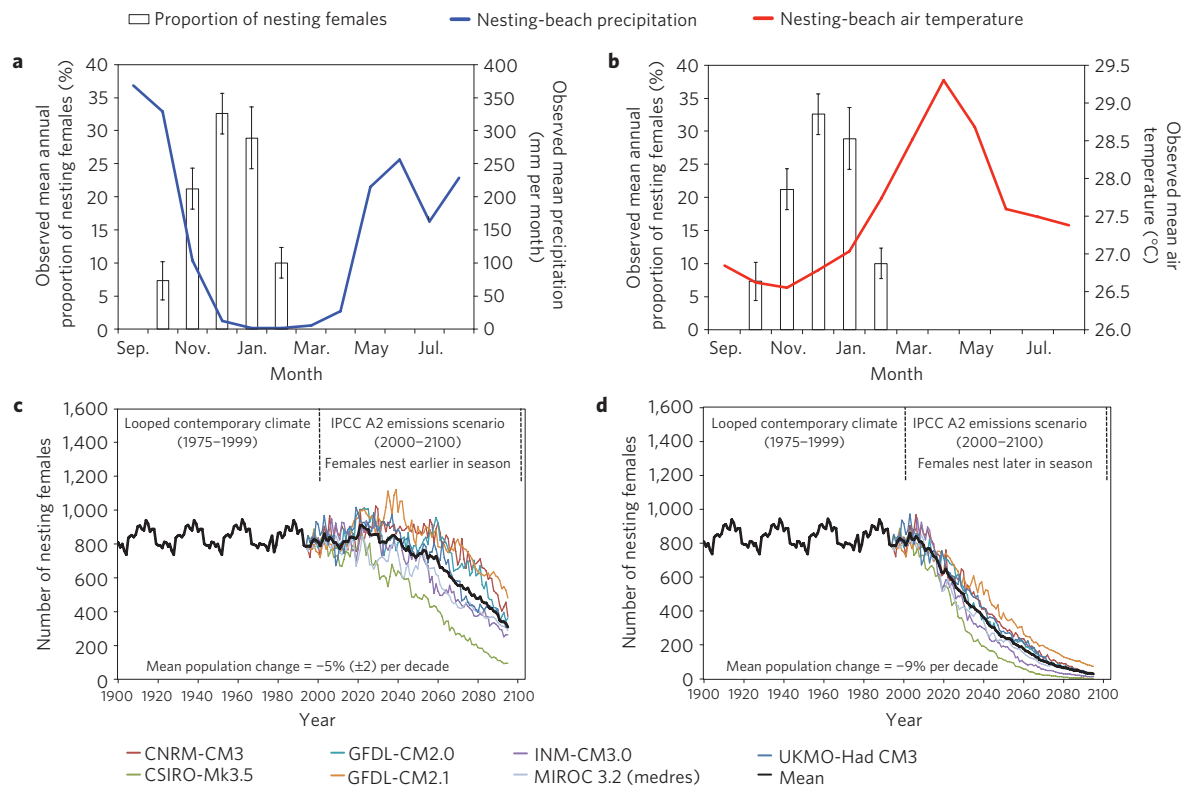


Figure 4 | Nesting phenology of leatherbacks in relation to the local climate at Playa Grande, Costa Rica. **a,b**, Observed mean annual proportion (\pm standard deviation) of nesting females during each month of the nesting season (October–February) compared with observed mean monthly precipitation at Playa Grande from 1975 to 1999 (from local airport; Supplementary Methods) (**a**) and observed mean monthly air temperature at Playa Grande from 1975 to 1999 (from local airport; Supplementary Methods) (**b**). **c,d**, CLIMPOP projections of annual numbers of nesting female leatherbacks at Playa Grande, Costa Rica, during SRES A2 (among seven climate models) when considering that the turtles exclusively nest in the earlier portion of the nesting season (**c**) and the later portion of the nesting season after the year 1999 (**d**).

