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# Phenological shift mitigates predicted impacts of climate change on sea turtle offspring

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ABSTRACT: Many studies have documented the impacts of climate change on species and ecosystems, but few have shown how species may respond to mitigate these effects. For species with temperature-dependent sex determination, rising temperatures directly impact offspring sex ratios. If species do not change their geographic ranges, phenology of breeding or thermal restrictions for incubation, sex ratios will become skewed towards that produced at higher temperatures and hatching success may be impacted. Using nearly 3 decades of empirical data (1993–2021) and a heuristic model, we show that if the seasonality of nesting remains unchanged, by 2100, loggerhead turtles *Caretta caretta* at our study site will produce almost no offspring. Modelling the advancement of nesting by 0.5 d $yr^{-1}$ stabilised offspring sex ratios at their current rate, but advancement of 0.7 d $yr^{-1}$ was required to stabilise hatching success. This population, however, has responded to rising temperatures, with advancements in both the mean day of the nesting season and onset of nesting (5th percentile ordinal day) by 0.23 and 0.43 d $yr^{-1}$, respectively, since 1993. However, returning females that have higher fidelity to the site have advanced the mean day of nesting and the onset of nesting by 0.54 and 0.78 d $yr^{-1}$, respectively, which is within range of those predicted by our heuristic models to stabilise offspring sex ratios. Our study suggests that loggerhead turtles at this site are currently compensating for the predicted negative impacts of rising temperatures on offspring sex ratios through a change in the phenology of breeding.

KEY WORDS: Phenology · Climate change · Sex ratios · Sea turtles · Loggerhead turtle

## 1. INTRODUCTION

Species may alter their spatial ranges (Doody et al. 2006) or the timing of key life-history behaviours in response to climate change (Todd et al. 2011, Saba et al. 2012, Gill et al. 2014); however, such alterations may result in trophic mismatch in the timing and synchrony of ecosystems, potentially leading to an alteration in niche overlap with other species (Todd et al. 2011, Du et al. 2023). Species undertaking such spatial or phenological alterations may be able to adapt to new environments; however, for long-lived species with extended generation times, there is concern that adaptation may not be possible within the timescales (~100 yr) during which the greatest rate of change in global temperature is predicted to occur (IPCC 2021).

One such group is marine turtles. Most species are wide-ranging, occupy entire ocean basins during their life cycle, take 20–50 yr to reach maturity, exhibit natal philopatry (return to breed at the same coastal area where they hatched) and have temperature-dependent sex determination (Miller 1997). In this taxon, female offspring are produced at higher nest incubation temperatures, and female-biased sex ratios are the norm (Witt et al. 2010). As such, it has been proposed that predicted increases in environmental

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temperature associated with global climate change will have wide-ranging impacts, including a change in habitat availability and altered offspring production, potentially leading to increased wide-scale feminisation and mortality, particularly under extreme climate warming scenarios (Patrício et al. 2021). There is little evidence to suggest that marine turtles might vary in their pivotal temperature (the temperature at which an equal offspring sex ratio is produced) or in the thermal tolerance range of developing embryos as an adaptation to climate warming (Mitchell & Janzen 2010, Patrício et al. 2021), although there is some evidence that the transitional range of temperature (when both sexes are produced) is variable across species and geographic regions (Lolavar & Wyneken 2020, Rivas et al. 2024, Santidrián Tomillo et al. 2024). Altering the timing of nesting to ensure that incubation occurs within a suitable thermal window for egg development is one method by which marine turtles may mitigate the impacts of climate change on incubating embryos (Fuentes et al. 2024). For some marine turtle species, the phenology of nesting has been found to be driven by temperature in the foraging grounds (Monsinjon et al. 2019b) or at the nesting beach (Pike et al. 2006, Hawkes et al. 2007, Weishampel et al. 2010), with some studies reporting a directional shift in the phenology of nesting over time (Pike et al. 2006, Mazaris et al. 2008, Lamont & Fujisaki 2014, Neeman et al. 2015, Monsinjon et al. 2019b). The majority of these studies of the loggerhead turtle *Caretta caretta* found higher temperatures related to earlier breeding (Mazaris et al. 2013, Lamont & Fujisaki 2014); however, in one study of leatherback turtles *Dermochelys coriacea* (Neeman et al. 2015), increasing temperatures at the foraging grounds delayed the onset of nesting. Higher temperatures have also been found to affect the duration of the nesting season, which itself will alter the thermal window of incubation but might also result from the changing demographics of the population or conditions at the foraging grounds affecting clutch production (Pike et al. 2006, Monsinjon et al. 2019a).

Understanding how species are responding to rising temperatures informs predictions of the impact of future climate scenarios and can guide mitigation methods. Although some studies have explored how rising temperatures might drive a change in the phenology or timing of the nesting season and the subsequent impacts on offspring sex ratios (Weishampel et al. 2010, Mazaris et al. 2013, Patel et al. 2016, Reneker & Kamel 2016, Almpanidou et al. 2018, Monsinjon et al. 2019a,b), none have compared these predictions with current responses in the phenology of nesting. Using empirical data at our long-term study site in Cyprus, we modelled the impact of rising sea surface temperatures on loggerhead turtle offspring sex ratios and hatch success and the phenological shift needed to mitigate these impacts. We compared these findings with empirical data to test whether this population is responding to rising temperatures by shifting the phenology of nesting and determined whether the current response is adequate to mitigate the predicted impacts of rising temperatures.

