

RESEARCH ARTICLE

Climate warming and sea turtle sex ratios across the globe

Jacques-Olivier Laloë¹  | Gail Schofield^{2,†}  | Graeme C. Hays¹ 

¹School of Life and Environmental Sciences, Deakin University, Geelong, Victoria, Australia

²School of Biological and Behavioural Sciences, Queen Mary University of London, London, UK

Correspondence

Graeme C. Hays, School of Life and Environmental Sciences, Deakin University, Geelong, VIC, Australia.
Email: g.hays@deakin.edu.au

Funding information

Fondation Bertarelli, Grant/Award Number: BPMS-2017-4 and 820633

Abstract

Climate warming and the feminization of populations due to temperature-dependent sex determination may threaten sea turtles with extinction. To identify sites of heightened risk, we examined sex ratio data and patterns of climate change over multiple decades for 64 nesting sites spread across the globe. Over the last 62 years the mean change in air temperature was 0.85°C per century (SD=0.65°C, range=-0.53 to +2.5°C, $n=64$ nesting sites). Temperatures increased at 40 of the 64 study sites. Female-skewed hatchling or juvenile sex ratios occurred at 57 of the 64 sites, with skews >90% female at 17 sites. We did not uncover a relationship between the extent of warming and sex ratio ($r_{62}=-0.03$, $p=.802$, $n=64$ nesting sites). Hence, our results suggest that female-hatchling sex ratio skews are not simply a consequence of recent warming but have likely persisted at some sites for many decades. So other factors aside from recent warming must drive these variations in sex ratios across nesting sites, such as variations in nesting behaviour (e.g. nest depth), substrate (e.g. sand albedo), shading available and rainfall patterns. While overall across sites recent warming is not linked to hatchling sex ratio, at some sites there is both a high female skew and high warming, such as Raine Island (Australia; 99% female green turtles; 1.27°C warming per century), nesting beaches in Cyprus (97.1% female green turtles; 1.68°C warming per century) and in the Dutch Caribbean (St Eustatius; 91.5% female leatherback turtles; 1.15°C warming per century). These may be among the first sites where management intervention is needed to increase male production. Continued monitoring of sand temperatures and sex ratios are recommended to help identify when high incubation temperatures threaten population viability.

KEYWORDS

conservation, environmental sex determination, extinction risk, ICOADS, latitudinal effect, marine turtles, population feminization, warming temperatures

1 | INTRODUCTION

For species with temperature-dependent sex determination (TSD) there is concern that with climate warming the sex produced at

warmer temperatures will increasingly dominate until eventually highly skewed populations may occur leading to population extinction (e.g. Booth et al., 2021; Jensen et al., 2018; Katselidis et al., 2012; Roberts et al., 2023). Sea turtles are a well-studied group that exhibit

[†]Gail Schofield deceased in March 2023.

TSD with males being produced at low incubation temperatures and females at high temperatures and hence there are concerns that climate warming may lead to all-female populations (Santidrián Tomillo & Spotila, 2020). Furthermore, at warmer temperatures there is high mortality of turtle embryos which provides an additional threat with climate warming (Hays et al., 2017; Santidrián Tomillo et al., 2012). In light of these concerns, a large number of studies have estimated sex ratios being produced at nesting beaches through histological examination of sacrificed hatchlings (King et al., 2013; Patrício et al., 2017), by estimating hatchling sex ratios from temperature models (Fuentes et al., 2009; Laloë, Monsinjon, et al., 2020), or by assessing sex ratios of juveniles through blood hormone analysis (Jensen et al., 2018). For example, at Raine Island (northern Great Barrier Reef, Australia), which hosts one of the world's largest green sea turtle populations, hatchling sex ratios have been estimated to be >99% female (Booth et al., 2020; Jensen et al., 2018). Highly female-biased hatchling sex ratios observed in sea turtle populations around the world (Hays et al., 2014) highlight the urgent need for further research to understand climate change impacts on this iconic group.

Predictive models are frequently used to show how sandy-beach species might respond to climate change (Schoeman et al., 2014). Air temperatures have repeatedly been shown to be closely linked to sand temperatures at sea turtle nest depth, including studies at nesting beaches in Ascension Island (South Atlantic; Hays et al., 2003), the Chagos Archipelago (Indian Ocean; Laloë, Chivers, et al., 2021), in Florida (West Atlantic; Hawkes et al., 2007) and around Australia (South Pacific; Fuentes et al., 2009, 2010). Predictions of sand temperatures from sand versus air temperature models have been shown to be close to measured sand temperatures (Laloë et al., 2017; Laloë, Chivers, et al., 2021) and so air temperature has been used many times as a proxy for predicting likely temporal changes in mean incubation temperatures at nest depths across decades (e.g. Fuentes et al., 2009, 2010; Hawkes et al., 2007; Jensen et al., 2018; Laloë, Chivers, et al., 2021). Therefore, air temperature records likely provide a good proxy for how mean incubation temperatures at nesting sites have changed over long periods.

Several studies have examined how incubation temperatures have likely changed over recent decades at sea turtles nesting sites (reviewed in Laloë, Chivers, et al., 2021). However, there has been no comprehensive examination of how incubation temperatures have likely changed at nesting sites across the world. Given the threats that rising temperatures pose for hatchling sex ratios, here we examine 62 years of temperature records at nesting sites around the world to gauge the spatial patterns and variability of temperature increases. In this way we identify where climate warming has likely been occurring most rapidly at sea turtle nest sites. Using hatchling and juvenile sex ratio estimates, we examine whether current highly skewed sex ratios are simply a consequence of the extent of warming over recent decades or, instead, whether some populations have experienced warm incubation conditions and hence likely had highly skewed sex ratio for a long time. In this way we gauge whether skewed sex ratios in sea turtles are only a negative consequence of recent warming or instead whether they might be adaptive and have likely existed for a long time.

