

# Importance of spatio-temporal data for predicting the effects of climate change on marine turtle sex ratios

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**ABSTRACT:** Species with temperature-dependent sex determination (TSD) are likely to be impacted by climate change. There is a paucity of data on the contemporary sex ratios of offspring produced by regional marine turtle populations. The lack of such information inhibits the ability of researchers to accurately predict how future meteorological and climate-driven changes may affect turtle populations. Moreover, these data are integral for the development of regional and global recovery plans for declining turtle populations. We estimate offspring sex ratios for the loggerhead turtle *Caretta caretta* at a range of beaches on the Mediterranean island of Cyprus over a 10 yr period (1997 to 2006; 40 beaches, 628 clutches, 29402 hatchlings). Based on hatchling sex determination, we found the pivotal incubation temperature (the temperature at which a 50:50 sex ratio occurs) to be 28.9°C, and the pivotal incubation duration to be 56.3 d. From the incubation durations of over 628 *in situ* clutches laid on different beaches, we estimate that 89% of the offspring produced from these clutches were female. There was, however, both inter-annual (74 to 95% female) and inter-beach (58–98% female) variability in mean offspring sex ratios. These findings highlight the need for wide-scale, long-term monitoring of primary sex ratios in order to accurately predict the likely impacts of climate change. Despite spatial and temporal variation in offspring sex ratios produced, male hatchlings are certainly in the minority in Cyprus. It is therefore highly likely that beaches producing males will become increasingly critical habitats for successful clutch incubation in the face of predicted rising temperatures.

**KEY WORDS:** Loggerhead turtle · *Caretta caretta* · Sex ratio · Pivotal incubation temperature · Climate change · Global warming · Conservation

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## INTRODUCTION

The extent to which animal populations may be impacted or adapt in relation to a changing climate is of great concern to conservation biologists (Parmesan et al. 1999, Walther et al. 2002, Thomas et al. 2004, Parmesan 2006, Hulin et al. 2009, Game et al. 2011). For those species for which temperature influ-

ences offspring sex, rising global temperatures may result in skewed sex ratios that could ultimately impact population viability. Migratory marine turtles are of great interest in this regard, since they depend on terrestrial habitats for reproduction and show temperature-dependent sex determination (TSD; Bull 1980, Yntema & Mrosovsky 1980, Ackerman 1997) and are thus likely to experience impacts of cli-

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mate change across all stages of their life cycle (Weishampel et al. 2004, Chaloupka et al. 2008, Hawkes et al. 2009, Robinson et al. 2009, Witt et al. 2010, Fuentes et al. 2011).

Rising temperatures may cause excessive feminisation of marine turtle offspring (Janzen 1994, Hays et al. 2003). The loggerhead turtle *Caretta caretta* has been the most extensively studied marine turtle species to date, with the majority of sex ratio studies reporting a female bias (Mrosovsky & Provanča 1992, Marcovaldi et al. 1997, Hanson et al. 1998, Houghton & Hays 2001, Öz et al. 2004, Hawkes et al. 2009, Witt et al. 2010). However, only 7 studies have estimated pivotal temperatures (the temperature at which a 50:50 sex ratio occurs) for this species (reviewed in Hawkes et al. 2009) and only 2 of these (Limpus et al. 1985, Kaska et al. 1998) have been based on field studies (Witt et al. 2010). One of the reasons for the lack of data is that the only reliable method of sexing marine turtle offspring is through histological examination of the gonads, a procedure that requires euthanasia of the offspring and is often considered difficult to justify for imperilled species. Most estimates of population sex ratios use predictive curves created in the laboratory under constant temperature conditions (Mrosovsky 1988, Marcovaldi et al. 1997, Mrosovsky et al. 2002). Field estimates have been based on either sand temperature (Glen & Mrosovsky 2004, Hawkes et al. 2007), clutch temperature (Godley et al. 2001a), or incubation duration (Marcovaldi et al. 1997, Mrosovsky et al. 1999). The latter method is based upon the negative correlation with incubation temperature and thus provides researchers with a cheap, non-invasive and easy to use inferential tool for quickly estimating a population's sex ratio. There is clearly a need for further research into the effects of climate change on offspring sex ratios, which is considered to be one of the highest research priorities to effectively inform marine turtle conservation (Hamann et al. 2010).

