

Title: Reconstructing past thermal conditions in microclimates

Authors: Jacques-Olivier Laloë¹, William J. Chivers², Nicole Esteban^{3*}, Graeme C. Hays¹

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

²School of Electrical Engineering and Computing, University of Newcastle, Callaghan, New South Wales, Australia

³Faculty of Science and Engineering, Swansea University, Swansea, Wales, United Kingdom

*corresponding author: n.esteban@swansea.ac.uk

Running headline: Modelling temperatures in unique microhabitats

Journal: Global Change Biology

Abstract

Reconstruction of past conditions provides important information on how ecosystems have been impacted by climate change, but generally for microhabitats worldwide there are no long-term empirical measurements. In these cases, there has been protracted debate about how various large-scale environmental proxies can best be used to reconstruct local temperatures. Here we help resolve this debate using sand temperature data at nest depths for sea turtle nesting sites across the world. We examine how well environmental proxies hindcast sand temperatures at nest depths at five sea turtle nesting sites across the world. We link instrumental air temperature and sea surface temperature records with empirical sand temperatures observations in the Atlantic (Ascension Island and Cape Verde), the Indian Ocean (Chagos Archipelago), the Caribbean (St Eustatius) and the Pacific (French Polynesia). We found strong correlations between sea surface temperatures, air temperatures and sand temperatures at all our study sites. Furthermore, Granger causality testing shows variations in sea surface temperature and air temperature precede variations in sand temperatures. We found that different proxies (air or sea temperature or a combination of both) predicted mean monthly sand temperatures within $< 0.5^{\circ}\text{C}$ of empirical observations. Reconstructions of sand temperatures over the last 170 years reveal a slight warming of temperatures (maximum 0.5°C per century). An analysis of 36 published datasets revealed that the gradient of the relationship between sand temperature and air temperature is

relatively constant, suggesting long-term changes in sand temperature could be extended around the world to include nesting sites where there are no empirical measurements of sand temperature. Our approaches are likely to have utility for a range of micro-habitats where there is interest in long-term changes in temperature.

Key words: microhabitat modelling, Granger causality testing, Hadley SST, temperature-dependent sex determination, climate change

1 | Introduction

Reconstructing past environmental conditions offers valuable information on the rate of climate change. Since the distribution of plant and animals is closely linked with the climate, reconstructing past climates also allows modelling of the past distributions of species as well as exploring processes behind distribution range shifts (Melo-Merino et al., 2020). Different components of the past climate can be inferred using different proxies. For example, coral cores provide reliable information on sea temperatures over several centuries, as well as giving indications of the rates of sea level change and salinity variations (Corrège, 2006). For terrestrial ecosystems, dendroecological techniques help reconstruct the climate over several millennia by studying tree rings (Touchan et al., 2008). To extend further back in time, paleoclimatologists rely on oxygen isotope ratios found in ice cores (Steiger et al., 2017) and pollen diversity preserved in sediment layers (Davis et al., 2003). Taken together, these techniques enable the reconstruction of past climates on regional and global scales, and for time frames ranging several decades to several 100s of millions of years.

To estimate recent global temperatures climatologists can rely on the instrumental record, which extends as far back as the mid-nineteenth century in some locations. For example, air temperatures, sea surface temperatures and precipitation data are monitored daily at countless locations around the world and are compiled in datasets that are widely made available (e.g. the Bureau of Meteorology in Australia, the Meteorological Office in the United Kingdom, the National Oceanic and Atmospheric Administration in the United States of America). In some cases, these data can be used to directly assess how climate change may have impacted taxa, for example marine species whose range is influenced by sea surface temperature (e.g. McMahon & Hays, 2006; Chivers et al., 2017; Richardson & Schoeman, 2004). For species that live in particular microhabitats (i.e. very small and localized habitats) correlative models that use large-scale environmental proxies to predict local environmental conditions can be used (Kearney et al., 2010; Pacifici et al., 2015). For example, for species

that live in the soil, soil temperatures can be modelled using proxies such as land surface temperatures (Huang et al., 2020).

For sea turtles, the correlative approach using either air temperature (AT) and/or sea surface temperature (SST) has been widely used to reconstruct sand temperatures at nesting sites (Hays et al., 2003; Fuentes et al., 2009; Jensen et al., 2018; Bentley et al., 2020a; Chatting et al., 2021). However, there has been debate about whether AT or SST provides the best proxy for these sand temperature reconstructions (Fuentes et al. 2009; Bentley et al. 2020a; Hays et al. 2021). Here we set out to resolve this debate using sand temperature data at nest depths for sea turtle nesting sites across the world. In addition to simple correlative models, we further explored the potential causal pathways between AT, SST and sand temperature by using Granger causality testing which provides a measure of forecasting over and above that provided simply by temporal correlations and helps point towards causal links (Thurman & Fisher, 1988). Combining our best models with historical environmental datasets, we then reconstruct sand temperatures at nest depths for > 100 years at each study site and show the utility of our approach for both other sea turtle nesting sites around the world as well as other micro-habitats where there are no long-term local temperature measurements. In this way we demonstrate how our approach may have broad utility for those studying a range of habitats where there is interest in assessing how temperatures have changed over the past century and identifying those sites that are most likely to have been strongly impacted by recent climate change.

2 | Materials and methods

2.1 | Sand temperatures

We used sand temperature records published from six sea turtle nesting beaches from five island locations (Figure 1). Data were obtained for Long Beach and North East Bay on Ascension Island (South Atlantic) (Hays et al., 2003), Cape Verde (North Atlantic) (Laloë et al., 2017), the Chagos Archipelago (Indian Ocean) (Esteban et al., 2016), French Polynesia (East Pacific) (Laloë et al., 2020a), and St Eustatius (Caribbean) (Laloë et al., 2016). In these studies, sand temperatures were recorded using loggers deployed at nest depth on sea turtle nesting beaches. Loggers were deployed at different sites along the nesting beach to capture the range of different thermal habitats in which the turtles nest. In all studies temperatures loggers were deployed adjacent to nests and at typical depths reported for each site. So although the depth of loggers varied between studies, changes in the recorded sand

temperatures from month to month reflected the temporal change in incubation conditions. Details of each dataset can be found in Supplemental table 1.