2 | MATERIALS AND METHODS

2.1 | Sex ratios

We assembled data on sea turtle hatchling sex ratios from published sources by searching the Thomson Reuters ISI Web of Science™ database. We searched for papers that included the terms 'sea turtle' and 'sex ratio' in the title, abstract or keywords. We performed a backward and forward citation search of the publications we found to identify additional articles. In some studies, the sex ratios were measured directly through the histological observation of the hatchling's gonads, while in other studies the sex ratios were estimated from recorded sand temperatures using the established relationship between sex ratio and sand temperature. In one study, sex ratios were estimated through endocrinology (i.e. Jensen et al., 2018). Sex ratio values were extracted from the sources' main text, tables or figures. When sex ratios estimated from histological studies and sex ratios estimated from temperature models were both available for a site, we used the sex ratio estimates from the histology study. For sites that had sex ratios available from different studies, we calculated a mean sex ratio. Details from the original datasets (e.g. species, years of study and sample sizes) can be found in Tables S1 and S2. For each site we found we noted which sea turtle regional management unit (RMU; Wallace et al., 2010) it was in to explore if there were regional patterns in warming.

2.2 | Air temperature records

We obtained air temperature records from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) through the National Center for Atmospheric Research (<http://rda.ucar.edu/datasets/ds540.1/>). ICOADS is the world's most extensive surface marine meteorological data collection and offers records spanning from 1662 to the present. Data sources range from moored buoys to surface drifters and research vessels. We used the Enhanced ICOADS Monthly Summary Statistics Release 3.0.0 to obtain temperatures between January 1960 and December 2022. We extracted air temperatures for the 4° by 4° quadrats that encompass the sea turtle sites for which we obtained sex ratio data. Previous studies from nesting sites across the world have shown that air temperatures in the 4° by 4° quadrats reflect sand temperatures at nest depth at nesting sites (e.g. Esteban et al., 2016; Hays et al., 2003) and typically a 1°C increase in air temperature equates to a 0.86°C increase in sand temperature at nest depth (Laloë, Chivers, et al., 2021). We obtained air temperatures for 1° by 1° boxes and calculated a mean monthly air temperature for each 4° by 4° quadrat weighing values by the number of observations in each 1° by 1° quadrat. We excluded from our analysis monthly means that were based on <10 observations, as is commonly done in similar studies (Fuentes et al., 2009; Hays et al., 2003). Hereafter 'mean monthly air temperature' refers to the mean of the mean air temperature for each month within the nesting window.

Nesting season information were extracted from the published literature for each study site. For each site we calculated the mean air temperature during the nesting season, as well as the mean air temperature of the month in the middle of the nesting season.

2.3 | Statistical analyses

To examine if air temperatures changed over the past 62 years (i.e. between 1960 and 2022), we used the time-slice approach where we compared temperatures between two eras (e.g. Cubasch et al., 1995). We calculated the mean monthly air temperatures during the nesting season from 1960 to 1969 and from 2013 to 2022 at each site to provide information on multidecadal changes. We then used a *t*-test to compare temperatures between these two eras. To account for the potential variation in nesting phenology across nesting sites, we ran the same analysis using the mean air temperature of the month in the middle of the nesting season for each site.

To explore if warming was linked to the latitude of each nesting site we built a second-order polynomial model with one quantitative predictor. 'Degree latitude' was entered as the predictor variable and 'air temperature difference between 1960–1969 and 2013–2022' was entered as the response variable. In addition, we explored if some regions (i.e. sea turtle RMUs) warmed more than others using an ANOVA and Tukey's HSD test.

We plotted 'female sex ratio' against 'air temperature difference between 1960–1969 and 2013–2022' and performed Pearson's product-moment correlation test to uncover the potential relationship between the two variables. To account for differences between species, we also separated data by species and performed Pearson's product-moment correlation tests if enough data were available for a species (i.e. $n \geq 9$).

All figures and tables present air temperature warming between 1960–1969 and 2013–2022, unless stated otherwise. For easy comparison with other studies, we estimated 'warming per century' by multiplying 'warming between 1960–1969 and 2013–2022' by 1.89. All statistical analyses were carried out in R version 4.0.3 (R Core Team, 2020).

3 | RESULTS

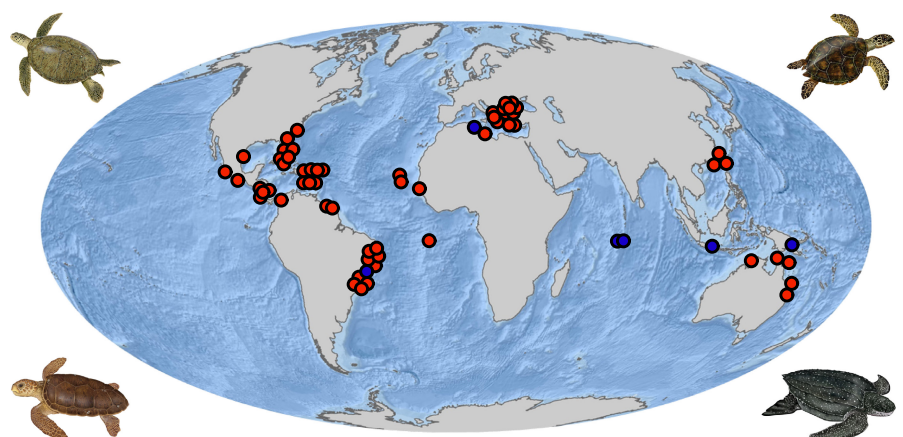
We obtained estimates of hatchling or juvenile sex ratios and air temperature records between 1960 and 2022 for 64 nesting sites spread across the world and across all seven sea turtle species (Figure 1). However, we appreciate that some sites are close together and so likely not independent (Table S1). We obtained data from 31 loggerhead rookeries, 14 green rookeries, nine leatherback rookeries, five hawksbill rookeries, three olive ridley rookeries, one Kemp's ridley rookery and one flatback rookery.