## 2. MATERIALS AND METHODS

### 2.1. Empirical data

Loggerhead turtle nesting has been monitored at the Alagadi rookery (North Cyprus, Eastern Mediterranean; 35.5° N, 33.8° E) since 1993 for the entire duration of each nesting season, from mid-May to early October (Omeyer et al. 2021). Females at this site have been tracked to foraging locations around the eastern Mediterranean and north African coast (Haywood et al. 2020). At this site, females are tagged after laying, using both flipper (since 1992) and passive integrated transponder tags (since 1997), which have increased the accuracy of recapture data (Omeyer et al. 2019). Nests are marked at laying and monitored daily throughout the reproductive season. Following hatching, clutches are excavated and data are gathered, including incubation duration (days), depth to the bottom of the egg chamber (cm), number of eggs laid and hatching success (the percentage of eggs laid that hatched). We removed relocated clutches from our analyses of these metrics, as relocation will alter the thermal environment for incubation. In addition, we removed clutches from 1993–1996 from analyses, as during these years only clutches that hatched were excavated to assess success, meaning that some clutches with low success rates may not have been detected, artificially increasing the annual hatching success for these years and potentially biasing data on incubation duration and depth. Data from these early years of monitoring (1993–1996) are, however, presented in the figures. Logistical constraints in 2000 and 2001 meant that surveying began shortly after the laying of the first nest; as such, data on nesting seasonality for those years have been excluded from analyses. In 2020 and 2021, because of COVID-19 restrictions, nightly patrols of the beach were not always possible and are not included in our analysis of remigrant (returning) turtle arrival dates. The onset of the nesting season in each year was set as the 5th percentile value of clutch lay dates at the rookery. Annual metrics, including mean ordinal day of nesting and nesting season duration (days elapsed between first and last nest), were also calculated from nest lay dates. Temporal patterns in sex ratios, hatching success, depth and incubation duration were analysed using general linear models with a Gaussian link identity, with sex ratio and hatching success data logit transformed.

A selection of clutches (n = 300, 1996–2021) were instrumented with temperature data loggers (Tinytag Plus 2 TGP 4017, Tinytalk TG 4005; Gemini Dataloggers; resolution 0.1–0.01°C, accuracy 0.2°C) checked against a calibrated unit under constant temperature. Data loggers were placed at the centre of the clutch during egg laying, recording ambient clutch temperature at an hourly frequency. For these clutches, we calculated the mean clutch temperature for the mid-third of incubation (mtCT), the thermosensitive period during which sex is determined (Yntema & Mrosovsky 1982). We obtained historic mean daily sea surface temperature (SST) for each mid-third period (mtSST) from the sea area adjacent to the rookery using ERA5 data (Copernicus Data Service; 0.25° square; horizontal resolution). We then determined (1) the relationship between mtSST and mtCT (linear regression, adjusted $R^2 = 0.47$, $F_{1,298} = 267.9$, $p < 0.001$; Fig. S1a in the Supplement at www.int-res.com/articles/suppl/n056p041_supp.pdf); (2) the relationship between mtCT and arcsin hatching success, given that hatching success values were skewed (quadratic regression, adjusted $R^2 = 0.18$, $F_{2,297} = 32.98$, $p < 0.001$; Fig. S1b); and (3) estimate offspring sex ratios using the actual or predicted (from mtSST) mtCT and the established temperature sex ratio curve for this population (Fuller et al. 2013). These relationships were used in the heuristic model and enabled us to estimate the proportion of female offspring produced for clutches at the Alagadi rookery, for which we did not have a direct measure of clutch temperature.

### 2.2. Heuristic model

The heuristic model operated on a daily time step and used the above 3 relationships that define key responses between marine turtle reproductive ecology and environmental temperature. The model operated as follows: for each day between 2022 and 2098, 3 model clutches started incubating, each with a defined incubation duration of 41, 48 and 63 d (observed min., mean and max. from empirical data). For each modelled clutch, we calculated the start and end dates of the mid-third period of incubation. We then determined the predicted future mean daily SST for this period from the sea area adjacent to the Alagadi rookery using data from the Hadley Centre Global Environment Model version 2 (HadGEM2; 0.25° square; horizontal resolution). We used daily predictions from model runs operating on the Representative Concentration Pathway (RCP) 8.5. Each predicted future daily SST used in the heuristic model was a mean ensemble from 4 realizations but with constant physical perturbations across model runs. This data set of future daily values was adjusted for mean and variance using the relationship between modelled SST (hindcast values from HadGEM2) and observed SST (from ERA5) during April–August for the period when both data sets had simultaneous temporal coverage (2006–2021), using the method of Sheppard (2003). Following this process, HadGEM2 daily SST values in future years (2022–2098) were adjusted upwards by 0.194°C, the error between the 2 models. Using these values, we determined the mtCT for each of the modelled clutches. This derived mtCT was then used to calculate sex ratio (proportion female), hatching success (percentage hatched) and offspring production for each modelled clutch (assuming an arbitrary value of 100 eggs per clutch). If estimated mean mtCT occurred outside thermal limits associated with clutches providing viable offspring (defined from empirical data; range: 28.8–35.4°C, n = 300 clutches), we assigned the proportion female, hatching success and offspring production for this clutch as zero.

The daily estimates of the proportion of females (sex ratio), hatching success and offspring production were then seasonally weighted prior to their contribution to respective annual estimates. This seasonal weighting represented a daily estimate of the proportion of annual nesting occurring on each day. This weighting was first developed from empirical data (2017–2021) and subsequently adjusted by moving the current mean day of nesting (Day 175) forward but retaining a constant seasonal width ($\sigma = 19.6$ d) to explore the effect of changing nesting phenology on sex ratio, hatching success and offspring production. A LOESS regression line was fitted to these data for visualisation of the direction of change.