We calculated monthly means from these sand temperature records to capture broad changes in sand temperatures as well as make these measurements directly comparable with the environmental datasets that are supplied as monthly means.

2.2 | Environmental datasets

We obtained air temperature records for our study sites from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) from the National Center for Atmospheric Research (<https://ncar.ucar.edu>). The ICOADS is an extensive set of surface marine data that extends as far back as 1854 and covers all oceans. Recent measurements (i.e. since the 1970s) are compiled from extensive arrays of drifting and moored buoys (Woodruff, 2001). We used the Enhanced ICOADS Monthly Summary Release 2.5 at the 2° spatial resolution. We used the same geographic area as defined in the original publications, which ranged from a 2° by 2° area (i.e. St Eustatius; Laloë et al., 2016) to a 10° by 10° area (i.e. the Chagos Archipelago; Esteban et al., 2016). We restricted the dataset to months with > 30 observations. We did not interpolate the data between months with missing data, so some gaps exist in these datasets.

We obtained Hadley sea surface temperature (SST) data for the same geographic areas from the United Kingdom Meteorological Office (www.metoffice.gov.uk). In this dataset, SSTs are reconstructed from *in situ* and remote-sensed measurements using reduced space optimal interpolation.

To examine if local AT is a better predictor for sand temperature than regional (i.e. ICOADS) AT, we obtained AT records from the Amílcar Cabral International Airport in Espargos, Cape Verde, from Weather Underground (www.wunderground.com). Local AT records were not available for our other study sites.

2.3 | Literature review

To explore if the relationship between sand temperature and air temperature is consistent at different sites across the world, we searched the literature for publications that present the relationship between sand temperature at nest depth and air temperature and/or sea surface temperature at sea turtle nesting sites. We entered the search terms “temperature” and “sea turtle” as TOPIC in Web of Science (apps.webofknowledge.com) for articles published between 1960 and 2021. We did a backward and a forward citation search on relevant articles to find further publications.

In some publications, relationships were not given but the data were available in figures or tables. For these cases, we digitized the data from the figures or tables using WebPlotDigitizer 4.4 (automeris.io/WebPlotDigitizer) and subsequently established the relationships ourselves.

It is important to note that although the depth at which loggers were buried might vary between studies, all studies present sand temperatures at nest depth. So regardless of specific depths at which loggers were deployed in each study, relationships are always given relative to sand temperature at nest depth.

2.4 | Statistical analyses

We investigated the relationship between sand temperature, ICOADS AT, and Hadley SST using a stepwise multiple regression. We further explored the time series using a Granger causality test. The Granger analysis was implemented using the “grangertest” function in the R library “lmtest” and with a lag = 1.

We also explored the relationships between sand temperature and AT found in the literature. We investigated whether the gradients and intercept of each relationship were different for different sites using an analysis of covariance. All statistical analyses were done in R version 4.0.3 (R Core Team, 2020).

3 | Results

3.1 | Best predictors for sand temperatures

Both ICOADS AT and Hadley SST were very good predictors for sand temperatures at our study sites, with R^2 values > 0.80 at all sites except in French Polynesia (Table 1; Figure 1). When we entered AT and SST in a stepwise regression, AT was found to be the best predictor for sand temperature for Ascension Island Long Beach, Ascension Island North East Bay, and Cape Verde. SST was the best predictor for sand temperature for the Chagos Archipelago and French Polynesia. Only at one study site, i.e. St Eustatius, using AT in combination with SST resulted in the best model fit (Table 1). We also found a strong relationship between air temperatures recorded at the airport on Cape Verde and sand temperatures ($R^2 = 0.88$, $p < 0.001$; Table 1).

To further examine the differences between model outputs we calculated the mean absolute difference between modelled sand temperatures and observed sand temperatures. For example, for Ascension Island Long Beach the model with the best fit (i.e. using AT as predictor; Table 1) modelled sand temperatures that were on average 0.36°C from the

observed sand temperature. The next best model (i.e. using both AT and SST as predictors; Table 1) modelled sand temperatures that were on average 0.37 °C from the observed sand temperature. Using SST alone as a predictor produced results that were on average 0.47°C from the observed sand temperature. Similarly, for Cape Verde, using local air temperatures or regional air temperatures produced results that were within 0.1 °C of each other (Table 1; Supplemental figure 1). In short, all examined models produced results that were on average within fractions of a degree of the recorded mean monthly sand temperatures, i.e. there were only marginal differences in whether either AT or SST or a combination of both was used to predict sand temperature.

We used Granger causality tests to further explore the relationships between our predictor variables and sand temperatures. We found significant Granger causality between air temperature and sand temperature ($p < 0.05$) at all study sites except Cape Verde, i.e. when past values of AT were used in a regression model to predict future values of sand temperature (with a lag of 1 month) after adjusting for past values of sand temperature. We also found significant Granger causality between SST and sand temperature ($p < 0.05$) at all study sites except Cape Verde and St Eustatius.

3.2 | Long term reconstructions

We reconstructed sand temperatures at our study sites using the historic instrumental records (i.e. ICOADS and Hadley datasets) and the relationships highlighted in Table 1. In two cases (i.e. both beaches on Ascension Island), we were able to reconstruct sand temperature as far back as 1805 (Supplemental figure 2). In general, our times series extend from the late 19th century to the present.

To explore if there has been a warming trend over the last centuries, we examined mean monthly sand temperatures during peak nesting season at each site (Figure 2). We found that there has been a warming trend at all our study sites bar one (i.e. St Eustatius). Sand temperatures during peak nesting month increased by up to 0.5 °C per century (minimum = 0.15 °C per century, maximum = 0.5°C per century).

3.3 | Sand vs air relationships

We found a total of 36 relationships between sand temperature and AT published for 23 different sea turtle nesting sites (Figure 3; Supplemental table 2). While the intercepts of the relationships found for different study sites vary (mean = 6.35, standard deviation = 7.40, $n = 36$), the gradient for all relationships remains relatively constant (mean = 0.86, standard

deviation = 0.26, $n = 36$; Figure 3). In other words, for every 1°C increase in air temperature, sand temperatures increase by an average 0.86°C .

