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RESEARCH ARTICLE

Short-term resilience to climate-induced temperature increases for equatorial sea turtle populations

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Abstract

Projection models are being increasingly used to manage threatened taxa by estimating their responses to climate change. Sea turtles are particularly susceptible to climate change as they have temperature-dependent sex determination and increased sand temperatures on nesting beaches could result in the 'feminisation' of hatchling sex ratios for some populations. This study modelled likely long-term trends in sand temperatures and hatchling sex ratios at an equatorial nesting site for endangered green turtles (*Chelonia mydas*) and critically endangered hawksbill turtles (*Eretmochelys imbricata*). A total of 1078 days of sand temperature data were collected from 28 logger deployments at nest depth between 2018 and 2022 in Papua New Guinea (PNG). Long-term trends in sand temperature were generated from a model using air temperature as an environmental proxy. The influence of rainfall and seasonal variation on sand temperature was also investigated. Between 1960 and 2019, we estimated that sand temperature increased by ~0.6°C and the average hatchling sex ratio was relatively balanced (46.2% female, SD = 10.7). No trends were observed in historical rainfall anomalies and projections indicated no further changes to rainfall until 2100. Therefore, the sex ratio models were unlikely to be influenced by changing rainfall patterns. A relatively balanced sex ratio such as this is starkly different to the extremely female-skewed hatchling sex ratio (>99% female) reported for another Coral Sea nesting site, Raine Island (~850 km West). This PNG nesting site is likely rare in the global context, as it is less threatened by climate-induced feminisation. Although there is no current need for 'cooling' interventions, the mean projected sex ratios for 2020–2100 were estimated 76%–87% female, so future interventions may be required to increase male production. Our use of long-term sand temperature and rainfall trends has advanced our understanding of climate change impacts on sea turtles.

KEYWORDS
AT, climate modelling, endangered species, ENSO, forecast, marine turtles, precipitation

1 | INTRODUCTION

The onset of rapid climate change around the world has triggered a response by wildlife managers to protect and conserve those species that are most threatened by a changing climate and increasingly extreme weather events (Gatto et al., 2023; Samways et al., 2020). Yet, it remains unknown how well most species will overcome or adapt to human-induced climate change (Poloczanska et al., 2016), especially as future conditions move beyond the envelope they experienced historically (Steinthorsdottir et al., 2021). Many reptiles, including sea turtles, may be particularly susceptible to climate warming because they have temperature-dependent sex determination (TSD), with their sex determined by the incubation temperature during a thermal sensitive period (TSP) in the middle of embryonic development (reviewed in Wibbels, 2003). For most populations of sea turtles, the pivotal temperature (PT; i.e. where the theoretical hatchling sex ratio is 1:1) is typically around 29°C (Mrosovsky & Pieau, 1991; Wibbels, 2003). At nesting sites around the world, female-biased hatchling sex ratios tend to dominate (Hays et al., 2014) and extreme feminisation is rare (Santidrián Tomillo, 2022). Despite this, there are grave concerns that climate warming will cause extreme feminisation for more populations and ultimately population decreases due to a lack of males (Hays et al., 2023; Schoeman et al., 2014).

There has been long-standing interest in assessing the likely changes in incubation conditions on sea turtle nesting beaches because of climate warming and hence likely changes in hatchling sex ratios (Hawkes et al., 2007; Hays et al., 2003; Laloë et al., 2014). Work in this area is largely built around a well-established methodological approach using tight relationships between environmental proxies (e.g. air temperature [AT], or sea surface temperature [SST]) and sand temperatures at nest depth (Fuentes et al., 2009; Hays et al., 2003). Therefore, the historical measurements of those proxies, as well as future projections, can then be used to estimate past and future sand temperatures over a timescale of several decades or even a century or more. One of the caveats of this widely used approach is that the envelope of conditions used to develop the relationship between sand temperature and AT or SST might change in the future. For example, focus has recently turned to the role of heavy rainfall in lowering sand temperatures and promoting greater male hatchling production (Laloë et al., 2020; Staines et al., 2020). However, projections of rainfall patterns are rarely considered in climate forecasts for sea turtle sex ratios (but see Saba et al., 2012; Santidrián Tomillo et al., 2020).

Here, an important advance is made by considering not only established environmental proxies, such as AT to project likely future sea turtle nest temperatures, but additionally consider the influence of changes in rainfall and intra-beach thermal variation in our estimates of hatchling sex ratios. In this way, we show how multiple lines of evidence can be used to establish the likely resilience of nesting populations to climate warming with respect to the feminisation of hatchling sex ratios. Hence, this paper establishes an approach for identifying those sea turtle nesting sites where feminisation is likely to be greatest (e.g. close to the equator) to isolate where management intervention might be needed to ensure the adequate production of male hatchlings. Modelling hatchling sex ratio trends will aid conservation managers by either avoiding unnecessary mitigations on nesting beaches (Santidrián Tomillo et al., 2021) or conversely, it may trigger a preventative management approach (e.g. relocation, irrigation or shading) where complete feminisation seems imminent (Esteban et al., 2018; Gatto et al., 2023).