Numerical modelling was conducted in Matlab 2023a (update 2); statistics and graphing were conducted in R (version 4.3.3; R Core Team 2023).

## 3. RESULTS

Mean daily April SST, the month when loggerhead turtles are observed in proximity to the nesting beach in advance of breeding, has increased at the site during the study period (Fig. 1) and is predicted to increase under the RCP 8.5 scenario from HadGEM2 by ~4°C over the next century.

Offspring sex ratios at this site are highly female-biased, with median annual sex ratios of clutches ranging from 87.8 to 97.6% female (Fig. 2a) and increasing across the study (1997–2021, $t_{1,649} = 1.964$, $p = 0.05$; Fig. S2a). Median annual hatching success ranged from 57.8 to 85.2% (Fig. 2b), with no significant trend in hatching success across the study period ($t_{1,739} = 0.043$, $p = 0.99$; Fig. S2b). There was no significant change in the depth at which clutches were laid across our study ($t_{1,727} = 0.566$, $p = 0.57$; Fig. S3c), with median annual depth ranging from 45 to 54.3 cm (Fig. 2c). Clutch incubation duration has, however, increased through time (1997–2021, $t_{1,649} = 4.552$, $p < 0.001$; Fig. S2d), with median annual incubation duration ranging from 45 to 50 d (Fig. 2d).

Our predictive model was initialised with a constant seasonal pattern of nesting (mean ordinal day of season: Day 174; seasonal width: 19.6 d [1 SD], derived from empirical data 2017–2021), representing a scenario of no phenological change. By 2100, this model predicts that the percentage of female offspring produced will increase to ~99% (Fig. 3a), hatching success will decline to less than 10% (Fig. 4a) and the number of offspring produced will also decline to less than 10% (Fig. 5a).

Advancement in the nesting season towards earlier nesting of 0.2, 0.5 and 0.7 d $\text{yr}^{-1}$ produced varying responses (Figs. 3–5). An advancement of 0.2 d $\text{yr}^{-1}$ resulted in a continued increase in the proportion of female offspring (Fig. 3b) and declines in hatching success (Fig. 4b) and offspring production (Fig. 5b). Advancing by 0.5 d $\text{yr}^{-1}$ stabilised the proportion of female offspring through to 2100 at ~90–95% (Fig. 3c); whereas advancement of 0.7 d $\text{yr}^{-1}$ was required to stabilise hatching success at its current levels (Fig. 4d).

There has, however, been a phenological change at this site. At the population level, the annual mean day of nesting advanced by 0.23 d $\text{yr}^{-1}$ (range: 166–191; linear regression, $F_{1,27} = 4.25$, $R^2 = 0.10$, $p = 0.0$; Fig. 6a) and the onset of nesting (5th percentile ordinal day) by 0.43 d $\text{yr}^{-1}$ (range: 132–168; linear regression, $F_{1,27} = 13.82$, $R^2 = 0.31$, $p < 0.001$; Fig. 6a). However, nesting females that have bred at the study site in more than one season (remigrants, n = 92 females) revealed a stronger phenological response, with the mean day of nesting advancing by 0.54 d $\text{yr}^{-1}$ (range: 161–190; linear regression, $F_{1,23} = 21.52$, $R^2 = 0.45$, $p < 0.001$; Fig. 6b) and the onset of nesting advancing by 0.78 d $\text{yr}^{-1}$ (range: 141–180; linear regression, $F_{1,23} = 41.64$, $R^2 = 0.63$, $p < 0.001$; Fig. 6b). There was no trend in nesting season duration (days elapsed between first and last nest) throughout the study period (linear regression, 1993–2021, $F_{1,27} = 4.17$, $R^2 = 0.10$, $p > 0.05$; Fig. S3).

Mean daily SST during April predicted the annual mean ordinal day of nesting (linear regression, $F_{1,27} = 15.47$, $R^2 = 0.34$, $p < 0.001$; Fig. S4a), advancing at a rate of 3.7 d for every 1°C rise. Mean daily SST during April also predicted the onset of the nesting season (5th percentile ordinal day) (linear regression, $F_{1,27} = 24.97$, $R^2 = 0.46$, $p < 0.001$; Fig. S4b) advancing at a rate of 5.1 d for every 1°C rise.

## 4. DISCUSSION

Without a considerable phenological change in the latter half of this century to ameliorate further acceleration of climate warming, the outlook for our population of loggerhead turtles could be bleak; male production would almost entirely cease by 2100. Our study, however, shows that if the mean day of nesting advances at between 0.5 and 0.7 d $\text{yr}^{-1}$, the impacts of predicted SST on offspring production would remain within the range estimated in our study. Indeed, our empirical data for remigrant turtles fall within this rate of change, suggesting that this response is in progress and may mitigate

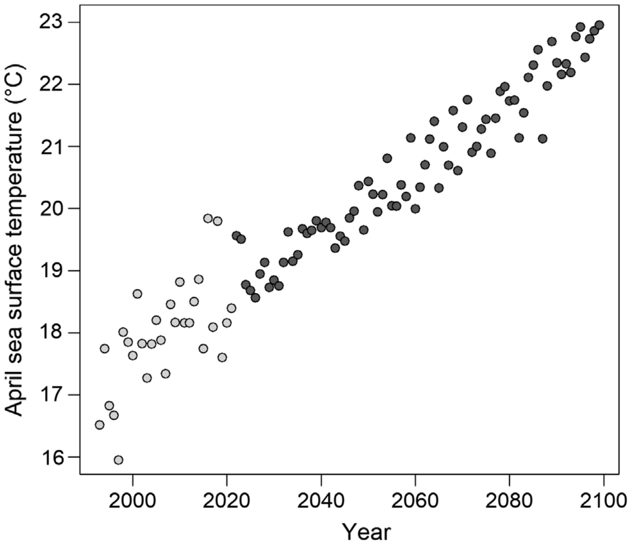

Fig. 1. Historic and future sea surface temperature time series at Alagadi rookery, North Cyprus, showing April daily mean sea surface temperature; observed data (1993–2022; ERA5, light grey circles) and predicted following adjustment (HadGEM2 RCP 8.5, dark grey filled circles)