The median number of observations used to calculate mean air temperature at a study site was 12,673 (range=534 to 63,782, $n=64$) for 1960–1969 and 15,473 (range=262 to 1,133,304, $n=64$) for 2013–2022. We found statistically significant differences between mean monthly air temperatures from 1960 to 1969 and mean monthly air temperatures from 2013 to 2022 at 40 sites ($p < .05$ for 40 of 64 *t*-tests). At these 40 sites air temperature increased between 1960 and 2022, with the mean warming being 0.65°C (SD=0.27, range=0.20 to 1.3°C, $p < .05$, $n=40$). This warming translates to a rate of 1.22°C per century (SD=0.51°C, range=0.38 to 2.5°C, $p < .05$, $n=40$). Across all sites (i.e. including sites at which no statistically significant differences were noted), mean warming was 0.45°C (SD=0.35, range=-0.28 to +1.32°C, $p < .05$, $n=64$), which translates to a rate of 0.85°C per century (SD=0.65°C, range=-0.53 to +2.5°C, $p < .05$, $n=64$).

There was a marked variation across sites in the extent of air temperature warming (Figure 2a–d; Figure S1), with warming being maximal at Kuriat Island (Tunisia; 2.49°C warming per century) where loggerhead turtles nest, and lowest at Pirambu Beach (Brazil; 0.38°C warming per century), which also hosts a loggerhead rookery. Some of this variation in warming between sites was linked to latitude, with warming tending to be less near the equator and more at higher latitudes ($r^2=0.21$, $F_{2,61}=8.106$, $p < .01$, $n=64$). Sites in the temperate zone generally warmed nearly twice as fast as sites in the tropics, but considerable residual variation remained (Figure S2).

An ANOVA revealed that some regions (i.e. sea turtle RMUs) warmed more than others ($F_{7,56}=9.145$, $p < .01$). Tukey's HSD test showed that, in general, sites in the Mediterranean have warmed the most, followed by sites in the South Pacific. There were no significant

FIGURE 1 Sites around the world with hatchling/juvenile sex ratios estimates and multidecadal air temperature records. Female-skewed hatchling/juvenile sex ratios are widely reported across the world. Red points indicate sites that report female-biased sex ratios ($\geq 50\%$ female) and blue points indicate male-biased sex ratios ($> 50\%$ male). Note that some points are offset to increase legibility. The turtle images were kindly provided by NOAA Fisheries (www.fisheries.noaa.gov).



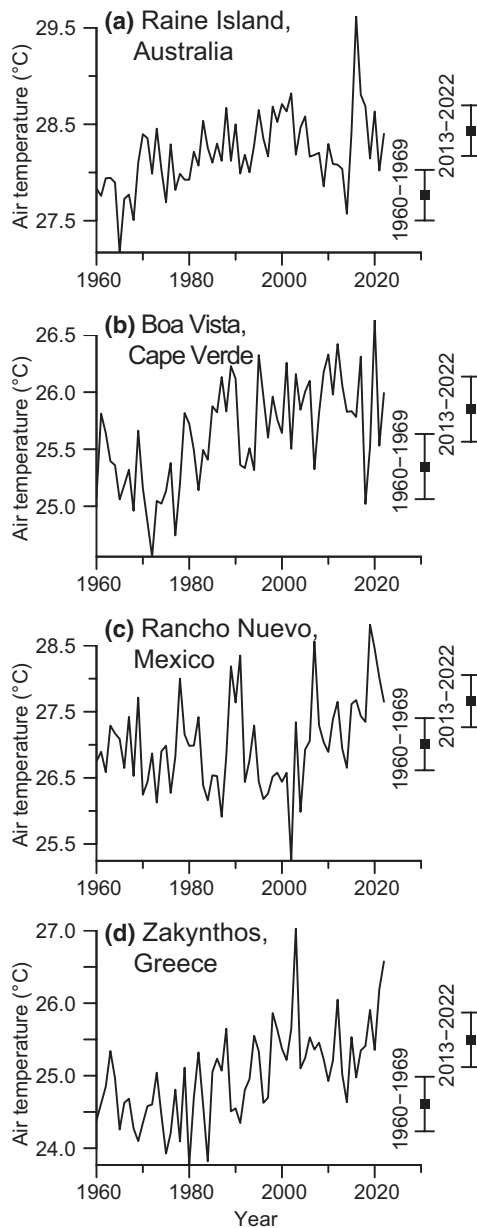


FIGURE 2 (a–d) Examples of air temperature records since 1960. Each plot shows mean monthly air temperature during the sea turtle nesting season across years. The vertical bars to the right indicate the mean \pm standard deviation of air temperatures for 1960–1969 and 2013–2022.

differences in warming for the remaining regions ($F_{5,37}=1.614$, $p=.181$).

There was no relationship between the most recent sex ratio estimate and the extent of warming over the past 62 years ($r_{62}=-0.03$, $p=.802$), that is, sites that had experienced the most marked warming did not always have the most extreme female bias in sex ratio (Figure 3). In addition, there was no relationship between sex ratio and warming when data were separated by species (for loggerheads: $r_{29}=-0.22$, $p=.238$; for greens: $r_{12}=0.47$, $p=.09$; for leatherbacks: $r_7=-0.10$, $p=.790$; Figure S3). In other words, the most extreme sex ratio skews do not seem to simply be the result of extreme warming

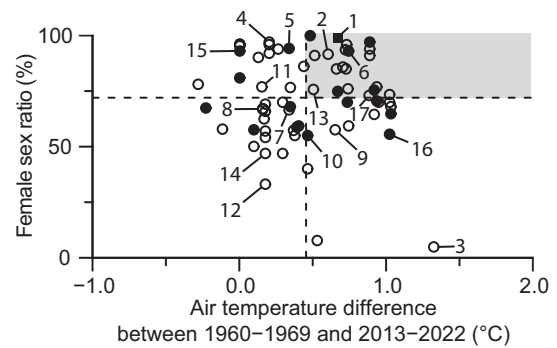


FIGURE 3 There is no direct relationship between current hatchling/juvenile sex ratios and the amount of warming a site has experienced over the past 62 years ($r_{62}=-0.03$, $p=.802$). Sex ratios were estimated using histological data (filled circles), in-nest sand temperatures (open circles) or endocrinology (filled square). The dashed lines represent the mean values for each variable. The top-right shaded box highlights sites of conservation concern where both high female biases and high warming are recorded (Table S1). Sites presented in Figure 2 and in the main text are indicated (1: Raine Island, Australia; 2: St Eustatius, Dutch Caribbean; 3: Kuriat Island, Tunisia; 4: Pirambu, Brazil; 5: Buck Island, US Virgin Islands; 6: Wan-An Island, Taiwan; 7: Sandy Point, US Virgin Islands; 8: Tortuguero, Costa Rica; 9: Rancho Nuevo, Mexico; 10: La Escobilla, Mexico; 11: Ascension Island, British Overseas Territory; 12: Diego Garcia, Chagos Archipelago; 13: Boa Vista, Cape Verde; 14: Guriri Beach, Brazil; 15: Archie Carr National Wildlife Refuge, USA; 16: Dalyan, Turkey; 17: Zakynthos, Greece).