2 | MATERIALS AND METHODS

2.1 | Study site

The Conflict Island group (10.777° S, 151.817° E) in the Coral Sea comprises 21 coral sand islands, and is located approximately 500 km East of Port Moresby, in the Milne Bay Province of Papua New Guinea (PNG; Figure 1). The islands are heavily shaded by dense tropical forests of coconut palms (*Cocos nucifera*), casuarina trees (*Casuarina equisetifolia*) and coastal pandanus (*Pandanus tectorius*). Due to rising sea level and loss of available beach, very few nesting areas are completely exposed to direct sunlight. Between 2017 and 2022, there have been annual nesting numbers of 50–670 endangered green turtles (*Chelonia mydas*) and 25–40 critically endangered hawksbill turtles (*Eretmochelys imbricata*) that return to nest on the islands within the Conflict Island Group (Mortimer et al., 2008; Seminoff, 2004; Versace et al., 2022). Both species typically nest between November and February, with only ~10 hawksbill turtle nesting events documented outside of the typical nesting season each year (Versace et al., 2022). The Conflict Island Group and surrounding islands of Milne Bay may be regionally important as they are thought to support the largest nesting populations of hawksbill and green turtles in PNG (Kinch, 2020). However, precise long-term data on nesting numbers for Milne Bay and other areas of PNG are lacking.

Since the establishment of annual turtle monitoring by the Conflict Islands Conservation Initiative in 2017, most clutches laid on Panasesa, Irai and Tupit Island have been relocated to shaded hatcheries on the south-east side of Panasesa Island (18 m above sea level; Versace et al., 2022). These hatcheries are shaded with coconut palm fronds to best replicate the natural nest environment of the islands. The primary purpose of the hatcheries is to protect the incubating eggs from monitor lizards (*Varanus* sp.), erosion and the harvesting of eggs (Versace et al., 2022). There is also a community-supported ban on the harvesting of sea turtles and their eggs from the Conflict Island Group (Versace et al., 2022).

2.2 | Sand temperature data collection

Sand temperature data for the Conflict Islands were collected during three time periods: (1) January–December 2018, (2) November 2019–October 2020 and (3) September 2021–August 2022. For

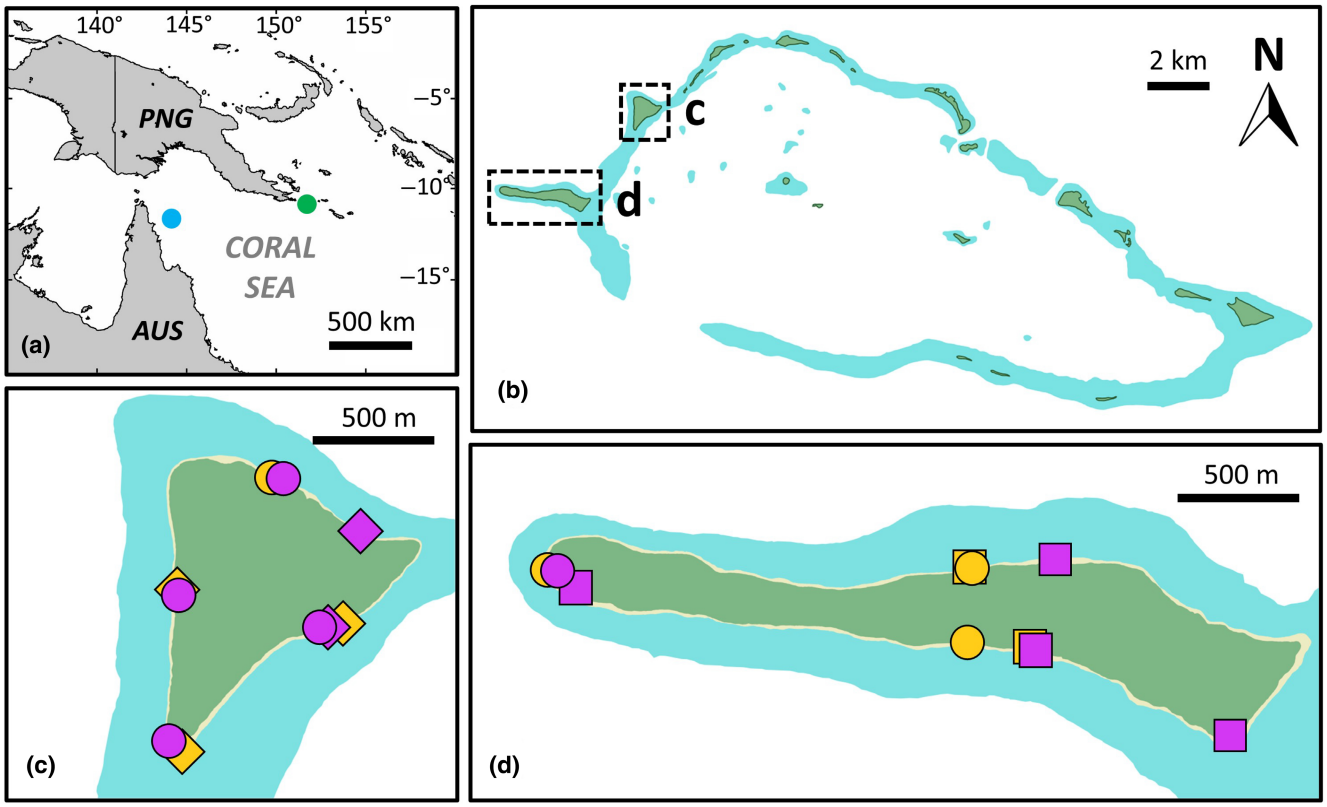

FIGURE 1 (a) Map of the Coral Sea with the locations of the Conflict Islands Group (green), Papua New Guinea (PNG) and Raine Island (blue), Australia (AUS). (b) The locations of the two study islands within the Conflict Island Group are highlighted in dashed boxes: (c) Panasesa Island and (d) Irai Island. (c-d) A total of 28 data loggers were used to record sand temperature over the 2018 (square), 2019–2020 (circle) and 2021–2022 (diamond) survey periods, in both shaded (purple) and unshaded (orange) sites. (b–d) The locations of shallow reef areas (blue), open sand (beige) and tree coverage (green). Map (a) was adapted from the seaturtle.org Map Tool using the Equidistant Cylindrical Projection. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