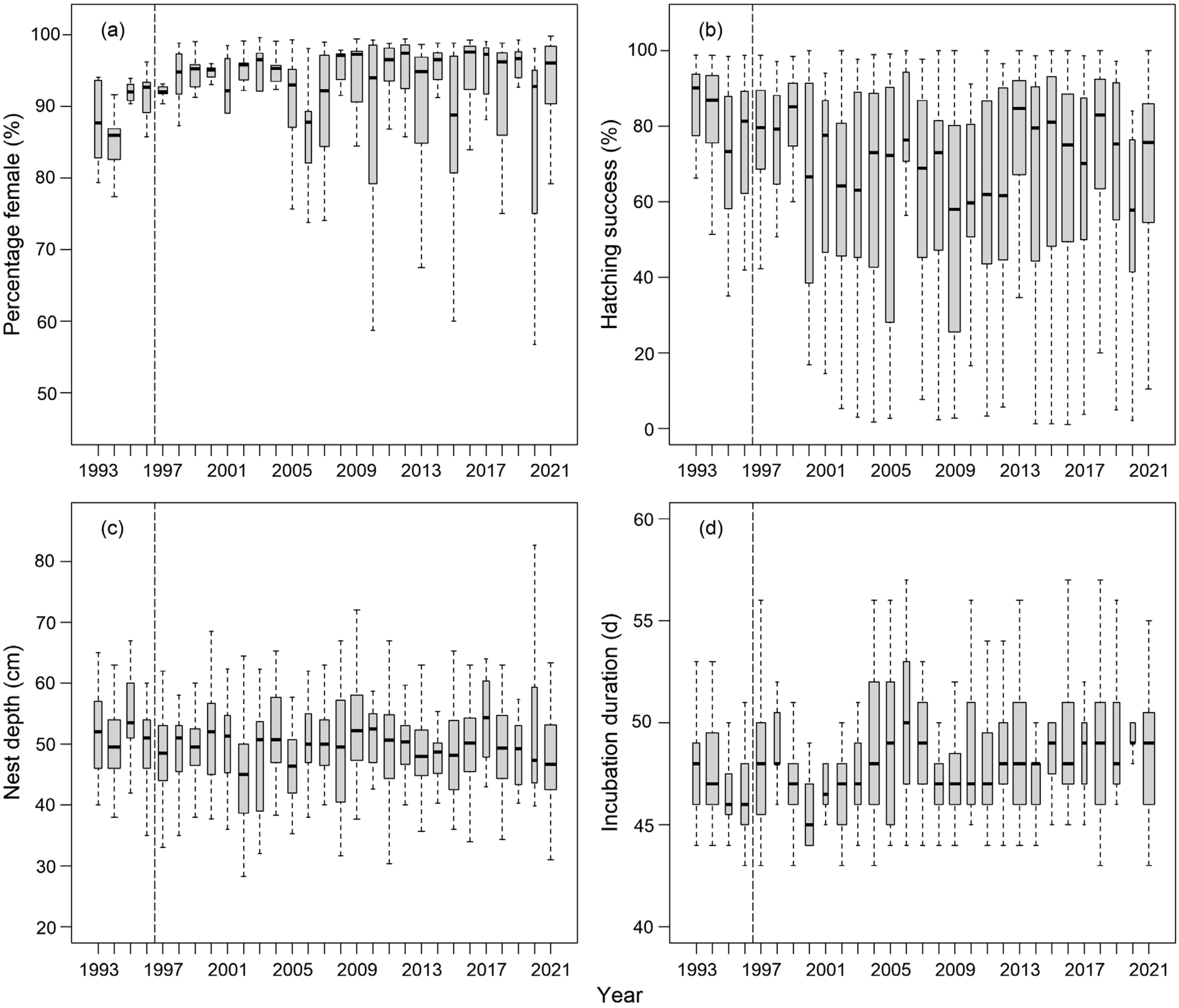

Fig. 2. Annual median (black horizontal line), interquartile range (upper and lower extents of vertical box) and tails (broken vertical lines) extending to approximately 2.5th and 97.5th percentiles (1993–2021) of (a) percentage female loggerhead turtle offspring, (b) percentage hatching success, (c) nest depth and (d) incubation duration at the Alagadi rookery. Box widths are indicative of relative differences in annual sample size. Vertical broad dashed line: data collected before (≤1996) and after (≥1997) changes in nest excavation protocols

at least some of the predicted impacts of increasing temperatures on loggerhead turtle offspring.

Our empirical data show advancement of the nesting season, a finding that has been previously reported elsewhere in this region and at other locations and a predicted response to global warming in multiple studies (Mazaris et al. 2013, Laloë & Hays 2023, Fuentes et al. 2024, Şirin & Başkale 2024). In addition, the predicted offspring sex ratios at our site have become more female-biased over the study period, although this is a weak relationship that appears to have stabilised in recent years. While the majority of marine turtle studies report female-biased offspring sex ratios (Witt et al. 2010, Fuller et al. 2013) and many predict further bias under future climate change scenarios (Katselidis et al. 2012), few have longer-term empirical data with which to explore changes over time (Reneker & Kamel 2016; those that do have reported the influence of rainfall and storms impacting incubation durations and resulting predicted offspring sex ratios (Reneker & Kamel 2016).