Within the Mediterranean, the loggerhead turtle has the most extensive nesting range, with the majority of nesting occurring around the eastern basin (Broderick et al. 2002). Most nesting sites to date have been assessed as having reported highly female-biased sex ratios (Margaritoulis et al. 2003, Witt et al. 2010). Loggerhead turtle clutches laid on the Mediterranean island of Cyprus have some of the shortest incubation durations and warmest temperatures recorded for marine turtles world-wide, and it has been inferred that this population has an extremely female-biased hatchling sex ratio (Kaska et al. 1998: 69 to 91%; Godley et al. 2001b:  $\geq 90\%$ ).

This may also be exacerbated by Cyprus loggerheads being the smallest and therefore potentially having shallower egg chambers than their conspecifics. These studies have, however, been based on data from 1 or 2 beaches in 1 or 2 study years. The present study provides data on the pivotal incubation durations and temperatures from *in situ* clutches of the loggerhead turtle in North Cyprus. Using these models, we predict the offspring sex ratios produced from over 600 clutches laid at 40 beaches in North Cyprus over the period of a decade (1997 to 2006).

## MATERIALS AND METHODS

### Study site and field monitoring

The present study was conducted on the Mediterranean island of Cyprus between 1997 and 2006 (encompassing 10 nesting seasons). During this period, we carried out regular surveying around the coastline of North Cyprus at over 40 beaches, including all major nesting sites. Beaches were surveyed every 1 to 3 d throughout the nesting and hatching season (May to October). Incubation durations were determined as the number of days between the night of laying and the night when the first hatchling tracks were discovered. It should be mentioned that field and laboratory incubation durations differ by approximately 4 d—the length of time hatchlings take to reach the sand surface after hatching (Godfrey & Mrosovsky 1997). Only nests which remained *in situ* (some clutches were relocated) and successfully hatched were included in this study. Beaches ranged in length from <100 m to a few kilometres, and in sand colour from very dark grey to near white (Hays et al. 2001). All beaches were typical of the Mediterranean with no natural shading. For displaying results, we grouped beaches into geographical zones 1 to 6 (Fig. 1) according to the protocol described in Broderick & Godley (1996). Beaches in Zones 1 to 3 were monitored in each year between 1997 and 2006, and those in Zones 4 to 6 were monitored from 1997 to 1999 (after which the local authority took over monitoring according to different methodologies). Data from Zones 4 to 6 are therefore omitted from the extended temporal analyses.

### Sex ratio estimation

Currently, the only reliable method of determining the sex of marine turtle offspring is by histological

examination of the gonads, which requires euthanasia of animals (Yntema & Mrosovsky 1980). Given that marine turtle populations in the Mediterranean are of acute conservation concern, in this study we sampled only dead offspring found in the nest after hatching. We sampled offspring from 7 clutches, in which hourly temperature was also recorded using Tinytag dataloggers (Gemini Data Loggers; accuracy 0.3°C). Dataloggers were placed in the centre of the clutch of eggs at laying, and the female was allowed to cover her eggs and camouflage her nest as normal. After hatching, nest contents were excavated, the datalogger was retrieved and data were downloaded. To allow for thermal equilibration of the datalogger, temperatures recorded for 4 h after covering of the nest were discounted, as were the temperatures recorded after midnight on the night of the first hatchling emergence. In addition, we included published data from 2 clutches in which live hatchlings were sampled (Kaska et al. 1998), also from Cyprus—increasing our sample for sex determination to 9 clutches and 48 hatchlings. We do not know female identity for all clutches, therefore we cannot be certain that there are not repeat clutches from the same female; however, it is unlikely since the clutches were laid at 4 separate beaches. There is the possibility that different females may have different pivotal temperatures, although currently there is no evidence to suggest that this is the case.