period (1), sand temperature data were collected using iButton® data loggers (DS1921G, resolution = 0.5°C; Maxim Integrated) enclosed in a rubber balloon (for waterproofing) and buried at 45 cm depth (i.e. typical hawksbill turtle nest depth) at 16 sites on Irai Island. Of the 16 sites, sand temperature data from seven shaded and four unshaded sites were recovered ($n = 11$). Each data logger was programmed to record sand temperature every 4 h. For period (2), sand temperature data were recovered from 12 of the 16 sites across the two islands, Panasesa ($n = 7$) and Irai ($n = 5$) in shaded ($n = 5$) and unshaded sites ($n = 7$) using iButton® data loggers (DS1922L, resolution = 0.0625°C) in rubber balloons. For period (3), sand temperature data were recovered at five of the eight deployment sites across Panasesa Island, in both shaded ($n = 2$) and unshaded sites ($n = 3$) using TinyTag® Plus 2 model data loggers (TGP-4017, resolution = 0.01°C; Gemini Data Loggers Ltd.). The data loggers used in the deployments for periods (2) and (3) were programmed to record sand temperature every 6 h and were buried at 60 cm in depth (typical green turtle nest depth). The dataset used in the analyses of this study amounted to 1078 days of temperature data collected from 28 data loggers in locations on the north, east, south and western sides of both Panasesa and Irai Island (Figure 1b–d). Previous research has shown that the accuracy and precision of these different logger types are closely comparable (Staines, Booth, et al., 2022).

2.3 | Hindcasted and projected sand temperatures and sex ratios

Historical mean AT data from 1960 to 2021 were extracted from the International Comprehensive Ocean–Atmosphere Dataset (ICOADS) through the National Center for Atmospheric Research (NCAR) data portal (http://rda.ucar.edu/datasets/ds548.1; NCEI et al., 2016). We identified the 2 × 2° geographical area (10–12°S and 151–153°E) that included the Conflict Island Group and downloaded data from the Enhanced ICOADS Mean Monthly Summary Release 3. Missing data from the ICOADs monthly mean dataset were not interpolated, and only the monthly means for November–March (i.e. when both species have nests incubating in the sand) were included. A stepwise multiple regression was used to select the most appropriate model for the relationships between sand temperature and the predictor variables (i.e. AT, shading, depth and year).

Projected near-surface AT anomalies for November–March (when nests are incubating) were obtained through the Koninklijk Nederlands Meteorologisch Instituut (KNMI) Climate Change Atlas data portal (climexp.knmi.nl/plot_atlas_form.py). The three climate scenarios used in this study were the Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathways (RCPs); these included RCP2.6, RCP4.5 and RCP8.5 (atmospheric

CO_2 concentrations of 420, 600 and 1130 ppm respectively by the year 2100; Arias et al., 2021). The projected AT anomalies stem from a combined multi-model ensemble (MME) simulation of 43 model experiments (Table S1) from the Coupled Model Intercomparison Project (CMIP5) in the IPCC fifth assessment report. Currently, most non-climate scientists have limited access to regionally-specific time series MME products from the more recent CMIP6. However, various studies have reported on the highly comparable outputs on the simulated temperature and rainfall anomalies from the CMIP5 and CMIP6, with CMIP6 products overall having marginally less variation in rainfall anomaly projections (Deng et al., 2021; Zhu & Yang, 2021). Therefore, in this study, CMIP5 products were used over CMIP6 due to the greater accessibility to region-specific data through the KNMI data portal. The historical AT data from the Climatic Research Unit (CRU) Time-Series (TS) dataset, version 4.06 (Harris et al., 2022; crudata.uea.ac.uk/) were used as reference data for the CMIP5 model experiments. Modelled AT from 2022 to 2100 was extracted for the same 2×2° geographical area used for extracting the ICOADS data. The 'delta' approach was used to bias-correct the mean value of the model output by adding the AT anomalies relative to the historic mean AT from 1997 to 2017 to the predicted AT values.

There was within-beach variability in sand temperature that was not explained by AT alone. From the empirical relationship between sand and AT, we assessed the extent of this unexplained variability and then added it as a predictive interval to our projections of the mean sand temperature across years. In this way, we considered the likely future mean sand temperature but also the likely variation across the beach between relatively warm and relatively cool sites.

For visualisation purposes, the interannual variability observed in the long-term historical temperature records (1960–2021) was measured and added as random interannual variability to the future sand temperature projections. Random variability was used in model visualisations to represent just one possible future scenario among many possible scenarios, however, the results presented in the main text will be from the means of the model output.

To estimate hatchling sex ratios, values for metabolic heating (MH) were added to the hindcasted and projected sand temperatures, to estimate nest temperature. We used values of MH equal to 0.5°C (conservative) and 1.1°C (moderate) to capture the likely variations in MH during the sex determination period (Gammon et al., 2020; Laloë et al., 2014; Patrício et al., 2017). The moderate MH estimate was the calculated average from the reported MH temperatures for green turtles during the middle-third of embryonic development reviewed in Gammon et al. (2020). Using the modelled nest temperatures, we estimated the primary hatchling sex ratio of both species for each nesting season using a standardised logistic model described by Hays et al. (2017), which assumes a PT = 29.1°C and a transitional range in temperatures (TRT) = 26–32°C. The formula used to estimate the proportion of female hatchlings (Y) produced at a given temperature (T) is as follows: $Y = 1 / \left(1 + e^{(-1.3\times(T-29.1))}\right)$.