Incubation durations at our site have also significantly increased over time (1997–2021), which we believe is at least partly related to a change in

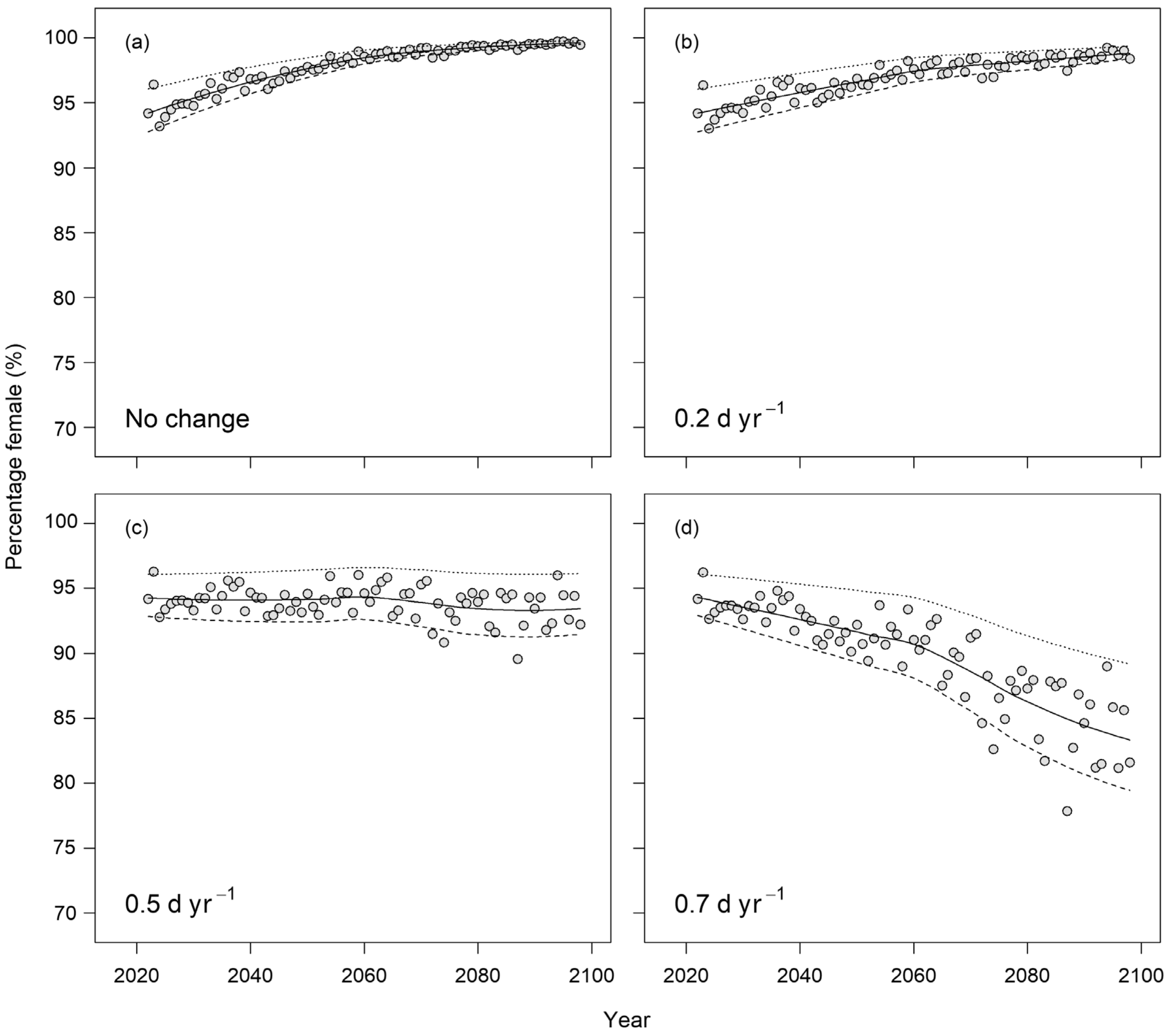

Fig. 3. Sex ratio (percentage female) of loggerhead turtle offspring under 4 scenarios of adaptation to climate change with respect to mean day of nesting: (a) no change, (b) advance of 0.2 d yr$^{-1}$, (c) advance of 0.5 d yr$^{-1}$ and (d) advance of 0.7 d yr$^{-1}$. Annual value (circles) for 48 d incubation duration model, LOESS regression for 41, 48 and 63 d model (dotted, solid and dashed lines, respectively)

management practice. In 2007, we began reducing the number of clutches that were relocated to safer locations further from the sea owing to concern that we might be further skewing sex ratios when relocating to potentially hotter locations. This resulted in more clutches being washed over, some of which failed as a result. However, for those that hatched, many had reduced hatching success and longer incubation durations as a result of cooling. In addition, maternal effects such as nest site selection, depth of clutch and clutch size will all impact incubation and may be driven by changes in the demographic of the population (Omeyer et al. 2021, Wu et al. 2022). In the past decade, we have also experienced more storms during the nesting season, leading to loss of clutches but also inundation and cooling of clutches, resulting in longer incubation durations, which may result in more male production but overall fewer offspring being produced.