### Sex ratio curve estimates

We used generalised linear models with binomial errors for curve estimates using R statistical software:

$$\text{Proportion of females} = 1/[1 + 1/e^{(-27.65 + 0.96 \times \text{temp})}] \quad (1)$$

$$\text{Proportion of females} = 1/[1 + 1/e^{(39.763 - 0.707 \times \text{ID})}] \quad (2)$$

## RESULTS

### Sex ratio curves

Curves were generated to estimate the relationships between sex ratio and temperature ( $\chi^2 = 5.764$ ,  $df = 1$ ,  $p = 0.016$ ; Fig. 2a; Eq. 1) and incubation dura-

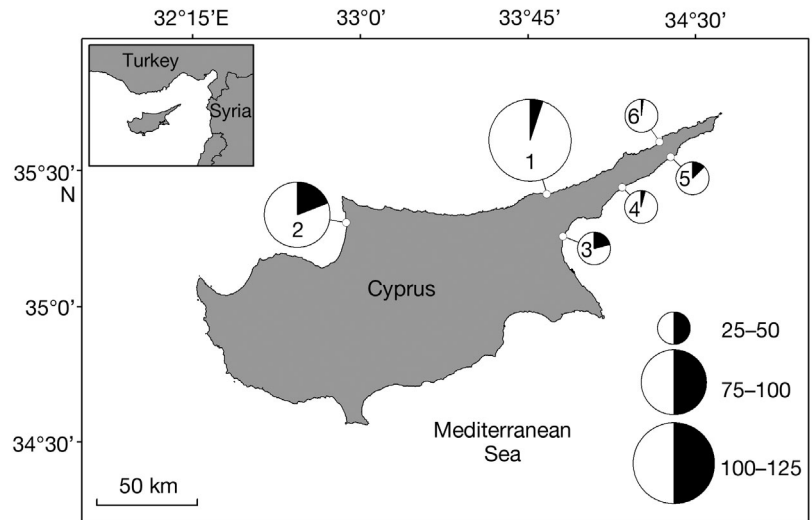


Fig. 1. *Caretta caretta*. Loggerhead turtle survey zones (pies = Zones 1 to 6) monitored in Cyprus, with estimated proportion of female (white) and male (black) turtle offspring produced in each zone. Pie diameter is scaled according to magnitude of clutches laid each year in each zone

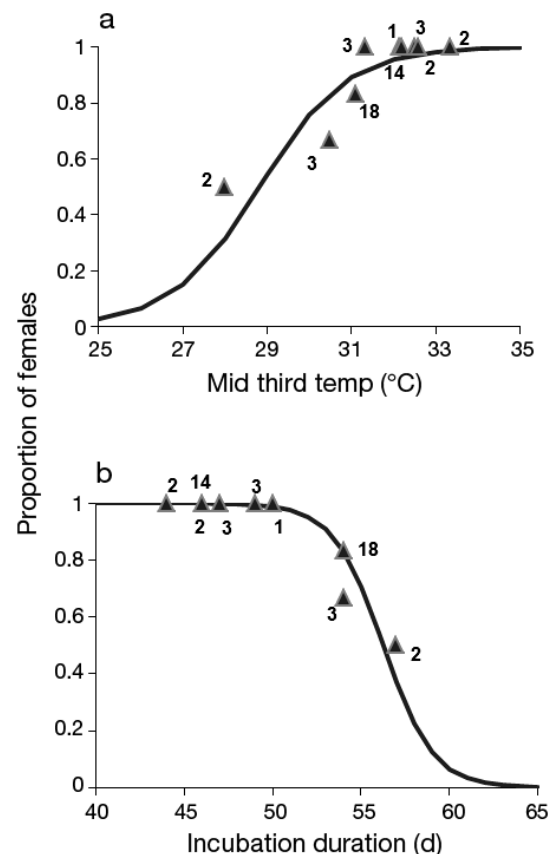


Fig. 2. *Caretta caretta*. Raw data and sex ratio curves for loggerhead turtles in Cyprus based on (a) mean clutch temperatures during the middle third of incubation and (b) incubation durations. Pivotal temperature is 28.9°C; pivotal incubation duration is 56.3 d