The resulting estimates of hatchling sex ratios were then reported and 'graded' into one of three ranges; 'balanced' was used to describe sex ratio estimates between 40% and 60% female, 'moderate female bias' for estimates between 60% and 85% female and 'extreme female bias' for estimates between 85% and 100% female. Given the uncertainties with hatchling sex ratio predictions, there is merit in reporting ratios in this type of grading system, instead of reporting and discussing the discrete values. The results and visualisations of hatchling sex ratio used only the projected sand temperatures under RCP4.5 as this scenario is the most probable outcome dictated by the IPCC (Hausfather & Peters, 2020).

2.4 | Historical and projected rainfall

Historical mean daily rainfall values for the Conflict Islands region during the nesting season (November–March) were also extracted from the KNMI Climate Change Atlas data portal. The source data were subsetted from the CRU TS dataset, version 4.06 (Harris et al., 2022). The three meteorological stations that have contributed to this dataset have been inactive since 1997, so only observations from 1960 to 1996 could be included in our investigation. The two closest stations were located 115 km east and north-west of Panasesa Island, respectively, and the third was located 155 km north-west.

Using a 30-year reference period (1967-1996) of observed rainfall, daily rainfall during the nesting season from 2021 to 2099 was projected under the IPCC climate change scenarios RCP2.6, RCP 4.5 and RCP8.0 with a modelled mean from 43 different models (Table S1). For visualisation purposes, interannual variation in the observed historical rainfall (1960–1996) was measured and added as random interannual variability to the projected rainfall anomalies. The results presented in the main text will be from the means of the model output, but the model visualisations represent just one possible future scenario among many possible scenarios.

3 | RESULTS

3.1 | Hindcasted and projected sand temperatures

We found that 62% of the variability in sand temperature was best explained by AT ($R^2 = .62$, AIC = −151.29, $p < .01$). The addition of other terms such as shading, depth and year only explained a further 2% of the variance ($R^2 = .64$, AIC = −168.41, $p < .01$; Figure 2a; Table 1) and so the more parsimonious model, which included only AT as the predictor variable was used to model sand temperature. The strength of the AT versus sand temperature relationship was evident in the observed versus predicted sand temperature profiles across the 3 years of data collection (Figure 2b). The mean difference between the predicted and observed mean monthly sand temperatures was 0.33°C and the absolute difference was examined (i.e. the modulus of the difference each month) was 0.55°C ($n = 36$ months). Therefore, the predicted and observed mean monthly sand temperatures were similar.

There was interannual variability in historic sand temperatures in addition to a long-term trend. For example, between 1960 and 2019

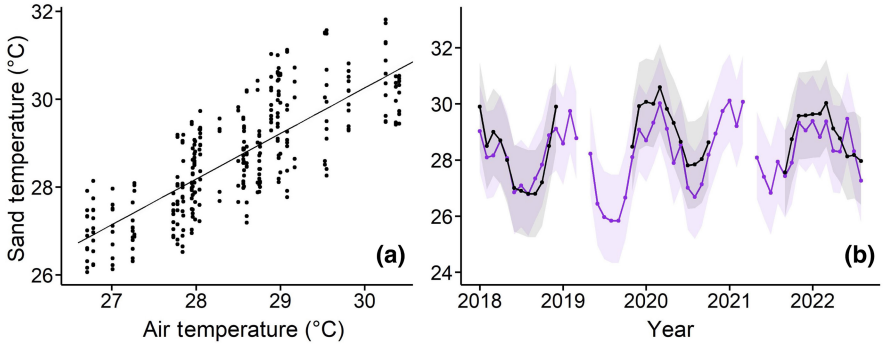

FIGURE 2 (a) Relationships between sand temperatures recorded at 45 and 60 cm depth and mean monthly air temperature. A single point represents the monthly mean sand temperature recorded by one data logger ($n = 28$) for each month of the 2018, 2019–2020 and 2021–2022 data collection periods. (b) The observed monthly mean sand temperature (black) and the mean monthly sand temperature predicted by the linear model (purple) using regional monthly mean air temperature data for the Conflict Island Group, Papua New Guinea. A single point represents the mean monthly sand temperature from January 2018 to August 2022. Grey shaded regions represent the 95% confidence limits calculated from the standard deviation of mean daily temperature values from the data loggers. Purple shaded regions represent the 95% predicitive interval from the relationship in panel (a), i.e., shaded region represents the likely variation in sand temperature across the beach.

TABLE 1 Comparison of four models to describe sand temperature across two islands over the three data collection periods (2018, 2019–2020 and 2021–2022) in the Conflict Islands, Papua New Guinea. Model predictors include AT, air temperature, and categorical covariates; D, depth of the logger; S, shading (unshaded/shaded); Y, year. The model with the best fit based on R^2 value and the Akaike's information criterion (AIC) value is in bold.

Model predictors	R^2	AIC	p	Equation
AT[a]	.618	−151.29	<.01	−0.73 + (1.03 × AT)
AT + S	.625	−155.75	<.01	−0.14 + (1.02 × AT) + (−0.22 × S)
AT + S + D	.632	−159.95	<.01	−0.94 + (1.08 × AT) + (−0.27 × S) + (−0.02 × D)
AT + S + D + Y	**.644**	**−168.41**	**<.01**	**−398.93 + (1.11 × AT) + (−0.27 × S) + (−0.04 × D) + (0.20 × Y)**

[a]Used as the final model.

there was a linear increase in the mean sand temperature during the nesting season of 0.1°C per decade, that is, an increase of 0.6°C in sand temperature over 60 years (Figure 3a). Superimposed on this trend, the SD of the residual variation in sand temperature was 0.29°C, reflecting warmer and cooler years. Over the more recent 20-year period (2000–2019), mean sand temperatures during the nesting season was 28.7°C (SD = 0.3°C), and the 2020 season had the highest mean temperature recorded across the time series at 29.6°C (Figure 3a).