The difference in both the onset of nesting and mean day of the season of remigrant turtles in comparison to the overall population, including females that have only ever been recorded nesting in one season, is likely a result of variation in reproductive output and fidelity recorded in these groups. At our study site, remigrant females lay more clutches in a breeding year (Omeyer et al. 2021), which may be a result of increasing reproductive output with age but is also a result of higher fidelity to Alagadi Beach. As

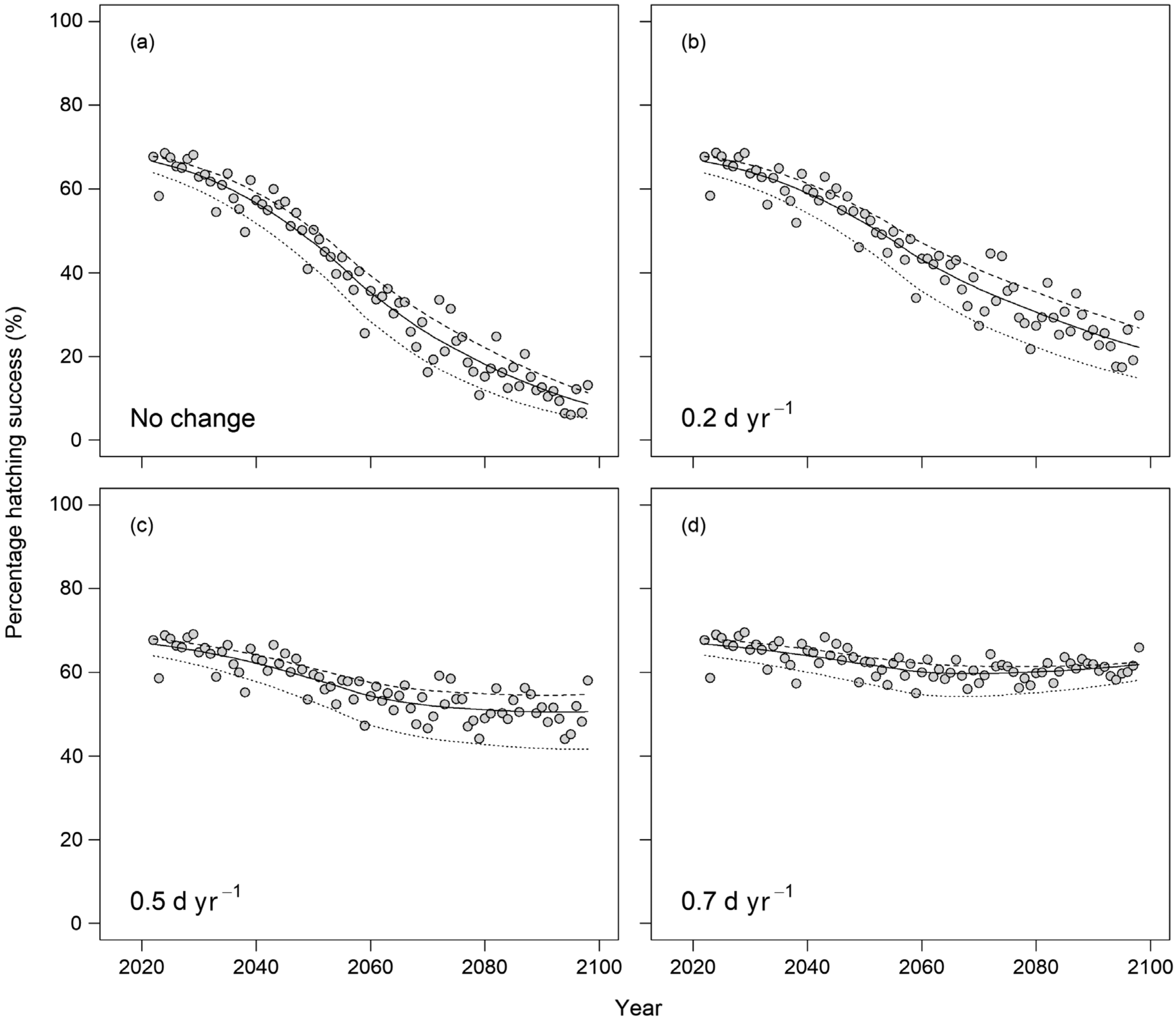

Fig. 4. Percentage hatching success of loggerhead turtle clutches under 4 scenarios of adaptation to climate change with respect to mean day of nesting: (a) no change, (b) advance of 0.2 d yr$^{-1}$, (c) advance of 0.5 d yr$^{-1}$, and (d) advance of 0.7 d yr$^{-1}$. Annual value (circles) for 48 d incubation duration model, LOESS regression for 41, 48 and 63 d model (dotted, solid and dashed lines, respectively)

a result, we recapture more nesting events for remigrant turtles at our study site, and we believe the advancement recorded for this group is likely to be more accurate. The demographics of the population, however, may also impact overall population offspring sex ratios, with remigrant females that are larger on average, arrive earlier and produce a greater number of eggs across the season (Omeyer et al. 2021, Wu et al. 2022). Understanding how demographics and maternal effects drive phenology is important but challenging, as it requires knowledge of the arrival dates of individual females.

In our study, we predicted the offspring sex ratio using a field-derived clutch thermal response model (Fuller et al. 2013) dependent upon the mean temperature of the middle third of incubation. The middle third of development and the middle third of incubation, however, are not the same in laboratory and field studies owing to the number of days (e.g. 3–4) for offspring to emerge from the nest. Studies have suggested methods to more accurately estimate this middle third period (Girondot & Kaska 2014) in field studies; however, the difference in these methods has been shown to be negligible (Fuentes et al. 2017, Patrício et al. 2017). To minimise this potential error and create realistic constraints around our predictions, we ran models using the minimum, mean and maximum incubation durations recorded in this study.