tion ( $\chi^2 = 8.06$ ,  $df = 1$ ,  $p = 0.0045$ ; Fig. 2b; Eq. 2). From these curves, we determined that the pivotal temperature at which a 50:50 sex ratio is produced is  $28.9^\circ\text{C}$  ( $\pm\text{SE}$  of 1.1), with a pivotal incubation duration of 56.3 d ( $\pm\text{SE}$  of 1.3).

### Incubation durations

We recorded incubation durations of 628 *in situ* clutches that successfully hatched (1997 to 2006) from all zones. Incubation durations ranged from 40 to 66 d (mean  $\pm$  SD:  $49 \pm 5$  d; Fig. 3). Although beaches in Zones 4 to 6 were only monitored over 3 yr (1997 to 1999) of this study, the incubation durations of clutches laid at these beaches ( $48 \pm 4.1$  d;  $n = 43$ ; range 41 to 58 d) were not significantly different from Zones 1 to 3 ( $50 \pm 5$  d;  $n = 585$ , range 40 to 66; *t*-test;  $F = 1.26$ ,  $p > 0.05$ ).

### Sex ratio estimations

Using the incubation duration curve (Fig. 2b), we estimate that from our 628 study clutches across the island, 89% of offspring produced were female (SD = 26%, range = 0 to 100%). All but one of our 40 study beaches produced highly biased (>70%) female sex ratios, although it should be noted that one beach produced an almost equal hatchling sex ratio (42% males) but supported very low levels of nesting (<5 clutches laid at this site per year). In Fig. 1, we present the mean sex ratio in each of the 6 study

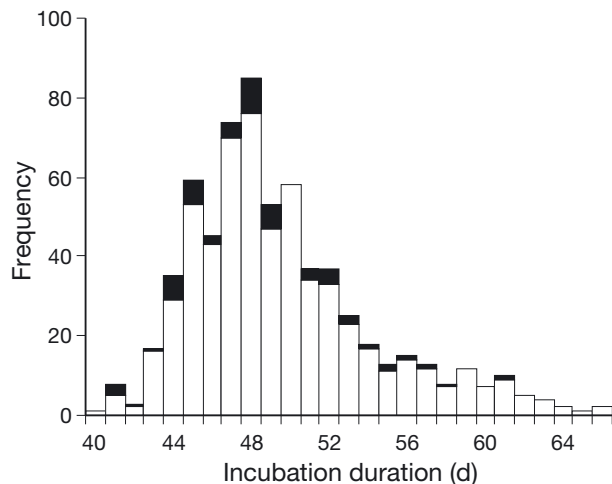


Fig. 3. *Caretta caretta*. Duration of loggerhead turtle clutch incubation in Zones 1 to 3 (unshaded) monitored from 1997 to 2006, and Zones 4 to 6 (shaded) monitored from 1997 to 1999

zones and the magnitude of nesting at these sites. Mean incubation durations of clutches laid in Zones 1 to 3 over the 10 yr study period ranged from 48 to 52 d (Fig. 4a), with mean sex ratios ranging from 74 to 95% female (Fig. 4b). Zones 4 to 6 were only monitored for 3 seasons (and thus were not included in this analysis), but their results are similar (incubation duration 47 to 58 d and mean sex ratio range 54 to 97%).