For 13 of these 23 sites, data were available in the publication either in tables or figures. For these sites, we investigated the relationships between sand temperatures and AT using an analysis of covariance. AT was modelled as the dependent variable with site as the factor and sand temperature as the covariate. We found a significant effect of AT on sand temperature ($F_{1,706} = 241.5$, $p < 0.01$) but no significant interaction ($F_{1,706} = 2.5$, $p = 0.111$), indicating that the slopes of the regression between sand temperature and AT is similar at all sites (Supplemental figure 3). This analysis confirms the above result that the gradient for all relationships remains relatively constant at all sites (Figure 3). At these 13 sites, a 1°C increase in air temperature resulted in mean monthly sand temperatures increasing by an average 0.84°C (95% confidence interval = $[0.79; 0.90]$, $n = 13$ sites). Site had a significant effect on sand temperature ($F_{1,706} = 71.8$, $p < 0.01$) indicating that different sites have different intercepts, i.e. that some sites are warmer than others. For example, sand temperatures at nest depths recorded on two beaches on Ascension Island were very different: Long Beach was an average 3.0°C warmer than North East Bay beach.

Site	n	Variable	AIC	R ²	p	Equation	Mean absolute difference
Ascension Island	29	AT	-44.64	0.80	< 0.001	10.38 + 0.67 x AT	0.35 °C
Long Beach		AT+SST	-42.64	0.80	< 0.001	10.42 + 0.68 x AT - 0.01 SST	0.34 °C
		SST	-29.86	0.67	< 0.001	9.81 + 0.68 x SST	0.47 °C
Ascension Island	25	AT	-33.15	0.82	< 0.001	11.22 + 0.75 x AT	0.36 °C
North East Bay		AT+SST	-32.36	0.83	< 0.001	10.15 + 0.58 x AT + 0.21 x SST	0.37 °C
		SST	-24.56	0.74	< 0.001	9.70 + 0.80 x SST	0.47 °C
Cape Verde	24	AT	-41.31	0.84	< 0.001	11.04 + 0.69 x AT	0.30 °C
		AT+SST	-39.94	0.85	< 0.001	10.47 + 0.55 x AT + 0.17 x SST	0.31 °C
		SST	-35.17	0.80	< 0.001	9.93 + 0.73 x AT	0.36 °C
		<i>local AT</i>	<i>NA</i>	<i>0.88</i>	<i>< 0.001</i>	<i>10.44 + 0.73 x local AT</i>	<i>0.28 °C</i>
Chagos Archipelago	15	SST	-33.93	0.82	< 0.001	3.65 + 0.86 x AT	0.23 °C
		AT+SST	-32.13	0.82	< 0.001	3.54 + 0.15 x AT + 0.71 x SST	0.23 °C
		AT	-30.36	0.77	< 0.001	4.86 + 0.84 x AT	0.25 °C
French Polynesia	23	SST	-35.77	0.58	< 0.001	13.32 + 0.52 x SST	0.31 °C
		AT+SST	-33.85	0.58	< 0.001	13.15 + 0.06 x AT + 0.46 x SST	0.31 °C
		AT	-31.3	0.49	< 0.001	14.48 + 0.49 x AT	0.38 °C
St Eustatius	14	AT+SST	-6.55	0.82	< 0.001	8.87 + 4.09 x AT -3.21 x SST	0.55 °C
		AT	0.44	0.70	< 0.001	-5.09 + 1.31 x AT	0.65 °C
		SST	6.32	0.49	0.005	-6.12 + 1.31 x SST	0.85 °C

220

221 TABLE 1 We found strong relationships between sand temperature (ST), air temperature (AT) and sea surface temperature (SST). For each site,
222 the model with the best fit (lowest Akaike's information criterion) is indicated in bold. For Cape Verde, we additionally examined the
223 relationship between sand temperature (ST) and air temperature from the international airport found on Sal (local AT; in italics). The sample size
224 (n) is the number of months for which sand temperatures are available.