primarily driven by declining hatching success and emergence rate owing to increasing air temperature. Increases/decreases in the amplitude of ENSO variability had a positive/negative effect, but the impact was relatively small over the ensemble considered. A limitation of the assessed ocean impact in CLIMPOP is that the ocean affects the turtle population only through ENSO-driven modulations of large phytoplankton primary productivity. Empirical data on nesting returns³ and overall dominance of ENSO in the climate of the region^{4,10} support this as a viable starting point, but more holistic treatment of the impacts of climate change on leatherback bioenergetics, foraging and thermoregulation during the ocean phase may reveal additional ocean effects. For example, adult leatherbacks are typically bound by the 15°C SST isotherm¹⁹ whereas juveniles ($<100\text{ cm}$ in length) may be bound by the 26°C SST isotherm²⁰ and thus a warming ocean may expand the eastern Pacific population's latitudinal range (south of 40°S ; ref. 21) rendering new foraging areas accessible. However, any additional unresolved ocean effects may not alter the strong negative influence of increasing air temperature on hatching success and emergence rate.

Long generation time of leatherbacks may prevent them from adapting through evolution to rapid climate change, though plastic responses may compensate²² (that is, active change of nesting beach or nesting season). We examined implications of plastic responses based on contemporary relationships between climate, nesting site location and nesting phenology (Figs 3 and 4).

Major leatherback nesting beaches (>40 nesting females per year) in the eastern Pacific are relatively scarce (Fig. 3a) suggesting that these beaches, local ecosystems and nearshore waters have particularly rare features that led to the establishment of a viable

nesting population through natural selection. Nesting sites are bound between 10°N and 20°N . They all fall within the northeast corner of the Intertropical Convergence Zone (ITCZ) and thus share similarly warm temperatures, moderate annual rainfall and seasonal dynamics (Fig. 3a,c). Adding projected ensemble mean air temperature and precipitation differences to these contemporary values suggests that all nesting beaches are subject to the same regional scale projected warming and drying trends (Fig. 3b,d). Maintaining present air temperature conditions by moving north of 20°N would thus require nesting in starkly drier subtropical regions with markedly different seasonal dynamics. The difference in precipitation between these two regions ($2\text{--}4\text{ mm d}^{-1}$) is far greater than the relatively small 0.5 mm d^{-1} decrease projected by the ensemble mean simulation at Playa Grande. Likewise, maintaining beach temperature conditions by moving south of 10°N towards the centre of the ITCZ would lead to starkly higher and more seasonally persistent precipitation. Although our modelling framework cannot extrapolate over such large climate differences, the extent of these changes in combination with the diversity of additional beach suitability conditions (that is, sand type, currents, predation) make viability of compensation for climate-driven temperature changes through simple latitudinal movement highly uncertain. At Playa Grande and other leatherback beaches in this region, there is no site fidelity in nest-site selection between the water and vegetation and there are no naturally shaded areas². Therefore, there is no opportunity for leatherbacks to nest in cooler portions of the beach.

Another potential plastic response is through nesting phenology (nesting earlier or later in the year). Leatherbacks at Playa Grande nest during the end and just after the rainy season (Fig. 4a) and

during the coolest portion of the year (Fig. 4b). However, the median nesting date at Playa Grande has increased 17 days since the mid-1990s (N. Robinson, unpublished observations). The timescale of this observed change is too short to attribute to climate change and is counterintuitive if leatherbacks are selecting for the cooler portion of the nesting season. The CLIMPOP projections for turtles nesting earlier in the season, when air temperatures are coolest and precipitation is higher, showed a delay in population decline by about 10–15 years (Fig. 4c). If the turtles nest later in the season, the decline begins even sooner (Fig. 4d) owing to warmer temperatures and drier conditions in the later portion of the season. Indeed, observations at Playa Grande show that nesting later in the season results in both low hatching success and emergence rate²³ and an increased probability of nest collapse due to the dry sand.