in the past 62 years. For example, at Buck Island (US Virgin Islands) there has been relatively little warming (0.64°C per century) but still a marked female bias in hatchling sex ratio (94.1% female). The implication is that some sites were likely warm and producing mainly females even 60+ years ago. However, in other cases highly skewed female sex ratios co-occurred with high warming such as at Raine Island (Australia; 99% female green turtles; 1.27°C per century warming) and Wan-An Island (Taiwan; 93% female green turtles; 1.40°C per century warming). At some sites there were relatively balanced sex ratio and relatively little warming over the last 62 years, including Sandy Point (US Virgin Islands; 66.6% female leatherbacks; 0.64°C per century warming), Tortuguero (Costa Rica; 67% female greens; 0.30°C per century warming) and Rancho Nuevo (Mexico; 57.5% female Kemps ridleys; 1.23°C per century warming). We reached the same broad conclusions of the relative differences in warming across sites if we simply looked at the month in the middle of the nesting season between eras. In other words, our conclusions are not dependent on the exact definition of the start and end of the nesting season across sites.

4 | DISCUSSION

Although warming has been previously reported at individual nesting sites (e.g. Jensen et al., 2018, 2022; Patrício et al., 2019; Turkozan et al., 2021), our study shows increasing temperatures across ocean

basins and across different species, reiterating concerns over warming that have been expressed at individual rookeries. Due to the close relationship between air temperature and sand temperature at nest depth (Fuentes et al., 2009; Hawkes et al., 2007; Hays et al., 2003; Jensen et al., 2018; Laloë, Chivers, et al., 2021), our key finding of generally rising air temperatures at nesting sites around the world over the last 62 years suggests that sand temperatures at nest depths have likely also risen by about the same extent. The mean extent of warming that we reported across 64 sites (0.85°C per century) is consistent with the Intergovernmental Panel on Climate Change (IPCC) reports that global surface temperatures have increased by about 1°C over the last century (IPCC, 2021). However, underlying this average rate of warming our study reveals a picture of considerable variation in warming across sites (range = -0.53 to +2.5°C per century), which may have important conservation implications. We found that warming increased at higher latitudes; a pattern similar to that reported in climatological studies (Ballantyne et al., 2010; Gaskell et al., 2022). For example, it is well known that areas near the Arctic are warming faster than areas near the equator (IPCC, 2021; Walsh, 2014) and this higher-than average warming is having profound impact for species such as polar bears (*Ursus maritimus*) in the Arctic where warming is associated with loss of sea ice (Wunderling et al., 2020). Our findings revealed, for the first time, this same general pattern of reduced warming at low latitudes for sea turtle rookeries.

Similarly, our result that sites in different sea turtle RMUs experienced different warming is consistent with climatology studies that have shown that ocean basins are warming at different rates (Wang et al., 2018). Our sites that experienced the most warming were found in the Mediterranean, which is known to be a climate change 'hotspot' (Giorgi, 2006). Interestingly, the Mediterranean region is warming at a rate similar to the global mean in winter and spring, but at a much higher rate in summer and autumn (Lionello & Scarascia, 2018), which is when turtles typically nest in the region. Knowing which sea turtle RMUs are warming the most may help identify sites not included in our study and where conservation intervention might be needed in the future to lower sand temperatures (Table S1).

Our results are broadly consistent with focal studies at individual nesting sites. For example, we report warming similar to that reported previously at Ascension Island (Hays et al., 2003), Raine Island (Jensen et al., 2018), the Chagos Archipelago (Hays et al., 2021) and the Cape Verde Islands (Laloë et al., 2014), even though different methodologies were used in each of these studies. By applying the same methodology across all sites, our work allows the relative extent of recent warming across sea turtle nesting sites to be gauged. As such, our work may help identify key areas where management intervention might be required to avoid severe hatchling sex ratio skews. While highly skewed hatchling sex ratios in a population do not necessarily lead to highly skewed adult sex ratios (Hays et al., 2014), populations with currently highly female-biased hatchling sex ratios are likely to see lower levels of hatchling production as incubation conditions change with climate warming (Hays et al., 2017).

There are clearly uncertainties and limitations when trying to quantify biological responses under a scenario of rapid climate change (Rangwala et al., 2021). We have shown that the extent of recent warming is not the cause of current sex ratio skews in sea turtles. Rather these sex ratio skews might be driven by differences between species and populations in nesting behaviour (e.g. nest depth; Bentley et al., 2020) microhabitat selection (e.g. shading available; Esteban et al., 2016) or variations in substrate (e.g. sand albedo; Hays et al., 2001), and rainfall patterns (Laloë, Tedeschi, et al., 2021). More details on these various factors might help tease apart the drivers of variations in hatchling sex ratios across populations. Furthermore, the adaptive capacity (e.g. microevolution; Tedeschi et al., 2016) of populations is unclear.

Scenarios of complete hatchling feminization will most likely be seen at sites that have (i) a current high female skew in hatchling production, (ii) high warming and (iii) current high temperatures. In this regard, Raine Island is of particular concern since estimates of current hatchling production are >99% female (Jensen et al., 2018) and there is appreciable warming. However, even at Raine Island, where hatchling sex ratios are >99% female, there is still no evidence of egg infertility (Booth et al., 2021). Given that our analysis indicates that Raine Island lies towards the extreme of hatchling sex ratio skew and recent warming, it is likely that issues of egg infertility, as a result of a lack of males, may not currently be an issue at the vast majority of nesting sites around the world. Hence, impacts of female-biased hatchling sex ratios may not yet be an issue needing management intervention to produce more males. However, as climate warming increases and accelerates (NOAA, 2022), continued monitoring of egg fertility may reveal when males are so scarce that not all breeding females can find a mate.