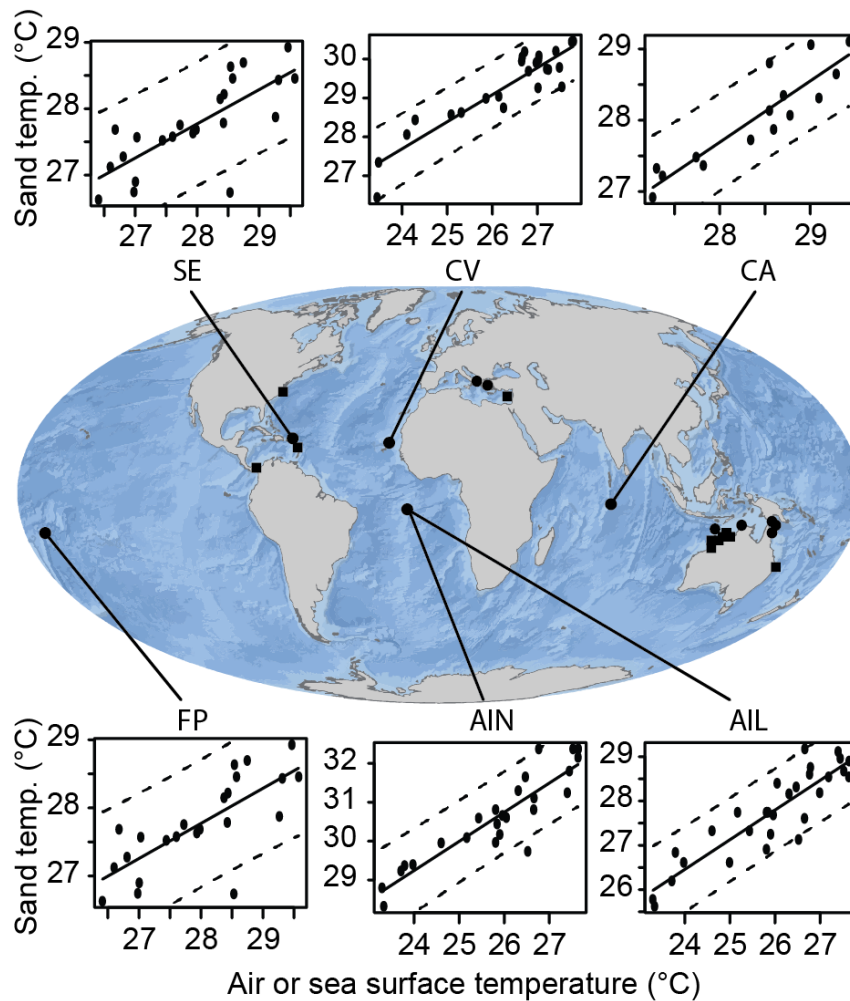


FIGURE 1 Location of sites used in our study. Relationships between sand temperature, air temperature and sea surface temperatures were given in the literature for all sites. Sites that gave the relationship as well as provided the data are indicated with circles. Sites which gave only the relationship are indicated by squares. We highlight the relationships presented in bold in Table 1. AIL: Ascension Island Long Beach; AIN: Ascension Island North East Beach; CA: Chagos Archipelago; CV: Cape Verde; FP: French Polynesia; SE: St Eustatius. The solid line in the regression line; the dashed lines define the 95% prediction interval.

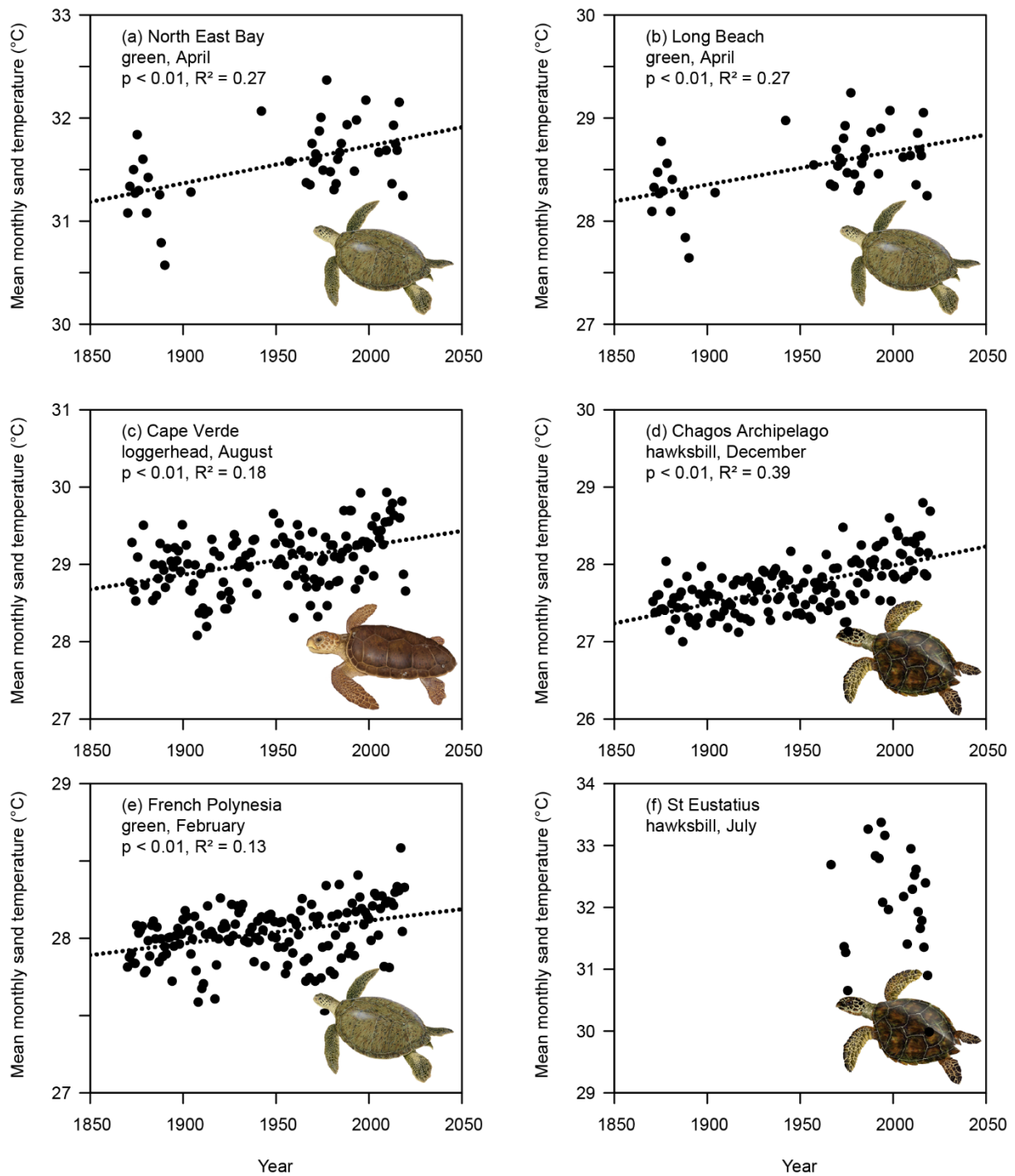


FIGURE 2 Mean monthly sand temperatures during peak nesting season have increased at the majority of our study sites. Sea turtle species and the month during peak nesting season shown are detailed in each sub-panel. For example, mean monthly sand temperature during December, a month during peak hawksbill nesting season in the Chagos Archipelago, has increased at an average rate of 0.5 °C per century since 1870 (subpanel b). There are gaps in our time series due to gaps in the historical records. Least squares fit regressions (dotted lines) are shown when significant.

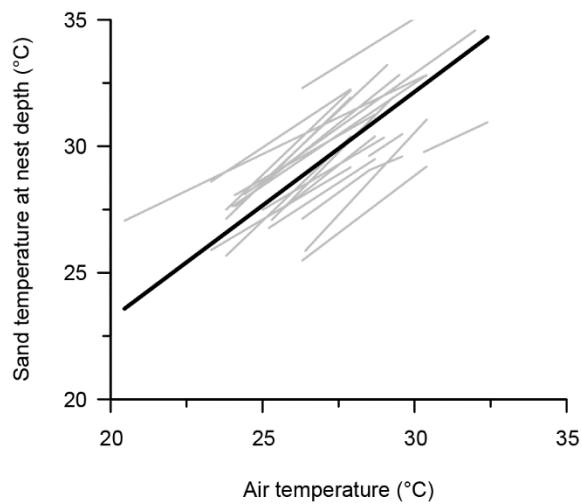


FIGURE 3 Warmer air temperatures consistently lead to warmer sand temperatures at sea turtle nesting beaches across the world. We found 36 relationships for 13 study sites (grey lines; Supplemental table 2). The black line represents the generic linear relationship defined by the mean intercept and the mean gradient of all relationships in grey (sand temperature = $0.86 \times \text{air temperature} + 6.35$).