Marine turtle life histories are profoundly affected by temperature (Godley et al. 2001, Hawkes et al. 2009, Poloczanska et al. 2009), and other biological changes might also be predicted within a warmer en-

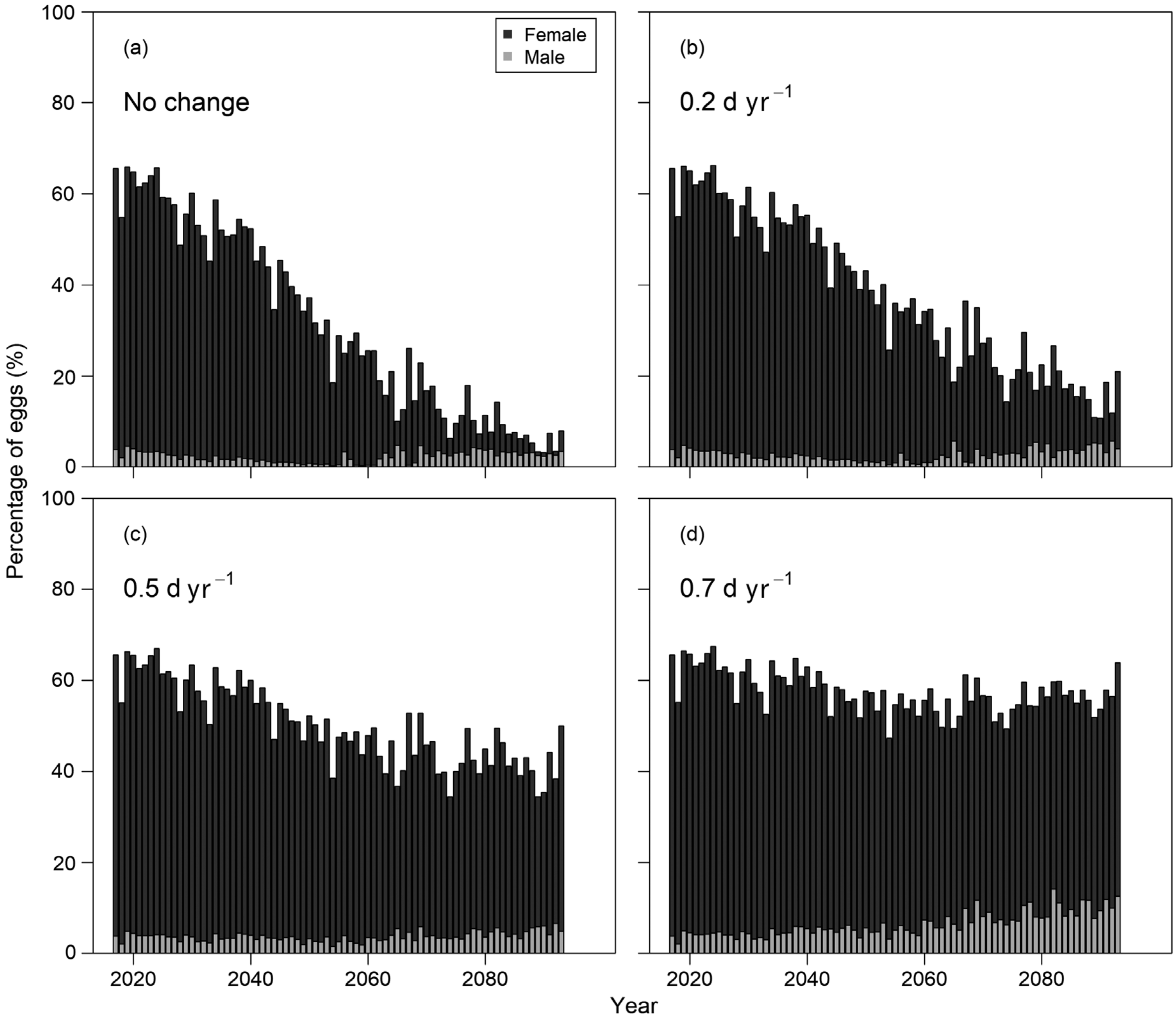

Fig. 5. Percentage of loggerhead turtle eggs surviving to hatching and their sex under 4 scenarios of adaptation to climate change with respect to mean day of nesting: (a) no change, (b) advance of 0.2 d yr$^{-1}$, (c) advance of 0.5 d yr$^{-1}$ and (d) advance of 0.7 d yr$^{-1}$. Showing data from 48 d incubation duration model

vironment. As capital breeders, turtles typically nest every 2–4 yr (Miller 1997), laying multiple clutches each year (2–3 clutches every 3–4 yr is typical for our population; Omeyer et al. 2021). This periodicity could change with rising temperatures, with females returning to reproductive readiness more quickly and potentially earlier in a warming world, laying more frequently, but perhaps fewer clutches per year in a shorter season or with altered offspring quality (Booth & Astill 2001). Alternatively, rising temperatures could result in longer nesting seasons, allowing more clutches to be laid and resulting in longer remigration intervals for recovery between nesting seasons. Although a change in the duration of the nesting season was not recorded in this study or at other Mediterranean nesting sites of this species to date (Mazaris et al. 2008), this has been found at other sites; for example, a reduction in the duration of the nesting season along with sequentially earlier nesting has been documented for loggerhead turtle populations on the Atlantic coast of the USA (Pike et al. 2006).