Our work also helps identify where feminization of populations is of low concern. For example, our comparison across sites shows that at Boa Vista (Cape Verde) hatchling sex ratios are not extremely skewed and warming has been moderate, supporting previous conclusions that nesting populations in Cape Verde will be resilient to climate change (Abella Perez et al., 2016; Laloë et al., 2014). Cape Verde hosts one of the largest loggerhead turtle rookeries in the world (Hays et al., 2022; Laloë, Cozens, et al., 2020). Other very large and likely climate-resilient nesting sites identified in our analysis include Tortuguero (Costa Rica; leatherbacks and green turtles) and the state of Espírito Santo (Brazil; loggerhead turtles). The likely resilience of these sites adds to the generally reported 'good news' for many sea turtle nesting sites around the world where nesting numbers are increasing (Mazaris et al., 2017).

There has been long-term consideration of whether TSD is adaptive or is simply an ancestral form of sex determination with no current adaptive significance (Mrosovsky, 1994; Shine, 1999). Some have suggested that TSD is not adaptive, however, it has also been proposed that sea turtles might generally benefit from producing more female than male hatchlings for several reasons. First, having more females may increase the per capita reproductive output of populations thereby allowing increased growth when females are in excess (Mazaris et al., 2017). Second, there is now strong theoretical

(Santidrián Tomillo, 2022) and empirical (Hays et al., 2010) evidence that adult male turtles breed more frequently than females and hence female-skewed hatchling sex ratios may be required in order to produce balanced operational (breeding) sex ratios.

It might be argued that sites with an extreme female bias in hatchling production are simply a consequence of high recent warming. If this were the case, we would predict a strong relationship between the extent of warming and current hatchling sex ratio estimates. However, this was not the case. For example, highly female-biased hatchling sex ratios occur at some sites that have experienced little warming in recent decades, such as at the Archie Carr National Wildlife Refuge (USA) which hosts one of the largest loggerhead nesting assemblages in the world (Ehrhart et al., 2014) and where we detected no significant warming. This evidence points to female-skewed hatchling sex ratios having existed at some sites, including highly successful sea turtle rookeries, prior to recent warming, and supports the suggestion that moderate biases in female production may be adaptive. In addition, some sites with relatively balanced sex ratios have experienced some extreme warming. This was the case in Dalyan (Turkey), one of the most important reproductive sites for loggerheads in the Mediterranean, where histological data revealed 55.6% female-biased sex ratios (Sarı & Kaska, 2015) and we detected high warming (i.e. 1.93°C per century).

Our analyses also highlight that there is considerable inter-annual thermal variability within sites. With regard to sex ratios, this may indicate that even when a population may be producing predominantly one sex in most years at a site, there can still be occasional years when the other sex is produced. In this manner, interannual thermal variability may drive the continued production of males over time (e.g. decades), but not consistently every year. Thus, production of male sea turtles might follow similar pattern as that seen in fisheries, where rare but highly successful recruitment events sustain the population (Beaugrand et al., 2003). In support of this theory is the fact that sea turtles are long lived, so males produced in a particularly cool year may sustain a population for several decades thereafter (Hays et al., 2022). It is worth noting that for some of our study sites, it is possible that sex ratio estimates were made during such an atypically cool year, so that the sex ratios from those studies do not reflect overall population sex ratio accurately. However, since the majority of sex ratio estimates come from multiple years of study (Table S2), this is unlikely to be a major issue in our analysis.

The temperature time series present in our study extends several decades. Over such long periods, it might be argued that phenological shifts in the timing of nesting might mitigate warming, that is, as air and sand temperatures increase, so turtles might shift to nesting at a cooler time of year (e.g. Alpanidou et al., 2018; Mazaris et al., 2008, 2009, 2013). However, several studies suggest that the pace of phenological shifts in nesting by sea turtles is insufficient to fully mitigate rising temperatures (Alpanidou et al., 2018; Blechschmidt et al., 2020; Laloë & Hays, 2023). Sea turtles could potentially adapt to warming temperatures through a combination of behavioural changes, such as by selecting cooler sites (e.g. shaded)

within their nesting beaches (Topping & Valenzuela, 2021) or by colonizing new nesting areas (Santidrián Tomillo et al., 2023).

In conclusion, our findings show general warming across sea turtle nesting sites, with temperatures warming at 40 of 64 sites. Female-skewed hatchling or juvenile sex ratios were found at 57 of the 64 sites. However, even where both female-hatchling sex ratio skews and warming are high, there are no issues with a lack of males causing egg infertility. Our analysis did not detect a relationship between sex ratio and extent of warming over the last 62 years, suggesting that female-hatchling sex ratio skews are not simply a consequence of recent warming but may have persisted at some sites for many decades and hence may be adaptive. However, while moderate female-hatchling sex ratio skews may help population growth rates, continued monitoring of egg survival and sand temperatures are recommended to identify the tipping point at which high incubation temperatures threaten population viability.

AUTHOR CONTRIBUTIONS

Jacques-Olivier Laloë: Conceptualization; data curation; formal analysis; writing – original draft; writing – review and editing. **Gail Schofield:** Data curation; formal analysis; writing – original draft; writing – review and editing. **Graeme C. Hays:** Conceptualization; formal analysis; funding acquisition; writing – original draft; writing – review and editing.

ACKNOWLEDGEMENTS

This work was supported by the Bertarelli Foundation as part of the Bertarelli Programme in Marine Science (grant numbers BPMS-2017-4 and 820633). Open access publishing facilitated by Deakin University, as part of the Wiley - Deakin University agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

No authors have a conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Supplementary information and data that support the findings of this study are available from Dryad at <https://doi.org/10.5061/dryad.w0vt4b8zh>.