4 | Discussion

Our findings highlight how environmental proxies can be used to accurately reconstruct temperatures in specific microclimates and so this approach may have wide utility across habitats, allowing current conditions to be placed into the context of likely conditions over the last century. So, for example, our approach could equally be applied to other coastal ecosystems such as mangroves, salt-marshes and coral reefs where there is intense interest in the impacts of climate change (Duarte, 2017). The same approach we used could also be applied to terrestrial habitats where there is interest in reconstructing past conditions but where local in-situ temperature records are lacking. In this way, this approach would allow an assessment of the extent to which climate change may already have impacted species and habitats.

For sea turtles, there are specific reasons why understanding past nest conditions is important. Sea turtles exhibit temperature-dependent sex determination (TSD), with females being produced from eggs incubating at high incubation temperatures (Standora & Spotila, 1985; Santidrián Tomillo, 2020; Bentley et al., 2020b). Hence there is concern that warming temperatures as a part of climate change may raise temperatures sufficiently to produce single-sex (female-only) hatchling cohorts and so ultimately population extinctions. In addition, high incubation temperatures cause embryonic mortality (Howard et al., 2014). For this reason, recording sand temperatures at sea turtle nesting beaches has become routine across the world (e.g. Hays et al., 1999; Rees and Margaritoulis, 2004; Fuentes et al., 2009; Bentley et al., 2020a). Set against this backdrop, our findings suggest that historic sea surface temperature or air temperature – both of which are freely available across the globe – can be used to accurately predict historic sand temperatures at nest depths. This conclusion in itself is not new, since reconstructing sand temperatures at sea turtle nesting sites has been widely done using the correlative approach (e.g. Hays et al., 2003; Hawkes et al., 2007; Fuentes et al., 2009; Chatting et al., 2021). However, there has been debate about which environmental variables are the best predictors of sand temperature and here our work adds value by showing there is little difference in the predictions made by using either sand or air temperature. For some sites air temperatures have previously been used to predict sand temperature (e.g. Laloë et al., 2017) while for other sites sea surface temperatures are better predictors (e.g. Fuentes et al., 2009). For yet other sites using both air and sea surface temperatures produce best results (Bentley et al, 2020a; Chatting et al., 2021). We show here that for sites across the globe all these approaches give good predictions of sand temperatures. So if air temperatures are not available for a specific nesting site, sea surface

temperatures can be readily used as a reliable substitute for sand temperatures reconstructions and vice-versa. It is likely that the applicability of air temperatures and/or sea surface temperatures for predicting sand temperatures are locally variable. In general, it is expected that at island sites sea surface temperatures will play a greater role in influencing sand temperatures than at mainland sites. Additionally, we show that predictions of sand temperature using large-scale records agree with those using local air temperature records at one of our study sites, i.e. large-scale proxies give a good indication of local conditions. This result agrees with the recent finding that broad-scale environmental measurements can reflect local measurements (Hays et al., 2021). However, one important point to note is that the more local records – such as the air temperature records obtained from the airport used in our study – may not extend as far back in time as other large-scale records, and so reconstruction of past sand temperatures will be limited.

Our demonstration that either large scale air or sea temperature measurements can be used to reconstruct local temperatures, will help a number of important questions to be addressed. It is well established that female-skewed hatchling sex ratios predominate at rookeries around the world (e.g. Cuong et al., 2008; Hays et al., 2014; Booth et al., 2020). For instance, the largest green sea turtle rookery in the world was recently shown to be extremely female-biased (Jensen et al., 2018) and for our study site in Cape Verde, primary sex ratios were estimated to be > 70% female (Laloë et al., 2014). An important question is whether these skewed sex ratios are a normal feature for sea turtles and have persisted for a long time, possibly being adaptive by allowing increased population growth rates (Santidrián Tomillo & Spotila, 2020), or whether these skews are a maladaptive consequence of climate warming. Reconstructing the last century or more of sand temperatures on nesting beaches across the globe will help answer this question. Interestingly, our long-term sand temperature reconstructions reveal that incubation conditions currently reported at our study sites are not very different to conditions for the several past decades, as temperatures have increased at a slow rate of < 0.5 °C per century. So, it is likely that sex ratio production at these sites will have stayed relatively stable over the last century. For example, the biased sex ratios estimated in Cape Verde (Laloë et al., 2014) are likely not a new occurrence. Similarly, on Ascension Island's North East Bay sand temperatures are well above the pivotal temperature for TSD (Figure 2a), so it is unlikely that sex ratios have changed drastically over the past 100 years. If similar results were found at other nesting sites, it might suggest that biased hatchling sex ratios, at least to a certain extent, may in fact be quite normal for sea turtles and might serve to increase hatchling production and population resilience by having more

breeding females (Hays et al., 2017). However, it is important to underline that because of the steepness of the relationship between incubation temperature and hatchling sex ratio at the pivotal temperature (Bentley et al., 2020b), a 0.3 °C change in temperature at or near the pivotal temperature can lead to a large change in hatchling sex ratio. Additionally, there is important variability in sand temperatures both at shorter time-scales (e.g. Staines et al. 2020) and also between sites on the same beach (Esteban et al. 2016). So to gain a full picture of the likely long-term changes in sand temperatures, these sources of variability need to be assessed in addition to long-term changes. For example, it may be that even when the mean sand temperature on a beach drives the production of one sex, that thermal variability within a beach or over short time-scales may help ensure at least some production of the other sex (e.g. Porter et al. 2021).