The projected sand temperatures for the region using the RCP 2.6 scenario (most stringent pathway of carbon emissions) showed that sand temperatures would remain around 29°C to 2100 (Figure 3a). Under an intermediate climate scenario for global carbon emissions (RCP 4.5), the projection showed that mean sand temperatures would approach 30°C by 2100 (Figure 3a). The worst-case scenario (RCP 8.5) would see mean sand temperatures during the nesting season approach 31.5°C by 2100 (Figure 3a). While the IPCC projects likely trends in AT given various scenarios, there may still be both warmer and cooler than average years. We used the SD of the residual variation in AT between 1960 and 2022 to randomly assign a value for the future interannual variability in AT from the long-term predicted mean, simply to visually show the extent of this interannual variability in possible future temperatures.

Importantly, in both our hindcasts and projections of sand temperature, we build in the variability in sand temperatures across the beach, that is, the residual variation not explained by AT alone. The SD of the residual variation was 0.79°C and was used to generate the predictive limits (±1.55°C) around the long-term models. Therefore, this analysis shows that even when the mean temperature is at a predominately male- or female-producing temperature, some nests on the beach would still be appreciably cooler or warmer. For example, in 1960 even though the mean temperature on the beach was likely around 27.7°C (i.e. a male-producing temperature), there would still be some nests incubating at 29.3°C and so producing females. Likewise, even in the most extreme climate warming scenario modelled, while the mean sand temperature would be around 31°C, there would still be some nests incubating below 30°C and producing males within the same nesting season.

3.2 | Hindcasted and projected sex ratios

The primary sex ratios for each nesting season were estimated for hindcasted and projected sand temperatures. Over a 60-year period, between 1960 and 2019, the primary sex ratios were estimated

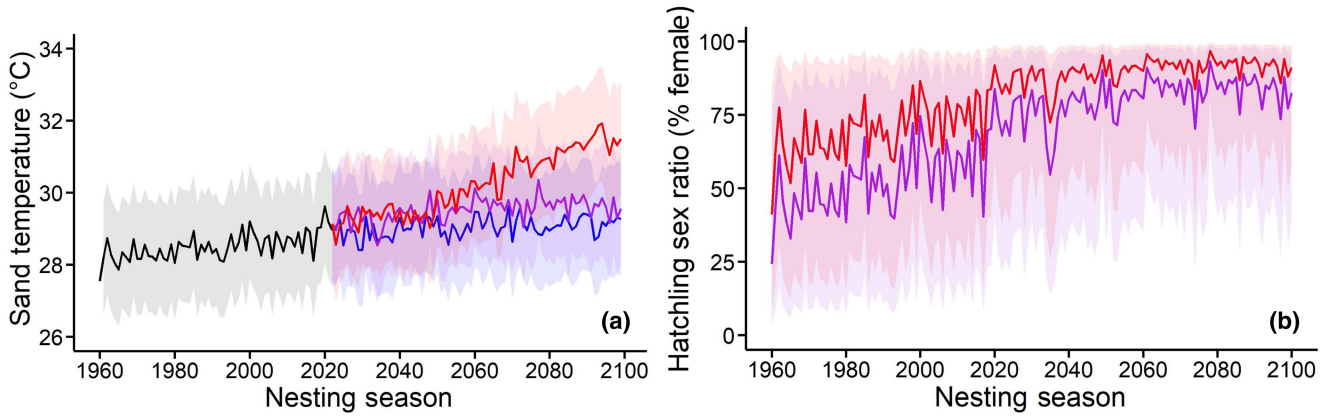

FIGURE 3 (a) Historical mean sand temperatures (at nest depth) for each nesting season from 1960 to 2022 (black line) based on the relationship between mean monthly air temperature and the mean monthly sand temperature recorded on Panasesa and Irai Island (Figure 2). The coloured lines represent the mean model values for sand temperature projections based on three Intergovernmental Panel on Climate Change climate scenarios; Representative Concentration Pathway (RCP) 2.6 (blue), RCP 4.5 (purple) and RCP 8.5 (red). Line traces from 2023 to 2100 represent one possible scenario using random variability among many possible scenarios. The shaded regions around the model represent the 95% predictive limits of the modelled sand temperatures. (b) Estimated mean primary sex ratio (% female hatchlings) of the Conflict Island Group modelled for each nesting season from 1960 to 2100 based on reconstructed and projected sand temperatures (Figure 2a) with two different estimates of metabolic heating; +0.5°C (purple) and +1.1°C (red). Sex ratios were estimated using a generalised pivotal temperature = 29.1°C. Line traces from 1960 to 2022 represent the mean primary sex ratios of each season from reconstructed sand temperatures. Line traces from 2023 to 2100 represent the projected sex ratios (under RCP 4.5) and show one possible scenario using random variability among many possible scenarios. The shaded regions around the model represent the 95% predictive limits of the modelled sex ratios across the 140-year time series.

to have been relatively balanced using a conservative estimate of MH (mean = 46.2% female, SD = 10.7) and had some female bias under a moderate estimate of MH (mean = 64.4% female, SD = 9.8; Figure 3b). Between 2020 and 2099, the primary sex ratios under RCP4.5 were estimated to have moderate female bias under a conservative estimate of MH (mean = 76.3%, SD = 6.6) and highly female-biased under a moderate estimate of MH (mean = 87.4%, SD = 4.1; Figure 3b).