ORCID

Jacques-Olivier Laloë  <https://orcid.org/0000-0002-1437-1959>

Gail Schofield  <https://orcid.org/0000-0002-8438-4181>

Graeme C. Hays  <https://orcid.org/0000-0002-3314-8189>

REFERENCES

- Abella Perez, E., Marco, A., Martins, S., & Hawkes, L. A. (2016). Is this what a climate change-resilient population of marine turtles looks like? *Biological Conservation*, 193, 124–132. <https://doi.org/10.1016/j.biocon.2015.11.023>
- Alpanidou, V., Katragkou, E., & Mazaris, A. D. (2018). The efficiency of phenological shifts as an adaptive response against climate change: A case study of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean. *Mitigation and Adaptation Strategies for*

- Global Change*, 23, 1143–1158. <https://doi.org/10.1007/s11027-017-9777-5>
- Ballantyne, A. P., Greenwood, D. R., Sinninghe Damsté, J. S., Csank, A. Z., Eberle, J. J., & Rybczynski, N. (2010). Significantly warmer Arctic surface temperatures during the Pliocene indicated by multiple independent proxies. *Geology*, 38, 603–606. <https://doi.org/10.1130/G30815.1>
- Beaugrand, G., Brander, K. M., Alistair Lindley, J., Souissi, S., & Reid, P. C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature*, 426, 661–664. <https://doi.org/10.1038/nature02164>
- Bentley, B. P., Kearney, M. R., Whiting, S. D., & Mitchell, N. J. (2020). Microclimate modelling of beach sand temperatures reveals high spatial and temporal variation at sea turtle rookeries. *Journal of Thermal Biology*, 88, 102522. <https://doi.org/10.1016/j.jtherbio.2020.102522>
- Blechs Schmidt, J., Wittmann, M. J., & Blüml, C. (2020). Climate change and green sea turtle sex ratio—Preventing possible extinction. *Genes*, 11, 588. <https://doi.org/10.3390/genes11050588>
- Booth, D. T., Dunstan, A., Bell, I., Reina, R., & Tedeschi, J. (2020). Low male production at the world's largest green turtle rookery. *Marine Ecology Progress Series*, 653, 181–190. <https://doi.org/10.3354/meps13500>
- Booth, D. T., Dunstan, A., Robertson, K., & Tedeschi, J. (2021). Egg viability of green turtles nesting on Raine Island, the world's largest nesting aggregation of green turtles. *Australian Journal of Zoology*, 69, 12–17. <https://doi.org/10.1071/ZO21024>
- Cubasch, U., Waszkewitz, J., Hegerl, G., & Perlwitz, J. (1995). Regional climate changes as simulated in time-slice experiments. *Climatic Change*, 31, 273–304. <https://doi.org/10.1007/BF01095150>
- Ehrhart, L., Redfoot, W., Bagley, D., & Mansfield, K. (2014). Long-term trends in loggerhead (*Caretta caretta*) nesting and reproductive success at an important western Atlantic rookery. *Chelonian Conservation and Biology*, 13, 173–181. <https://doi.org/10.2744/CCB-1100.1>
- Esteban, N., Laloë, J. O., Mortimer, J. A., Guzman, A. N., & Hays, G. C. (2016). Male hatchling production in sea turtles from one of the world's largest marine protected areas, the Chagos Archipelago. *Scientific Reports*, 6, 20339. <https://doi.org/10.1038/srep20339>
- Fuentes, M. M. P. B., Hamann, M., & Limpus, C. J. (2010). Past, current and future thermal profiles of green turtle nesting grounds: Implications from climate change. *Journal of Experimental Marine Biology and Ecology*, 383, 56–64. <https://doi.org/10.1016/j.jembe.2009.11.003>
- Fuentes, M. M. P. B., Maynard, J. A., Guinea, M., Bell, I. P., Werdell, P. J., & Hamann, M. (2009). Proxy indicators of sand temperature help project impacts of global warming on sea turtles in northern Australia. *Endangered Species Research*, 9, 33–40. <https://doi.org/10.3354/esr00224>
- Gaskell, D. E., Huber, M., O'Brien, C. L., Inglis, G. N., Acosta, R. P., Poulsen, C. J., & Hull, P. M. (2022). The latitudinal temperature gradient and its climate dependence as inferred from foraminiferal $\delta^{18}\text{O}$ over the past 95 million years. *Proceedings of the National Academy of Science*, 119, e2111332119. <https://doi.org/10.1073/pnas.2111332119>
- Giorgi, F. (2006). Climate change hot-spots. *Geophysical Research Letters*, 33, L08707. <https://doi.org/10.1029/2006GL025734>
- Hawkes, L. A., Broderick, A. C., Godfrey, M. H., & Godley, B. J. (2007). Investigating the potential impacts of climate change on a marine turtle population. *Global Change Biology*, 13, 923–932. <https://doi.org/10.1111/j.1365-2486.2007.01320.x>
- Hays, G. C., Ashworth, J. S., Barnsley, M. J., Broderick, A. C., Emery, D. R., Godley, B. J., Henwood, A., & Jones, E. L. (2001). The importance of sand albedo for the thermal conditions on sea turtle nesting beaches. *Oikos*, 93, 87–94. <https://doi.org/10.1034/j.1600-0706.2001.930109.x>
- Hays, G. C., Broderick, A. C., Glen, F., & Godley, B. J. (2003). Climate change and sea turtles: A 150-year reconstruction of incubation temperatures at a major marine turtle rookery. *Global Change Biology*, 9, 642–646. <https://doi.org/10.1046/j.1365-2486.2003.00606.x>
- Hays, G. C., Chivers, W. J., Laloë, J.-O., Sheppard, C., & Esteban, N. (2021). Impact of marine heatwaves for sea turtle nest temperatures. *Biology Letters*, 17(5), 20210038. <https://doi.org/10.1098/rsbl.2021.0038>
- Hays, G. C., Fossette, S., Katselidis, K. A., Schofield, G., & Gravenor, M. B. (2010). Breeding periodicity for male sea turtles, operational sex ratios, and implications in the face of climate change. *Conservation Biology*, 24, 1636–1643. <https://doi.org/10.1111/j.1523-1739.2010.01531.x>
- Hays, G. C., Mazaris, A. D., & Schofield, G. (2014). Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Frontiers in Marine Science*, 1, 43. <https://doi.org/10.3389/fmars.2014.00043>
- Hays, G. C., Mazaris, A. D., Schofield, G., & Laloë, J. O. (2017). Population viability at extreme sex-ratio skews produced by temperature-dependent sex determination. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20162576. <https://doi.org/10.1098/rspb.2016.2576>
- Hays, G. C., Shimada, T., & Schofield, G. (2022). A review of how the biology of male sea turtles may help mitigate female-biased hatchling sex ratio skews in a warming climate. *Marine Biology*, 169, 89. <https://doi.org/10.1007/s00227-022-04074-3>
- IPCC. (2021). Climate change 2021: The physical science basis. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Contribution of working group I to the sixth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, in press. <https://doi.org/10.1017/9781009157896>
- Jensen, M. P., Allen, C. D., Eguchi, T., Bell, I. P., LaCasella, E. L., Hilton, W. A., Hof, C. A., & Dutton, P. H. (2018). Environmental warming and feminization of one of the largest sea turtle populations in the world. *Current Biology*, 28, 154–159. <https://doi.org/10.1016/j.cub.2017.11.057>
- Jensen, M. P., Eguchi, T., FitzSimmons, N. N., McCarthy, M. A., Fuentes, M. M. P. B., Hamann, M., Limpus, C. J., Bell, I. P., & Read, M. A. (2022). Integrating climate change and management scenarios in population models to guide the conservation of marine turtles. *Bulletin of Marine Science*, 98, 131–154. <https://doi.org/10.5343/bms.2021.0033>
- Katselidis, K. A., Schofield, G., Stamou, G., Dimopoulos, P., & Pantis, J. D. (2012). Females first? Past, present and future variability in offspring sex ratio at a temperate sea turtle breeding area. *Animal Conservation*, 15, 508–518. <https://doi.org/10.1111/j.1469-1795.2012.00543.x>
- King, R., Cheng, W. H., Tseng, C. T., Chen, H., & Cheng, I. J. (2013). Estimating the sex ratio of green sea turtles (*Chelonia mydas*) in Taiwan by the nest temperature and histological methods. *Journal of Experimental Marine Biology and Ecology*, 445, 140–147. <https://doi.org/10.1016/j.jembe.2013.03.016>
- Laloë, J. O., Chivers, W. J., Esteban, N., & Hays, G. C. (2021). Reconstructing past thermal conditions in beach microclimates. *Global Change Biology*, 27, 6592–6601. <https://doi.org/10.1111/gcb.15903>
- Laloë, J.-O., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2014). Effects of rising temperature on the viability of an important sea turtle rookery. *Nature Climate Change*, 4(6), 513–518. <https://doi.org/10.1038/nclimate2236>
- Laloë, J. O., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2017). Climate change and temperature-linked hatchling mortality at a