In recent years, elegant mechanistic microclimate modelling approaches that rely on a suite of environmental variables have been used to reconstruct sand temperatures at turtle nesting sites (Fuentes and Porter, 2013; Bentley et al., 2020a). Advantages of the mechanistic model include that it can be forced with novel combinations of environmental variables to explore the impacts of climate change on sea turtle nesting grounds (Patrício et al., 2021) and that it is also possible to model sand temperatures over fine temporal scales (e.g. days or hours). However, microclimate models often require locally-calibrated input parameters (e.g. sand and beach properties as well as meteorological variables). Furthermore, projections are equally difficult to parametrize due to a lack of information regarding future environmental regimes (Patrício et al., 2021). Regardless, when applied correctly, mechanistic microclimate models can predict sand temperatures at sea turtle rookeries accurately, which in turn can help explore the impacts of climate change on beach temperatures (Bentley et al., 2020a). As mechanistic models are becoming readily accessible (e.g. through different R packages) alongside vast volumes of gridded climate data, they provide a powerful tool for investigating climate impacts in particular microhabitats.

Thanks to accessible online climate data repositories, the correlative approach is also easy to implement. One advantage of the correlative model is that it requires fewer input parameters than typical mechanistic models and so is usually easier to implement. On the other hand the correlative method may not be as reliable as the mechanistic model when making projections that fall outside of the range of observed values. However this was not an issue in our study since we were able to record large intra- and inter-seasonal variation by having temperature loggers deployed year-round and over multiple nesting season at all our study sites, and hence had a wide range of observations upon which to base our model. This

is confirmed by the fact that very few hindcasted values fell outside the range of values used to inform our models (Supplemental figure 2). Finally, both the mechanistic approach and the correlative method were shown to produce very similar results (Kearney et al., 2010; Bentley et al., 2020a) and, as detailed above, each approach has its advantages and drawbacks (Patrício et al., 2021). Our work and that of others (Bentley et al. 2020a), suggests that, when used appropriately, both mechanistic and correlative models will have broad utility as approaches for assessing how thermal conditions have changed on turtle nesting beaches, and other habitats, over the last century.

Ideally, more *in situ* sand temperature data will become available for nesting sites around the world both as temperature loggers become more widely used and data availability improves in academic publishing (Alsheikh-Ali et al., 2011; Munafò et al., 2017; Shin et al., 2020). However, it is likely that there will remain a huge number of nesting sites where *in situ* data continues to be lacking and so it would be useful to be able to estimate trends in nest temperatures for such sites. While absolute sand temperatures at a site may be influenced by physical and environmental factors such as sand colour (i.e. dark beaches are warmer Hays et al., 2003; Laloë et al., 2014), extent of shading (Esteban et al., 2016) and rainfall (Houghton et al., 2007; Laloë et al., 2020b, Staines et al., 2020), we found that the gradient of the relationship between sand temperature at nest depth and air temperature was relatively constant across nesting sites. So, by knowing simply the change in air or sea temperature for the last century at a site where there are no *in situ* sand temperature measurements, it might be possible to make a fairly accurate prediction of the likely changes in sand temperature at nest depths. In this way our finding of little change in sand temperatures at nest depths for several nesting sites could be extended to many more sites globally.

In summary, we show the broad utility of how environmental proxies may be used to reconstruct past conditions and we highlight how this approach could be used, not only for sea turtle nesting sites around the globe, but also for other species and habitats where predictions of temperatures in specific microclimates are difficult. Furthermore, there is intense interest in how climate change is impacting a number of coastal environments, such as coral reefs, mangroves and salt-marshes. Given the strong links we show between local temperature measurements and large-scale environmental proxies, it is likely that historic temperatures can reliably be reconstructed across this broad range of coastal habitats, allowing current conditions to be placed into a longer-term perspective.

Acknowledgments

This work was supported by the Bertarelli Foundation as part of the Bertarelli Programme in Marine Science (BPMS-2017-4). The turtle images used in Figure 2 were kindly provided by NOAA Fisheries (www.fisheries.noaa.gov).

Authors' contribution

G.C.H., J.-O.L. and N.E. conceived the ideas and designed the study. J.-O.L. and W.J.C. developed the statistical methods and analysed the data. J.-O.L. and G.C.H. led the manuscript writing. All authors contributed critically to manuscript drafts and gave final approval for publication.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

- Alsheikh-Ali, A. A., Qureshi, W., Al-Mallah, M. H., & Ioannidis, J. P. (2011). Public availability of published research data in high-impact journals. *PloS One*, 6, e24357. <https://doi.org/10.1371/journal.pone.0024357>
- Bentley, B. P., Kearney, M. R., Whiting, S. D., & Mitchell, N. J. (2020a). Microclimate modelling of beach sand temperatures reveals high spatial and temporal variation at sea turtle rookeries. *Journal Thermal Biology*, 88, 102522. <https://doi.org/10.1016/j.jtherbio.2020.102522>
- Bentley, B. P., Stubbs, J. L., Whiting, S. D., & Mitchell, N. J. (2020b). Variation in thermal traits describing sex determination and development in Western Australian sea turtle populations. *Functional Ecology*, 34, 2302-2314. <https://doi.org/10.1111/1365-2435.13645>
- 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>
- Chatting, M., Hamza, S., Al-Khayat, J., Smyth, D., Husrevoglu, S., & Marshall, C. D. (2021). Feminization of hawksbill turtle hatchlings in the twenty-first century at an important regional nesting aggregation. *Endangered Species Research*, 44, 149-158. <https://doi.org/10.3354/esr01104>