## DISCUSSION

Godley et al. (2001a,b) reported that high intranest temperatures and very short incubation durations of loggerhead turtle nests at Alagadi Beach, North Cyprus (Zone 1), were likely to result in an extremely female-biased hatchling sex ratio. The calculations used to make these conclusions were based on the assumption that the TSD mechanism in

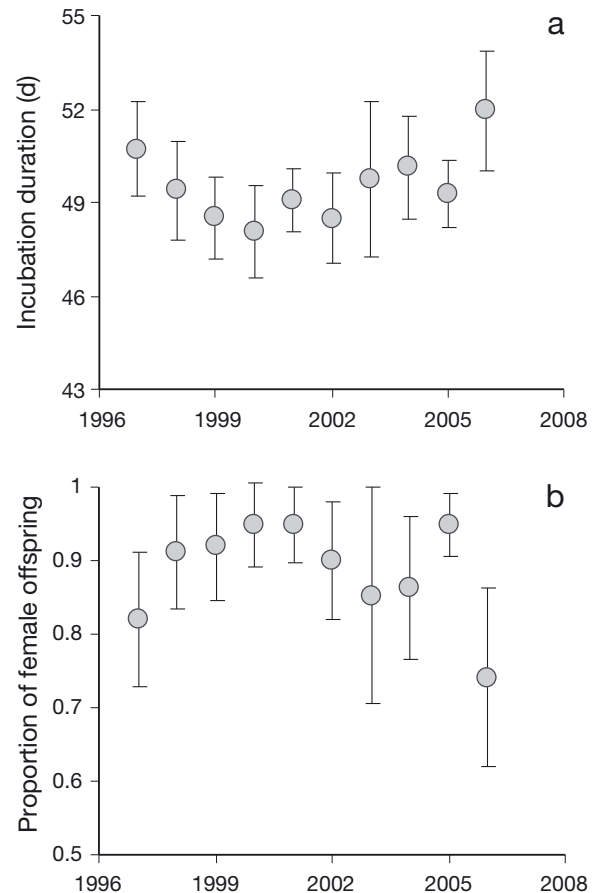


Fig. 4. *Caretta caretta*. Mean annual (a) incubation durations and (b) resultant sex ratios (with 99% confidence intervals) of loggerhead turtle clutches that successfully hatched between 1997 and 2006 in Zones 1 to 3

Mediterranean turtles was similar to conspecifics elsewhere (USA: Godfrey & Mrosovsky 1997; Brazil: Marcovaldi et al. 1997). The sex ratio curves generated in this study confirm that they are indeed similar to those produced for other conspecific populations. Additionally, the estimated pivotal incubation temperature and duration are also in line with previous studies (Mrosovsky 1994, Marcovaldi et al. 1997, Kaska et al. 1998, Mrosovsky et al. 2002), and the relationship between temperature and sex ratio appears relatively conserved within and among marine turtle species (Mrosovsky et al. 2002, Godfrey & Mrosovsky 2006)

Our site-specific curves enabled us to generate more robust and population specific estimates of the hatchling sex ratios produced over a decade, and are cause for conservation concern. It is very clear that the offspring sex ratio in Cyprus is highly female biased and is likely to become further biased with the predicted increase in temperatures in this region (IPCC 2000, 2007, Witt et al. 2010)—potentially leading to a reduction in reproductive males.

In the present study, we have shown variation in incubation durations and sex ratios over wide temporal (10 yr) and spatial scales (40 beaches, covering a coastline of >300 km and a latitudinal range of approximately 60 km). Previous loggerhead turtle sex ratio estimates in northern Cyprus have been restricted spatially to a single beach, and temporally to a period of 4 and 6 yr (Godley et al. 2001a,b). Other studies within the Mediterranean region also have a restricted coverage in both time and space. Zbinden et al. (2007) encompassed a period of 2 yr and 6 beaches on the island of Zakynthos, Greece (covering a total distance of approximately 10 km). Even within this relatively restricted time frame and spatial coverage, incubation durations varied considerably among beaches (40 to 85 d,  $n = 545$ ). Two beaches within this study site were significantly different in sex ratio estimates (male biased) compared to the other 4 (female biased). However, Rees & Margaritoulis (2004) found little variation in mean incubation durations among nesting areas of Kyparissa Bay, Greece. This study comprised one section of beach (10 km) during the 2003 nesting season and produced a female-biased hatchling sex ratio. Loggerhead turtles nesting at Fethiye beach, Turkey, demonstrated a relatively wide variation in mean nest temperatures and incubation durations (49 to 67 d,  $n = 21$ ) although spatially (8 km) and temporally (2000 to 2002) the scale was relatively small (Kaska et al. 2006). It is clear from the above-mentioned studies and the present study that in order to make accurate