Between 1960 and 2059 with projected sex ratios based on temperatures under RCP4.5, there was a significant increase in the percentage of females produced under both the conservative MH and moderate MH estimates ($R^2 = .76$, $F_{1,98} = 318$, $p < .001$ and $R^2 = .73$, $F_{1,98} = 260.4$, $p < .001$ respectively). Depending on whether 0.5°C or 1.1°C was added as MH, the relative change to the primary sex ratio was estimated to increase by 0.45% and 0.37% female per season (i.e. year) respectively (Figure 3b). Between 2060 and 2099 under RCP4.5, there was still a significant effect of season on the future projected hatchling sex ratios ($R^2 = .59$, $F_{1,38} = 54.2$, $p < .001$ and $R^2 = .59$, $F_{1,38} = 54.4$, $p < .001$ respectively), resulting in relative change to primary sex ratios, estimated to increase by 0.1% and 0.06% per season respectively (Figure 3b).

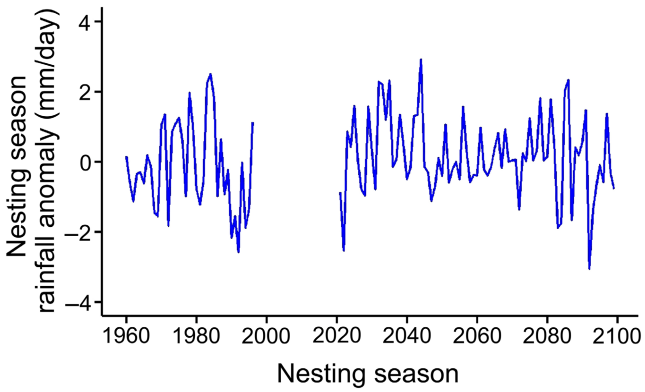

FIGURE 4 The historical mean rainfall anomaly (mm/day) for each nesting season (November–March) from 1960 to 1996 with respect to the mean from a 30-year reference period (1967–1996) for the region of the Conflict Islands. Also shown is the projected mean daily rainfall anomaly (mm/day) for each nesting season from 2021 to 2099, modelled under the Intergovernmental Panel on Climate Change climate change scenario Representative Concentration Pathway 4.5. Line traces from 2021 to 2099 represent one possible scenario using random variability among many possible scenarios. Rainfall data were not recorded between 1997 and 2020 due to weather station closures.

3.3 | Historical and projected rainfall

There was no detectable historical trend in the mean rainfall anomaly (mm/day) for each nesting season from 1960 to 1996 and no significant difference across nesting seasons ($F_{1,35} = 0.28$, $R^2 = .08$, $p = .6$; Figure 4). Observed records of rainfall for the region across those 36 nesting seasons ranged from 1010 to 1858 mm, with a mean of 1395 mm (SD = 216 mm). The linear regression for the projected rainfall anomalies under all three climate scenarios for 2021–2100 similarly demonstrated that rainfall will not be significantly different across the nesting seasons. For example, there were no long-term

changes in rainfall projected for this region under the IPCC climate change scenario RCP 4.5 ($F_{1,77}=0.07$, $R^2=.001$, $p=.79$; Figure 4).

4 | DISCUSSION

Our findings identify the short-term resilience of an equatorial nesting site to climate-induced 'feminisation' and our projections illustrate that both sexes will continue to be produced in the future. It is unknown how common male-producing sites are throughout the Asia-Pacific region, as evidence of male-biased or even balanced sex ratios has been rarely reported globally (e.g. Madden Hof et al., 2023; Patrício et al., 2017; Pilcher et al., 2015). Yet, these male-producing sites may be critical to the survival of future nesting populations both in the Coral Sea and globally. Here we make the step-advance of including (a) consideration of projected rainfall trends in the forecasts for changing hatchling sex ratios and (b) the variation in sand temperature across a beach not explained by environmental proxies. There have been widespread efforts to project the likely impact of climate change on key life-history features of different species such as changes in their geographic range or timing of reproduction (André et al., 2010; Green, 2017; Laloë & Hays, 2023; Lambert et al., 2014; McMahon & Hays, 2006; Pike, 2013). Across various studies, projections will also be improved as more data become available allowing better forecast models and, in some cases, model projections can start to be tested as long ecological time series become available (Edwards et al., 2010). In this regard, by incorporating consideration of impacts of changing rainfall as well as variation in temperatures across beaches, we improved how environmental proxies can be used for estimating past and future sand temperatures and likely impact on sex ratios of sea turtle hatchlings at key nesting beaches.

In corroboration with previous studies (e.g. Fuentes et al., 2009; Laloë et al., 2021), we showed that AT is strongly correlated with sand temperatures at the nest depth on sea turtle nesting beaches. There are likely several reasons for the residual variation on plots of sand temperature explained by environmental proxies. For example, the sand temperature might vary with the aspect of a nesting beach (e.g. north or south-facing; Booth & Freeman, 2006), the colour (albedo) of the sand, which can vary both within and between beaches (Hays et al., 2001), or the extent of natural tree shade (Hays et al., 1995; Reboul et al., 2021; Staines et al., 2019). By positioning temperature loggers across the range of nesting zones on beaches, we attempted to capture this intra-beach thermal variation. This variation was then incorporated into the hindcasts and forecasts of nest temperatures as a predictive limit. This variation is important to try and quantify because even when the mean temperature might only produce female hatchlings, some nests may be cool enough to still produce males. The ecological significance of 'mean conditions' versus the 'range of conditions experienced around that mean' is known to be important with other species in various environments, particularly ectothermic organisms (Davey et al., 1992; Isaak et al., 2017). There is also a substantial interest in improving species distribution models by incorporating the microclimatic conditions of a species' niche and increasing the resolution of the projected distribution (Lembrechts et al., 2019). For sea turtles, it may become increasingly important to identify sites where hatchling sex ratios are extremely female-biased and then triage the protection of the cooler male-producing zones on those nesting beaches (Laloë et al., 2014; Schoeman et al., 2014). Therefore, assessing within-beach thermal variation remains an important priority for sea turtle nesting sites.