- Chivers, W. J., Walne, A. W., & Hays, G. C. (2017). Mismatch between marine plankton range movements and the velocity of climate change. *Nature Communications*, 8, 14434. <https://doi.org/10.1038/ncomms14434>
- Corrège, T. (2006). Sea surface temperature and salinity reconstruction from coral geochemical tracers. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 232, 408-428. <https://doi.org/10.1016/j.palaeo.2005.10.014>
- Cuong, T. C., Booth, D. T., & Limpus, C. J. (2008). Estimating the sex ratio of loggerhead turtle hatchlings at Mon Repos rookery (Australia) from nest temperatures. *Australian Journal of Zoology*, 56, 57-64. <https://doi.org/10.1071/ZO08004>
- Davis, B. A., Brewer, S., Stevenson, A. C., & Guiot, J. (2003). The temperature of Europe during the Holocene reconstructed from pollen data. *Quaternary Science Reviews*, 22, 1701-1716. [https://doi.org/10.1016/S0277-3791\(03\)00173-2](https://doi.org/10.1016/S0277-3791(03)00173-2)
- Duarte, C. M. (2017). Reviews and syntheses: Hidden forests, the role of vegetated coastal habitats in the ocean carbon budget. *Biogeosciences*, 14, 301-310. <https://doi.org/10.5194/bg-14-301-2017>
- Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677-697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- 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, 1-8. <https://doi.org/10.1038/srep20339>
- 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>
- Fuentes, M. M. P. B., & Porter, W. P. (2013). Using a microclimate model to evaluate impacts of climate change on sea turtles. *Ecological Modelling*, 251, 150-157. <https://doi.org/10.1016/j.ecolmodel.2012.12.020>
- Fuentes, M. M., Monsinjon, J., Lopez, M., Lara, P., Santos, A., dei Marcovaldi, M. A., & Girondot, M. (2017). Sex ratio estimates for species with temperature-dependent sex determination differ according to the proxy used. *Ecological Modelling*, 365, 55-67. <https://doi.org/10.1016/j.ecolmodel.2017.09.022>

- Glen, F., & Mrosovsky, N. (2004). Antigua revisited: the impact of climate change on sand and nest temperatures at a hawksbill turtle (*Eretmochelys imbricata*) nesting beach. *Global Change Biology*, 10, 2036-2045. <https://doi.org/10.1111/j.1529-8817.2003.00865.x>
- Godley, B. J., Broderick, A. C., Downie, J. R., Glen, F., Houghton, J. D., Kirkwood, I., Reece, S., & Hays, G. C. (2001). Thermal conditions in nests of loggerhead turtles: further evidence suggesting female skewed sex ratios of hatchling production in the Mediterranean. *Journal of Experimental Marine Biology and Ecology*, 263, 45-63. [https://doi.org/10.1016/S0022-0981\(01\)00269-6](https://doi.org/10.1016/S0022-0981(01)00269-6)
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8, 993-1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- 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>
- Hawkes, L. A., Broderick, A. C., Godfrey, M. H., Godley, B. J., & Witt, M. J. (2014). The impacts of climate change on marine turtle reproductive success. *Coastal Conservation*. Cambridge University Press, Cambridge, 287-310.
- Hays, G. C. , Godley, B. J., & Broderick, A. C. (1999). Long-term thermal conditions on the nesting beaches of green turtles on Ascension Island. *Marine Ecology Progress Series*, 185, 297-299. <http://www.jstor.org/stable/24853219>
- 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., 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>

484 Hays, G. C., Chivers, W. J., Laloë, J. O., Sheppard, C., & Esteban, N. (2021). Impact of
 485 marine heatwaves for sea turtle nest temperatures. *Biology Letters*, 17, 20210038.
 486 <https://doi.org/10.1098/rsbl.2021.0038>

487 Houghton, J. D. R., Myers, A. E., Lloyd, C., King, R. S., Isaacs, C., & Hays, G. C. (2007).
 488 Protracted rainfall decreases temperature within leatherback turtle (*Dermochelys*
 489 *coriacea*) clutches in Grenada, West Indies: Ecological implications for a species
 490 displaying temperature dependent sex determination. *Journal of Experimental Marine*
 491 *Biology and Ecology*, 345, 71-77. <https://doi.org/10.1016/j.jembe.2007.02.001>

492 Howard, R., Bell, I., & Pike, D. A. (2014). Thermal tolerances of sea turtle embryos: current
 493 understanding and future directions. *Endangered Species Research*, 26, 75-86.
 494 <https://doi.org/10.3354/esr00636>

495 Huang, R., Huang, J.-X., Zhang, C., Ma, H.Y., Zhuo, W., Chen, Y.-Y., Zhu, D.-H., Wu, Q.,
 496 & Mansaray, L. R. (2020). Soil temperature estimation at different depths, using
 497 remotely-sensed data. *Journal of Integrative Agriculture*, 19, 277-290.
 498 [https://doi.org/10.1016/S2095-3119\(19\)62657-2](https://doi.org/10.1016/S2095-3119(19)62657-2)

499 Jensen, M. P., Allen, C. D., Eguchi, T., Bell, I. P., LaCasella, E. L., Hilton, W. A., Hof, & C.
 500 A., Dutton, P. H. (2018). Environmental warming and feminization of one of the
 501 largest sea turtle populations in the world. *Current Biology*, 28, 154-159.
 502 <https://doi.org/10.1016/j.cub.2017.11.057>

503 Katselidis, K. A., Schofield, G., Stamou, G., Dimopoulos, P., & Pantis, J. D. (2012). Females
 504 first? Past, present and future variability in offspring sex ratio at a temperate sea turtle
 505 breeding area. *Animal Conservation*, 15, 508-518. <https://doi.org/10.1111/j.1469-1795.2012.00543.x>

507 Kearney, M. R., Wintle, B. A., & Porter, W. P. (2010). Correlative and mechanistic models
 508 of species distribution provide congruent forecasts under climate change.
 509 *Conservation Letters*, 3, 203-213. <https://doi.org/10.1111/j.1755-263X.2010.00097.x>

510 Laloë, J. O., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2014). Effects of rising
 511 temperature on the viability of an important sea turtle rookery. *Nature Climate*
 512 *Change*, 4, 513-518 (2014). <https://doi.org/10.1038/nclimate2236>

513 Laloë, J. O., Esteban, N., Berkel, J., & Hays, G. C. (2016). Sand temperatures for nesting sea
 514 turtles in the Caribbean: Implications for hatchling sex ratios in the face of climate
 515 change. *Journal of Experimental Marine Biology and Ecology*, 474, 92-99.
 516 <https://doi.org/10.1016/j.jembe.2015.09.015>