assessments of hatchling sex ratios at beach level, multi-year data should be incorporated into any assessment. From our data, we would recommend using a minimum of 6 years of incubation data when providing hatchling sex ratio estimates—which in the present study would cover all but the extreme years. For regional assessments, multi-beach and multi-year data gathering are key, and should particularly include rookeries covering a range of physical aspects (such as albedo), and not just concentrate on those beaches with the highest nesting levels. Although the data have a wide temporal coverage there is no apparent trend as a result of climate warming (i.e. shortening of incubation durations); in fact, between 2000 and 2006 there was a slight increase in incubation durations. However, it is unlikely that results of climate warming would be recognisable over such a short timeframe.

As a result of varying sand reflectance, there is spatial variation in incubation temperatures, as has been found at other rookeries for this and other species (Baptistotte et al. 1999, Hays et al. 2001, Godley et al. 2002, Zbinden et al. 2007). In Cyprus, some of the beaches on the west (Zone 2) and east (Zone 3) coasts have some of the highest albedo levels and therefore longer incubation durations than those found on the north coast (Zone 1), which have some of the lowest, although aspect and relative degree of insolation cannot be ruled out. The only nesting regions in Cyprus not represented in the present study are the nesting beaches of southern Cyprus (Demetropoulos & Hadjichristophorou 1989), which support 159 to 256 nests each year (Margaritoulis et al. 2003). It is unlikely, however, that these regions represent significant male-producing beaches, as our study area encompasses beaches consisting of a wide range of albedos (Hays et al. 2001). Instead, it appears that there are local beaches that produce fewer females (albeit still biased towards females) than other rookery beaches in Cyprus. It is possible that these beaches that produce low-end, female-biased sex ratios could represent critical habitats for the production of male loggerhead turtles in Cyprus and the adjacent Mediterranean.

Although some study beaches were not monitored daily, patrols were never interrupted for more than 1 or 2 d, and these pauses in survey effort had no marked effect on the ability of workers to identify and locate nests deposited since the previous survey. It should be noted that some nests examined for the present study contained an estimated 1:1 hatchling sex ratio, although these were extremely few in number. To date, no extreme sex ratio bias has been iden-



tified in conspecific juveniles in the Mediterranean Sea (Casale et al. 2005, 2006), and genetic analyses suggest that significantly more male green turtles *Chelonia mydas* mate annually than female turtles, despite female-biased primary sex ratios observed on nesting beaches in Cyprus (Godley et al. 2001b, Wright et al. 2012a). This may suggest that there is highly female-biased mortality in hatchlings (Warner & Shine 2008), or that an alternative mating strategy is employed by sea turtles to compensate for skewed offspring sex ratios (Wright et al. 2012b).

The temperatures encountered during the present study should be considered to be close to the maximum value for each clutch, as dataloggers were placed in the centre of each clutch and likely experienced the greatest amount of metabolic heating. Metabolic heating primarily occurs during the final third of the incubation period, thereby reducing its effect on hatchling sex ratios (which is determined during the middle third of incubation; Broderick et al. 2001, Zbinden et al. 2006). Differences in incubation temperatures within a single nest do exist, and previous studies indicate that there is a measured maximum mean of 0.9°C between the top and bottom of clutches (Hanson et al. 1998, Kaska et al. 1998, Houghton & Hays 2001). Due to generally small clutch sizes and shallow nest depths, positioning the datalogger in the centre of each clutch likely provides the best representative temperature, as those at the top of the clutch would be warmer, but experience less metabolic heating.