Our finding that sex ratios have likely remained relatively balanced for the past 60 years has seldom been reported elsewhere (Patrício et al., 2017). In some places, such as the Arabian Gulf, sand temperatures are expected to exceed the range where male hatchlings would be naturally produced, however, the dominant sex in juvenile cohorts of the hawksbill turtle population is male (Pilcher et al., 2015). Male-producing sand temperatures have also been recently identified for several hawksbill turtle nesting islands in north-east Queensland and Torres Strait, Australia (Madden Hof et al., 2023). More commonly observed is a warming trend in estimated nest temperatures and so estimated hatchling sex ratios become more feminised over time (Jensen et al., 2018; Laloë et al., 2014). Approximately 850 km west of the Conflict Island Group is the largest green turtle rookery in the world, Raine Island in the northern Great Barrier Reef of Australia (Jensen et al., 2018). It is estimated that nest temperatures have been consistently above the PT on Raine Island since the mid-1970s, and as a result, over 99% of hatchlings are female (Jensen et al., 2018). Such extreme sex ratio biases will likely lead to substantial demographic consequences such as reductions in the incidence of multiple paternity within clutches and clutch infertility as males become scarcer (Hays et al., 2023; Jensen et al., 2022). Our conclusions in this study that climate warming is unlikely to lead to extreme feminisation of populations at an equatorial nesting site is important because recent studies have suggested that phenological shifts in nesting are an unlikely avenue by which sea turtles can mitigate rapid climate warming (Almpanidou et al., 2018; Laloë & Hays, 2023; Monsinjon et al., 2019). In essence, as temperature warms, female sea turtles could tend to nest earlier in the season (Mazaris et al., 2009; Weishampel et al., 2004) or change nesting beaches (Carreras et al., 2018; Kamel & Mrosovsky, 2004), but this phenological shift will only partially mitigate climate warming (Laloë & Hays, 2023). Similarly, evidence of inter-clutch variation for PT and TRTs within a population has recently emerged. Porter et al. (2021) showed that from a sample of four green turtle clutches (PT = 28.1°C), one clutch had a much greater propensity to produce males, even producing some males at a typical female-producing incubation temperature. So, there may be limited avenues for turtles to adapt fully to climate warming, prompting concerns that direct intervention may be required at many sites (including the Conflict Islands Group) to promote greater male hatchling production (Gatto et al., 2021; Smith et al., 2021).

A limitation of our study is that there have not been any assessments of the PT of PNG's hawksbill and green turtle populations. We used a species-wide logistical model described by Hays et al. (2017) to estimate the hatchling sex ratios of hawksbill and

green turtles. However, there is some variability in the PT and TRT between populations and species (reviewed in Wibbels, 2003). Clearly, an assessment of the specific PT for the PNG nesting populations would improve hatchling sex ratio estimates. Nevertheless, our key conclusion that male hatchling production will persist in this region is likely robust and non-sensitive to the specific PT used. While global assessments have shown that the majority of nesting sites produce female-biased hatchling ratios, some researchers have suggested that an increase in female production may be an adaptative response to climate change. The argument being that if more females nest annually, this will increase egg production and therefore increase the growth of the future population (Santidrián Tomillo et al., 2015; Santidrián Tomillo & Spotila, 2020). However, this scenario would only be a viable solution if there were enough males present to fertilise all clutches, and populations were not already in decline from more prominent human threats. Indeed, female-skewed hatchling production might be a contributing factor to a stronger population recovery (Mazaris et al., 2017). Furthermore, aspects of the biology of adult males, such as their more frequent breeding, likely mean that female-biased hatchling sex ratios translate into more balanced operational (breeding) sex ratios (Hays et al., 2014, 2022). This view has also been supported by estimates of operational sex ratios made by recent drone surveys in both Greece and Australia (Schofield et al., 2017; Staines, Smith, et al., 2022). Overall, evidence of sea turtle populations that are not threatened by climate-induced feminisation is currently limited (Esteban et al., 2016; Madden Hof et al., 2023; Maulany et al., 2012; Patrício et al., 2019), and trends in sand temperature and hatchling sex ratios across the Asia-Pacific region remain largely unknown (Hays et al., 2014; Madden Hof et al., 2023). Lastly, precise long-term data on nesting numbers for Milne Bay and other areas of PNG are still lacking. Obtaining these data should be viewed as a priority for future work given both the male production from the region and the fact that green and hawksbill turtles are currently listed as endangered and critically endangered respectively by the IUCN (Mortimer et al., 2008; Seminoff, 2004).