The nesting season in Cyprus is relatively short (May–September) compared to the tropics, with temperatures at the peak of summer approaching lethal levels for successful incubation. As temperatures continue to rise, we anticipate that we might see a change in the duration of the season, with the window of suitable incubation temperatures within a year reducing over time or a possible splitting of the season, with nesting in spring and autumn as peak summer temperatures reach lethal levels.

For marine turtles, however, rising temperature is not the only problem they face under climate change (Patrício et al. 2021). Sea level rise is predicted to

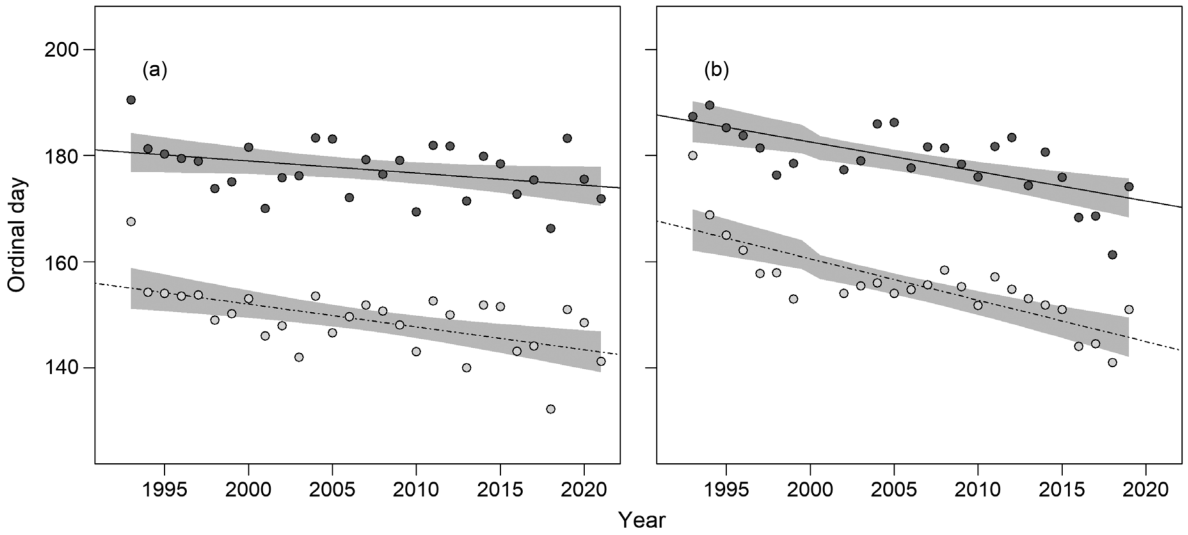

Fig. 6. (a) Population annual mean day of nesting for loggerhead turtle nesting at Alagadi rookery, considering all turtles (dark grey circles) with statistically significant linear regression (solid line, $y = -0.23x + 632.04$), and 5th percentile day of annual nesting onset (light grey circles) with statistically significant linear regression (dot-dashed line, $y = -0.43x + 1010.7$). (b) Remigrant annual mean day of nesting (dark grey circles) and 5th percentile day of nesting onset (light grey circles) with linear regressions (solid and dot-dashed lines, respectively: $y = -0.56x + 1293.45$, $y = -0.78x + 1720.07$). Grey shading: 95% confidence intervals for linear regressions (solid and dot-dashed lines)

result in a reduction in nesting habitat (Baker et al. 2006), a phenomenon which is likely to be worsened by anthropogenic changes leading to coastal squeeze (Fish et al. 2005). In addition, increased rainfall and extreme weather events may lead to clutch failure through inundation or destruction (Houghton et al. 2007, Pike & Stiner 2007, Van Houtan & Bass 2007, Fuentes et al. 2011, Martins et al. 2022). At our study site in Cyprus, it is predicted that with a 0.63 m rise in sea levels, 42−50% of loggerhead nesting habitat currently used will be lost (Varela et al. 2019). Fortunately, Alagadi Beach is a protected area and the dune habitat surrounding the beach has been largely preserved, ensuring there is habitat for nesting females to move inland as sea levels rise. However, for many nesting beaches, shifting inland is not an option owing to loss of habitat due to coastal development (Biddiscombe et al. 2020). In recent years, loggerhead turtles have been recorded in increasing numbers nesting on beaches in Italy and Spain at the edge of their current range within the Mediterranean Sea, and it has been suggested that this expansion is a result of climate change (Hochscheid et al. 2022). This further illustrates the ability of this reptilian group to respond to changes in temperature that may provide resilience under predicted scenarios of warming.

We assume that for a species that takes an estimated 20−50 yr to reach maturity, adaptation to rising temperatures through natural selection will not be possible. Yet marine turtles have persisted for many millennia, so there must be the potential for evolutionary adaptation. Thus far, there has been only minor variation described in the pivotal temperatures at which a 1:1 sex ratio is produced, in lab- and field-based studies (Witt et al. 2010, Patrício et al. 2021), although more variation is reported in the transitional range of temperatures at which successful incubation has been recorded (Lolavar & Wyneken 2020, Fuentes et al. 2024). However, studies have been limited in the number of populations, clutches and individuals subjected to investigation because the methods to date have been destructive; as such, gaining robust estimates of primary sex ratios from methods other than direct histology remains challenging but should be a priority for this field of research, as should more studies of the importance of humidity in sex determination (Wyneken & Lolavar 2015).

For this population, the future under climate change may not be as bleak as we have imagined. A phenological advancement in breeding, such as observed here, appears to offer a strong possibility for mitigation of the effects of climate change, at least in the mid term (multiple decades). In the longer term (centuries), if climate change advances as predicted, evolutionary adaptation will be required for survival.

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