Another notable point regarding our methodology is that in order to minimise the impact on a protected species we chose to sample only dead hatchlings. This may have introduced some bias into our sampling. However, irrespective of the fact that hotter nests are likely to have greater mortality than cooler nests, it is hard to see how this could introduce a systematic bias in the inferred sex ratio of a given nest unless there was a temperature- and sex-specific mortality bias. In future studies, it may be useful to augment sampling of dead hatchlings and developed embryos from the first laid nests in any season and from beaches which support longer incubation durations. It may also be helpful to fully investigate the thermal profiles experienced that so far have been suggestive of highly skewed sex ratios (Godley et al. 2001a), and to fully investigate the physical properties of these beaches, e.g. sand albedo, which has been shown to affect incubation temperatures (Hays et al. 2001).

The transitional range for temperature-dependent sex determination described here is rather wide com-

pared to some other curve predictions due to the slope of the curve; the flat slopes produced in the present study are almost certainly due to the absence of all-male clutches found during the sex determination part of this study. This is primarily due to the fact that the present study used only natural nests; consequently, temperature manipulation was not possible, with most clutches experiencing only feminising temperatures. This will be further exacerbated in the light of predicted warming and drying within the Mediterranean region as a result of future climate change scenarios (IPCC 2007).

From the results of this study, it is clear that in order to estimate population hatchling sex ratios accurately, sampling should be undertaken on as wide a spatial and temporal scale as possible. It is conceivable that future conservation management strategies may not simply have to prioritise the protection of sites with the highest number of nesting females, but should also focus on those that produce slightly more male hatchlings (Baptistotte et al. 1999, Zbinden et al. 2007). From the present study, we have been able to identify beaches and zones with a higher percentage of male-producing clutches, which could be used for further conservation measures. It is worth noting that the beaches within Zone 3 are not under special protection and are under threat from building construction. However, the picture for beaches within Zone 2 is currently much brighter, as they are protected under local legislation and are a Special Environmentally Protected Area (SEPA) and part of a potential Natura 2000 site (Fuller et al. 2010).

Relocation of nests in Mediterranean turtle conservation projects is widespread, often involving transplanting nests that are at risk of being destroyed through inundation and erosion. Nests that experience occasional wash-over may be cooler, and therefore may produce more males; however, nests with no chance of survival because of inundation should be relocated to enhance clutch success (LeBlanc et al. 2012). Transplanted nests may not truly reflect the dimensions and conditions of the original nest, and if so, conservation managers may need to artificially alter incubation temperatures, either *in situ* or in hatcheries (Shaver 1996, Mrosovsky & Godfrey 2010, Patino-Martinez et al. 2012). Unfortunately, artificial incubation conservation strategies (either *in situ* or *ex situ*) would incur huge financial and human resources which, for many sea turtle conservation groups, would prove prohibitive. Additionally, before selecting the sex ratio of choice (or assuming that a 1:1 sex ratio would be the best option in all cases), many factors would need to be incorporated into the

decision making process, such as the operational sex ratio within particular rookeries. Some may argue that in order to increase population size it would be preferable to produce a female-biased sex ratio (Vogt 1994). However, it could also be argued that the increasing environmental pressures of climate warming (to levels which will either produce all female hatchlings or be lethal to developing embryos) needs urgent attention. Fuentes et al. (2012) identified a suite of possible mitigation measures which could provide management tools in answer to the threat of global warming. The main recommendation from their study was (as we have accomplished here) to identify and improve the protection and population levels of male-producing beaches. This will become of paramount importance in the future should predicted increases in global temperatures become reality, leading to (1) a point where near zero male hatchling production is reached and/or (2) increased embryo mortality due to high incubation temperatures (Ackerman 1997).