517 Laloë, J. O., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2017). Climate change and
 518 temperature-linked hatchling mortality at a globally important sea turtle nesting site.
 519 *Global Change Biology*, 23, 4922-4931. <https://doi.org/10.1111/gcb.13765>
 520 Laloë, J. O., Monsinjon, J., Gaspar, C., Tournon, M., Genet, Q., Stubbs, J., Girondot, M., &
 521 Hays, G. C. (2020a). Production of male hatchlings at a remote South Pacific green
 522 sea turtle rookery: Conservation implications in a female-dominated world. *Marine*
 523 *Biology*, 167, 1-13. <https://doi.org/10.1007/s00227-020-03686-x>
 524 Laloë, J. O., Tedeschi, J. N., Booth, D. T., Bell, I., Dunstan, A., Reina, R. D., & Hays, G. C.
 525 (2020b). Extreme rainfall events and cooling of sea turtle clutches: Implications in the
 526 face of climate warming. *Ecology and Evolution*, 11, 560-565.
 527 <https://doi.org/10.1002/ece3.7076>
 528 McMahon, C. R., & Hays, G. C. (2006). Thermal niche, large scale movements and
 529 implications of climate change for a critically endangered marine vertebrate. *Global*
 530 *Change Biology*, 12, 1330-1338. <https://doi.org/10.1111/j.1365-2486.2006.01174.x>
 531 Melo-Merino, S. M., Reyes-Bonilla, H., & Lira-Noriega, A. (2020). Ecological niche models
 532 and species distribution models in marine environments: A literature review and
 533 spatial analysis of evidence. *Ecological Modelling*, 415, 108837.
 534 <https://doi.org/10.1016/j.ecolmodel.2019.108837>
 535 Munafò, M. R., Nosek, B. A., Bishop, D. V., Button, K. S., Chambers, C. D., Du Sert, N. P.,
 536 Simonsohn, U., Wagenmakers, E.-J., Ware, J. J., & Ioannidis, J. P. (2017). A
 537 manifesto for reproducible science. *Nature Human Behaviour*, 1, 1-9.
 538 <https://doi.org/10.1038/s41562-016-0021>
 539 Patino-Martinez, J., Marco, A., Quiñones, L., & Hawkes, L. (2012). A potential tool to
 540 mitigate the impacts of climate change to the Caribbean leatherback sea turtle. *Global*
 541 *Change Biology*, 18, 401-411. <https://doi.org/10.1111/j.1365-2486.2011.02532.x>
 542 Patrício, A. R., Hawkes, L. A., Monsinjon, J. R., Godley, B. J., & Fuentes, M. M. (2021).
 543 Climate change and marine turtles: recent advances and future directions. *Endangered*
 544 *Species Research*, 44, 363-395. <https://doi.org/10.3354/esr01110>
 545 Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E., Butchart, S. H., Kovacs, K. M.,
 546 Scheffers, B. R., Hole, D. G., Martin, T. G., Akçakaya, H. R., & Corlett, R. T. (2015).
 547 Assessing species vulnerability to climate change. *Nature Climate Change*, 5, 215-
 548 224. <https://doi.org/10.1038/nclimate2448>
 549 R Core Team (2020). R: A language and environment for statistical computing. R Foundation
 550 for Statistical Computing, Vienna, Austria. <https://www.R-project.org>

551 Santidrián Tomillo, P., & Spotila, J. R. (2020). Temperature-dependent sex determination in
 552 sea turtles in the context of climate change: uncovering the adaptive significance.
 553 *BioEssays*, 42, 2000146. <https://doi.org/10.1002/bies.202000146>
 554 Shin, N., Shibata, H., Osawa, T., Yamakita, T., Nakamura, M., & Kenta, T. (2020). Toward
 555 more data publication of long-term ecological observations. *Ecological Research*, 35,
 556 700-707. <https://doi.org/10.1111/1440-1703.12115>
 557 Standora, E. A., & Spotila, J. R. (1985). Temperature dependent sex determination in sea
 558 turtles. *Copeia*, 711-722. <https://doi.org/10.2307/1444765>
 559 Rees, A. F., & Margaritoulis, D. (2004). Beach temperatures, incubation durations and
 560 estimated hatchling sex ratio for loggerhead sea turtle nests in southern Kyparissia
 561 Bay, Greece. *Testudo*, 6, 23-36.
 562 Richardson, A. J., & Schoeman, D. S. (2004). Climate impact on plankton ecosystems in the
 563 Northeast Atlantic. *Science*, 305, 1609-1612. <https://doi.org/10.1126/science.1100958>
 564 Staines, M. N., Booth, D. T., Hof, C. A. M., & Hays, G. C. (2020). Impact of heavy rainfall
 565 events and shading on the temperature of sea turtle nests. *Marine Biology*, 167, 1-11.
 566 <https://doi.org/10.14264/c90b3d0>
 567 Steiger, N. J., Steig, E. J., Dee, S. G., Roe, G. H., & Hakim, G. J. (2017). Climate
 568 reconstruction using data assimilation of water isotope ratios from ice cores. *Journal*
 569 *of Geophysical Research: Atmospheres*, 122, 1545-1568.
 570 <https://doi.org/10.1002/2016JD026011>
 571 Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y.
 572 C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L.,
 573 Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A.,
 574 Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk
 575 from climate change. *Nature*, 427, 145-148. <https://doi.org/10.1038/nature02121>
 576 Thurman, W. N., & Fisher, M. E. (1988). Chickens, eggs, and causality, or which came first.
 577 *American Journal of Agricultural Economics*, 70, 237-238.
 578 <https://doi.org/10.2307/1242062>
 579 Touchan, R., Meko, D. M., & Aloui, A. (2008). Precipitation reconstruction for Northwestern
 580 Tunisia from tree rings. *Journal of Arid Environments*, 72, 1887-1896.
 581 <https://doi.org/10.1016/j.jaridenv.2008.05.010>
 582 Woodruff, S. D. (2001). COADS updates including newly digitized data and the blend with
 583 UK Meteorological Office Marine Data Bank and Quality control in recent COADS
 584 updates. In: Proceedings of Workshop on Preparation, Processing and Use of

585 Historical Marine Meteorological Data, 28-29 November 2000, Tokyo, Japan. Japan
586 Meteorological Agency and the Ship and Ocean Foundation, pp. 9-13.