- globally important sea turtle nesting site. *Global Change Biology*, 23, 4922–4931. <https://doi.org/10.1111/gcb.13765>
- Laloë, J. O., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2020). Conservation importance of previously undescribed abundance trends: Increase in loggerhead turtle numbers nesting on an Atlantic Island. *Oryx*, 54, 315–322. <https://doi.org/10.1017/S0030605318001497>
- Laloë, J. O., & Hays, G. C. (2023). Can a present-day thermal niche be preserved in a warming climate by a shift in phenology? A case study with sea turtles. *Royal Society Open Science*, 10, 221002. <https://doi.org/10.1098/rsos.221002>
- Laloë, J. O., Monsinjon, J., Gaspar, C., Touron, M., Genet, Q., Stubbs, J., Girondot, M., & Hays, G. C. (2020). Production of male hatchlings at a remote South Pacific green sea turtle rookery: Conservation implications in a female-dominated world. *Marine Biology*, 167, 70. <https://doi.org/10.1007/s00227-020-03686-x>
- Laloë, J. O., Tedeschi, J. N., Booth, D. T., Bell, I., Dunstan, A., Reina, R. D., & Hays, G. C. (2021). Extreme rainfall events and cooling of sea turtle clutches: Implications in the face of climate warming. *Ecology and Evolution*, 11, 560–565. <https://doi.org/10.1002/ece3.7076>
- Lionello, P., & Scarascia, L. (2018). The relation between climate change in the Mediterranean region and global warming. *Regional Environmental Change*, 18(5), 1481–1493. <https://doi.org/10.1007/s10113-018-1290-1>
- Mazaris, A. D., Kallimanis, A. S., Pantis, J. D., & Hays, G. C. (2013). Phenological response of sea turtles to environmental variation across a species' northern range. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20122397. <https://doi.org/10.1098/rspb.2012.2397>
- Mazaris, A. D., Kallimanis, A. S., Sgardelis, S. P., & Pantis, J. D. (2008). Do long-term changes in sea surface temperature at the breeding areas affect the breeding dates and reproduction performance of Mediterranean loggerhead turtles? Implications for climate change. *Journal of Experimental Marine Biology and Ecology*, 367, 219–226. <https://doi.org/10.1016/j.jembe.2008.09.025>
- Mazaris, A. D., Kallimanis, A. S., Tzanopoulos, J., Sgardelis, S. P., & Pantis, J. D. (2009). Sea surface temperature variations in core foraging grounds drive nesting trends and phenology of loggerhead turtles in the Mediterranean Sea. *Journal of Experimental Marine Biology and Ecology*, 379, 23–27. <https://doi.org/10.1016/j.jembe.2009.07.026>
- Mazaris, A. D., Schofield, G., Gkazinou, C., Almpandou, V., & Hays, G. C. (2017). Global sea turtle conservation successes. *Science Advances*, 3, e1600730. <https://doi.org/10.1126/sciadv.1600730>
- Mrosovsky, N. (1994). Sex ratios of sea turtles. *Journal of Experimental Zoology*, 270, 16–27. <https://doi.org/10.1002/jez.1402700104>
- NOAA National Centers for Environmental Information. (2022). 2022 Monthly National Climate Report for Annual 2021. Published online in January 2022. Retrieved from <https://www.ncei.noaa.gov/access/monitoring/monthly-report/national/202113>
- Patrício, A. R., Marques, A., Barbosa, C., Broderick, A. C., Godley, B. J., Hawkes, L. A., Rebelo, R., Regalla, A., & Catry, P. (2017). Balanced primary sex ratios and resilience to climate change in a major sea turtle population. *Marine Ecology Progress Series*, 577, 189–203. <https://doi.org/10.3354/meps12242>
- Patrício, A. R., Varela, M. R., Barbosa, C., Broderick, A. C., Catry, P., Hawkes, L. A., Regalla, A., & Godley, B. J. (2019). Climate change resilience of a globally important sea turtle nesting population. *Global Change Biology*, 25, 522–535. <https://doi.org/10.1111/gcb.14520>
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org>
- Rangwala, I., Moss, W., Wolken, J., Rondeau, R., Newlon, K., Guinotte, J., & Travis, W. R. (2021). Uncertainty, complexity and constraints: How do we robustly assess biological responses under a rapidly changing climate? *Climate*, 9, 177. <https://doi.org/10.3390/cli9120177>