Our projections suggest that climate change could drive eastern Pacific leatherbacks in Costa Rica to extirpation, even in the absence of fisheries mortality. Our modelling framework was based on empirical relationships between climate and leatherback biology. We assumed that these relationships would remain unchanged throughout this century because intense selection pressure and long generation time will reduce genetic variability on which natural selection works. Additional uncertainty in our projections can arise if these relationships have the ability to change.

Present adult survival rates are unsustainable (Supplementary Methods) and it is apparent that fisheries mortality must be reduced before any population recovery can occur. If mortality in the ocean continues, climate-induced reduction in hatchling recruitment will only exacerbate the impacts of fisheries. The importance of the beach-phase climate response suggests that anthropogenic climate mitigation of leatherback nests in Costa Rica may sustain present-day hatching success, emergence rate and sex ratio, and therefore maintain a sustainable nesting population. Future recovery plans should consider potential climate-mitigation programmes for nests (for example, shading and irrigation)⁷. Artificial shading of leatherback nests in the Caribbean has reduced nest temperatures without compromising hatching success⁸. We caution against widespread action unless observations show long-term declines in hatching success and emergence rate with a changing nesting-beach climate.

Methods

We developed a CLIMPOP (Supplementary Methods) based on almost two decades of empirical data at Parque Nacional Marino Las Baulas (Playa Grande) located on the northwest coast of Costa Rica. The beach component of CLIMPOP estimates hatching success within the nests, hatchling emergence rates from the nests and the sex ratios as a function of the local climate in northwestern Costa Rica. Hatching success and emergence rate of leatherback nests in Playa Grande are strongly associated with both local air temperature during the months of egg incubation (October–February) and precipitation in the second half of the rainy season (August–December)². The sex ratio of nests in Playa Grande is strongly associated with annual precipitation¹. Precipitation may contribute both beneficial wetting and cooling effects to the nest environments at Playa Grande².

The ocean component of the CLIMPOP model estimates the reproductive frequency of eastern Pacific females as a function of annual SST anomalies in the eastern equatorial Pacific and these anomalies serve as a proxy for changes in large phytoplankton and higher-trophic-level productivity^{4,24}. To reconcile the exclusive impacts of climate change on the population, CLIMPOP includes no effects of additional anthropogenic factors including incidental fisheries mortality, egg poaching, or coastal development. We assumed the present climate can sustain the nesting population in the absence of additional anthropogenic factors and calibrated survival rates in the model to give a stable population under climate conditions observed over the last quarter of the twentieth century (Supplementary Methods). Changes to this stable population under climate change then provided a measure of the nature and extent of the climate change sensitivity of eastern Pacific leatherbacks.

Barring rapid changes in ice flow, globally averaged sea-level rise over the twenty-first century is projected to be 0.23–0.51 m (ref. 25) under a relatively high emissions scenario (SRES A2) (ref. 26). Sea-level rise on the west coast of Central America is projected to be less than the global average regardless of ice flow uncertainties²⁶. The primary nesting area at Playa Grande lies on a berm one metre above the mean high-tide line²⁷. Moreover, protected areas extending 125 m inland

from the highest tide line should facilitate gradual beach adjustment to rising sea level. We thus assumed no effect of sea-level rise for this study.

Nesting population model equations. The nesting population dynamics model (CLIMPOP) is a combination of existing nesting-beach models^{1,2} and an expanded version of the leatherback remigration model³ for the leatherback population at Playa Grande, Costa Rica. The CLIMPOP model can be described with the following equations:

$$N_y = M_y + \sum_{i=1}^7 M_{i,y} + R_{2,y} + R_{3,y} + \sum_{i=4}^7 R_{i,y}$$

where N_y = number of nesting females at Playa Grande in year y ; M_y = number of 15-year-old, first-time-nesting females in year y where:

$$M_y = s(n_{y-15})(S^{12})p_y z$$

n_{y-15} = number of female hatchlings that entered the ocean from Playa Grande in year $y-15$ (age of maturity = 15 years; Supplementary Methods):

$$(n_{y-15}) = (N_{y-15})(E_{\text{clutch}})(F_{\text{clutch}})(h_{y-15})(e_{y-15})(r_{y-15})(B_{\text{survival}})$$