Another potential avenue for sea turtles to mitigate climate-induced feminisation of hatchlings is if there is considerable interannual variability in sand temperatures. In this study, the interannual variability in AT had a SD of 0.29°C, compared to the residual variation in sand temperature across the nesting beach having a SD of 0.79°C. In the future, males will be more likely produced (i) in cooler than average years and (ii) at cooler than average sites on the beach. Certainly, large numbers of males do not need to be produced every nesting season. Rather, since sea turtles are long-lived and breed multiple times, it is likely that just one big male-producing year each decade might be enough to sustain a population at risk of extreme feminisation (Hays et al., 2022; Santidrián Tomillo, 2022; Santidrián Tomillo et al., 2014). In this regard, we might consider male production to be akin to the 'boom-bust' population dynamics commonly seen in fisheries biology where a combination of biotic and abiotic factors culminates into the occasional (e.g. once per decade or rarer) highly successful recruitment event that sustains the fishery (Beaugrand et al., 2003; McClatchie et al., 2017). For example, applying this phenomenon to sea turtles, we found that the mean sand temperature in the 2017 nesting season was ~1.5°C lower than the mean temperature in 2020, resulting in a greater production of male hatchlings in 2017. Similarly, lower sand temperatures during the Austral winter months 2019–2022 would have likely supported some male hatchling production for the few out-of-season hawksbill turtle nests reported for the Conflict Islands. Therefore, for important nesting beaches, it is imperative that managers prioritise the protection of nests in the cooler, male-producing years as well as out-of-season clutches that are laid in the cooler months. Equally, our results show occasional much warmer than average years. Such years should not necessarily be considered disastrous, even if they result in high embryo mortality and fewer males, as long as there are sufficient cool years still occurring.

One concern is that changes in rainfall might alter the relationship between sand temperature on sea turtle nesting beaches and an environmental proxy such as AT. Interest in the environmental drivers of sea turtle nest temperatures has developed further with growing observations that heavy rainfall and tidal overwash can have profound cooling effects on the sand and incubating nests (Houghton et al., 2007; Laloë et al., 2016, 2020; Staines et al., 2020). This observed cooling effect of rainfall on sea turtle nests also extends to various other ovigerous taxa including lizards, crocodiles, freshwater turtles and tortoises (Booth, 1998; Campos, 1993; Gatto & Reina, 2022; Spotila et al., 1994; Webb & Cooper-Preston, 1989). Hence, consideration of projected changes in rainfall should be included in future ecological studies, especially with TSD species (Almpanidou et al., 2018; Saba et al., 2012). We acknowledge that rainfall projections are still less well-developed than projections for AT. Furthermore, rainfall may change markedly over small spatial scales, for example, associated with topography and wind direction leading to rain shadow areas (Stockham et al., 2018). Our mean modelled rainfall projections come from a reliable ensemble of 43 model outputs from 25 research institutions. Nevertheless, as rainfall projections become more nuanced and there are increased deployments of on-site permanent weather stations, this will improve the overall confidence in the model implications for ecological systems. Despite the lack of changes to rainfall anomalies that may have influenced our projected sex ratio models, the rainfall that this site do receive is likely a leading factor to the greater production of male hatchlings (e.g. Staines et al., 2020).

The lack of significant changes in long-term rainfall trends at this study site was also supported by observations of minimal changes to annual rainfall anomalies when averaged across all of PNG (McGregor, 1992) and even more localised rainfall observations for the region (McGree et al., 2014). However, as well as trends in mean seasonal rainfall, some areas may have received less annual rainfall but experienced more frequent extreme rainfall events over time (Doaemo et al., 2022). This interplay between

rainfall totals over a nesting season versus the occurrence of episodic extreme events remains poorly resolved, but as understanding improves it will allow a more refined estimate of the impacts of rainfall changes for future populations of sea turtles and other taxa. This interaction along with changes in regional rainfall patterns are an important factor to consider when assessing sex ratio models for other areas around the world. Much of the existing literature in this area predominantly shows examples of sites with reduced projected rainfall or no projected change. For example, Chatting et al. (2021) chose to exclude projected rainfall from their sex ratio models for a hawksbill turtle population in Qatar, as the region has an extremely dry climate so modelling rainfall would be irrelevant. Saba et al. (2012) demonstrated that certain areas of Costa Rica will become drier with climate change and likely lead to a decline in the leatherback turtle (*Dermochelys coriacea*) nesting population because of reduced hatching success. Additionally, Almpanidou et al. (2018) assessed the phenological response to climate change for 45 different loggerhead turtle (*Caretta caretta*) nesting beaches in Greece by investigating the projected changes in rainfall and temperature. Although the expected phenological shifts may not keep up with the rates of precipitation changes, they concluded that there would be no negative impacts on hatching success from reduced rainfall (Almpanidou et al., 2018). A holistic approach to assessing the impacts of climate change on sea turtle populations would be to also consider any changes to hatching success because of a warming and drying climate (Saba et al., 2012; Santidrián Tomillo et al., 2020). Some researchers have also chosen to take the additional step of considering other human impacts (e.g. harvesting) and management in their population models under different climate scenarios (Jensen et al., 2022).

In conclusion, our analyses of the estimated trends in sand temperature and sex ratios demonstrate that the sea turtle populations nesting within the Conflict Island Group of PNG have likely maintained balanced hatchling sex ratios since the 1960s and will also be moderately safe guarded against extreme feminisation in future decades. This study demonstrates an approach for identifying those sea turtle nesting sites where feminisation is likely to be greatest. As the IPCC models for global emission scenarios are further refined, researchers will also be able to update our forecasted models of sand temperature and sex ratios within the next decade. An important future objective is to identify what features (e.g. rainfall) characterise such climate-resilient nesting areas versus others that are being severely impacted by climate warming and facing the threat of extinction.

AUTHOR CONTRIBUTIONS

Graeme C. Hays, Melissa N. Staines and Christine A. Madden Hof conceived the study and designed the methodology. Melissa N. Staines, Caitlin E. Smith, Hayley Versace and Christine A. Madden Hof planned fieldwork logistics and collected the field data. Melissa N. Staines processed the data. Melissa N. Staines and Jacques-Olivier Laloë conducted the analyses for the study. Melissa N. Staines and Graeme C. Hays led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

No authors have a conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data used in this study is available via The University of Queensland's (UQ eSpace) data repository https://doi.org/10.48610/b7814cd.

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