- Roberts, H. P., Willey, L. L., Jones, M. T., Akre, T. S., King, D. I., Kleopfer, J., Brown, D. J., Buchanan, S. W., Chandler, H. C., de Maynadier, P., & Winters, M. (2023). Is the future female for turtles? Climate change and wetland configuration predict sex ratios of a freshwater species. *Global Change Biology*, 29(10), 2641–2642. <https://doi.org/10.1111/gcb.16625>
- Santidrián Tomillo, P. (2022). When population-advantageous primary sex ratios are female-biased: Changing concepts to facilitate climate change management in sea turtles. *Climatic Change*, 175, 15. <https://doi.org/10.1007/s10584-022-03470-4>
- Santidrián Tomillo, P., Pujol, F., Félix, G., Núñez-Reyes, V., Saba, V. S., Tomás, J., & Marco, A. (2023). Colonization of new nesting areas could provide climate refuge to loggerhead turtles under climate change. *Biological Conservation*, 284, 110146. <https://doi.org/10.1016/j.biocon.2023.110146>
- Santidrián Tomillo, P., Saba, V. S., Blanco, G. S., Stock, C. A., Paladino, F. V., & Spotila, J. R. (2012). Climate driven egg and hatchling mortality threatens survival of Eastern Pacific leatherback turtles. *PLoS One*, 7, e37602. <https://doi.org/10.1371/journal.pone.0037602>
- Santidrián Tomillo, P., & Spotila, J. R. (2020). Temperature-dependent sex determination in sea turtles in the context of climate change: Uncovering the adaptive significance. *BioEssays*, 42, 2000146. <https://doi.org/10.1002/bies.202000146>
- Sari, F., & Kaska, Y. (2015). Loggerhead Sea turtle hatchling sex ratio differences between two nesting beaches in Turkey. *Israel Journal of Ecology and Evolution*, 61, 115–129. <https://doi.org/10.1080/15659801.2015.1047681>
- Schoeman, D. S., Schlacher, T. A., & Defeo, O. (2014). Climate-change impacts on sandy-beach biota: Crossing a line in the sand. *Global Change Biology*, 20, 2383–2392. <https://doi.org/10.1111/gcb.12505>
- Shine, R. (1999). Why is sex determined by nest temperature in many reptiles? *Trends in Ecology & Evolution*, 14, 186–189. [https://doi.org/10.1016/S0169-5347\(98\)01575-4](https://doi.org/10.1016/S0169-5347(98)01575-4)
- Tedeschi, J. N., Kennington, W. J., Tomkins, J. L., Berry, O., Whiting, S., Meekan, M. G., & Mitchell, N. J. (2016). Heritable variation in heat shock gene expression: A potential mechanism for adaptation to thermal stress in embryos of sea turtles. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20152320. <https://doi.org/10.1098/rspb.2015.2320>
- Topping, N. E., & Valenzuela, N. (2021). Turtle nest-site choice, anthropogenic challenges, and evolutionary potential for adaptation. *Frontiers in Ecology and Evolution*, 9, 808621. <https://doi.org/10.3389/fevo.2021.808621>
- Turkozán, O., Almpandou, V., Yilmaz, C., & Mazaris, A. D. (2021). Extreme thermal conditions in sea turtle nests jeopardize reproductive output. *Climatic Change*, 167, 30. <https://doi.org/10.1007/s10584-021-03153-6>
- Wallace, B. P., DiMatteo, A. D., Hurley, B. J., Finkbeiner, E. M., Bolten, A. B., Chaloupka, M. Y., Hutchinson, B. J., Abreu-Grobois, F. A., Amorcho, D., Bjørndal, K. A., & Bourjea, J. (2010). Regional management units for marine turtles: A novel framework for prioritizing conservation and research across multiple scales. *PLoS One*, 5, e15465. <https://doi.org/10.1371/journal.pone.0015465>
- Walsh, J. E. (2014). Intensified warming of the Arctic: Causes and impacts on middle latitudes. *Global and Planetary Change*, 117, 52–63. <https://doi.org/10.1016/j.gloplacha.2014.03.003>
- Wang, G., Cheng, L., Abraham, J., & Li, C. (2018). Consensuses and discrepancies of basin-scale ocean heat content changes in different ocean analyses. *Climate Dynamics*, 50, 2471–2487. <https://doi.org/10.1007/s00382-017-3751-5>
- Wunderling, N., Willeit, M., Donges, J. F., & Winkelmann, R. (2020). Global warming due to loss of large ice masses and Arctic summer

sea ice. *Nature Communications*, 11, 5177. <https://doi.org/10.1038/s41467-020-18934-3>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Laloë, J.-O., Schofield, G., & Hays, G. C. (2024). Climate warming and sea turtle sex ratios across the globe. *Global Change Biology*, 30, e17004. <https://doi.org/10.1111/gcb.17004>