E_{clutch} = number of eggs per clutch = 62; F_{clutch} = clutch frequency = 6.6; B_{survival} = survival rate on the beach after emerging from the nest = 0.87 (ref. 2); h_{y-15} = average monthly hatching success for each clutch laid in the nesting season during year $y-15$ as a function of air temperature and precipitation in northwestern Costa Rica²; e_{y-15} = average monthly emergence rate for each clutch laid in the nesting season during year $y-15$ as a function of air temperature and precipitation in northwestern Costa Rica²; r_{y-15} = average proportion female for each clutch laid in the nesting season during year $y-15$ as a function of annual precipitation in northwestern Costa Rica¹; S = annual survival after age three = 0.90; s = survival from hatchling (after entering the ocean) to age three = 0.0195. The value for s is calculated assuming the annual survival S of leatherbacks older than three years is 0.90 and that the population remains stable in a looped contemporary climate (see below); p_y = the probability a mature female will nest in year y based on the prior year's ENSO phase as indicated by SST in the eastern equatorial Pacific³:

$$p_y = \frac{\exp[\beta_0 + \beta_1(\text{SST}_y)]}{1 + \exp[\beta_0 + \beta_1(\text{SST}_y)]}$$

SST_y = SST (detrended) averaged in the eastern equatorial Pacific (2.5° N to 2.5° S, 125° W to 85° W) from September of year y to September of year $y-1$; $\beta_0 = 11.219$, $\beta_1 = -0.540$, $z = 2.599$ and these parameters were based on the remigration model³ fit to observed remigration data at Playa Grande from 1995 to 2009 using SST_y from the Hadley Centre from 1994 to 2010. The factor z is based on a bioenergetics study²⁸ suggesting that the foraging rate required for females to nest again decreases when a female has had more than two years to recover since last nesting. Essentially, the probability that nesting females will remigrate to Playa Grande after only two years does not get an enhancement term z because the required foraging rate to do so is significantly greater than the foraging rate required to nest in \geq three years^{3,28} (see below descriptions for R). This same principal was applied to first-time nesting females (M) such that the probability of nesting within seven years of reaching sexual maturity (age 15) is never penalized because they have not nested previously.

$M_{i,y}$ = number of 15 + i years old first-time nesting females in year y that did not nest in year $y-i$ where i is between one and seven years and:

$$M_{i,y} = s(n_{y-(15+i)})(S^{(12+i)})p_y z \prod_{j=1}^i (1 - (p_{y-j}z))$$

Consistent with the seven-year maximum remigration interval at Playa Grande (99% of all observations)³, we assumed that if newly mature females do not nest after seven years of reaching sexual maturity (by age 22), they have a very low probability of nesting at all and thus we assumed a zero probability.

$R_{2,y}$ = number of remigrant nesting turtles in year y that have not nested since year $y-2$:

$$R_{2,y} = (N_{y-2})(S^2)p_y$$

$R_{3,y}$ = number of remigrant nesting turtles in year y that have not nested since year $y-3$

$$R_{3,y} = (N_{y-3})(S^3)(1 - p_{y-1})p_y z$$

$R_{i,y}$ = number of remigrant nesting turtles in year y that have not nested since year $y-i$ where i is between four and seven years and:

$$R_{i,y} = (N_{y-i})(S^i)p_y z (1 - p_{y-(i-2)}) \prod_{j=1}^{i-3} (1 - (p_{y-j}z))$$

Consistent with observed data at Playa Grande³, we assumed that females remigrate within two to seven years after nesting.

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Author contributions

V.S. formulated the hypotheses, experiments, CLIMPOP model and conducted the simulations and analyses. C.S. assisted with the CLIMPOP model formulation, simulations, and analyses. P.S.T. led the nesting-beach field study in Costa Rica and formulated the hatchling recruitment component of the nesting-beach model. J.S. and F.P. also led the field campaign in Costa Rica. V.S. and C.S. wrote the manuscript and all authors discussed the analyses and manuscript text.

Additional information

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