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#### LITERATURE CITED

- Ackerman R (1997) The nest environment and the embryonic development of sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 83–106
- Baptistotte C, Scalfoni JT, Mrosovsky N (1999) Male-producing thermal ecology of a southern loggerhead turtle nesting beach in Brazil: implications for conservation. *Anim Conserv* 2:9–13
- Broderick AC, Godley BJ (1996) Population and nesting ecology of the green turtle *Chelonia mydas* and the loggerhead turtle *Caretta caretta* in Northern Cyprus. *Zool Middle East* 13:27–46
- Broderick AC, Godley BJ, Hays GC (2001) Metabolic heating and the prediction of sex ratios from green turtles (*Chelonia mydas*). *Physiol Biochem Zool* 74:161–170
- Broderick A, Glen F, Godley B, Hays G (2002) Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. *Oryx* 36:227–235
- Bull JJ (1980) Sex determination in reptiles. *Q Rev Biol* 55:3–21
- Casale P, Freggi D, Basso R, Argano R (2005) Size at male maturity, sexing methods and adult sex ratio in loggerhead turtles (*Caretta caretta*) from Italian waters investigated through tail measurements. *Herpetol J* 15:145–148
- Casale P, Lazar B, Pont S, Tomás J and others (2006) Sex ratios of juvenile loggerhead sea turtles *Caretta caretta* in the Mediterranean Sea. *Mar Ecol Prog Ser* 324:281–285
- Chaloupka M, Kamezaki N, Limpus C (2008) Is climate change affecting the population dynamics of the endangered Pacific loggerhead sea turtle? *J Exp Mar Biol Ecol* 356:136–143
- Demetropoulos A, Hadjichristophorou M (1989) Sea turtle conservation in Cyprus. *Mar Turtle Newsl* 44:4–6
- Fuentes MM, Limpus CJ, Hamann M (2011) Vulnerability of sea turtle nesting grounds to climate change. *Glob Change Biol* 17:140–153
- Fuentes MM, Fish MR, Maynard JA (2012) Management strategies to mitigate the impacts of climate change on sea turtle's terrestrial reproductive phase. *Mitig Adapt Strategies Glob Change* 17:51–63
- Fuller WJ, Yalinca GK, Seffer J, Sefferova Stanova V, Ozden O, Hessenberg C, Kara C (2010) Management plan for Akdeniz SEPA. Project Europe Aid/125695/C/SER/CY/7, Technical assistance for management and protection of potential Natura 2000 sites in the northern part of Cyprus, Nicosia
- Game ET, Lipsett-More G, Saxon E, Peterson N (2011) Incorporating climate change adaptation into national conservation assessments. *Glob Change Biol* 17:3150–3160
- 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. *Glob Change Biol* 10:2036–2045
- Godfrey MH, Mrosovsky N (1997) Estimating the time between hatching of sea turtles and their emergence from the nest. *Chelonian Conserv Biol* 2:581–585
- Godfrey MH, Mrosovsky N (2006) Pivotal temperature for green turtles, *Chelonia mydas*, nesting in Suriname. *Herpetol J* 16:55–61
- Godley BJ, Broderick AC, Downie JR, Glen F and others (2001a) Thermal conditions in nests of loggerhead turtles: further evidence suggesting female skewed sex ratios of hatchling production in the Mediterranean. *J Exp Mar Biol Ecol* 263:45–63
- Godley BJ, Broderick AC, Mrosovsky N (2001b) Estimating hatchling sex ratios of loggerhead turtles in Cyprus from incubation durations. *Mar Ecol Prog Ser* 210:195–201
- Godley BJ, Broderick AC, Glen F, Hays GC (2002) Temperature-dependent sex determination of Ascension Island green turtles. *Mar Ecol Prog Ser* 226:115–124
- Hamann M, Godfrey MH, Seminoff JA, Arthur K and others (2010) Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endang Species Res* 11:245–269
- Hanson J, Wibbels T, Martin RE (1998) Predicted female bias in sex ratios of hatchling loggerhead sea turtles from a Florida nesting beach. *Can J Zool* 76:1850–1861
- Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2007) Investigating the potential impacts of climate change on a marine turtle population. *Glob Change Biol* 13:923–932
- Hawkes LA, Broderick AC, Godfrey MH, Godley BJ (2009) Climate change and marine turtles. *Endang Species Res* 7:137–154

- Hays GC, Ashworth JS, Barnsley MJ, Broderick AC and others (2001) The importance of sand albedo for the thermal conditions on sea turtle nesting beaches. *Oikos* 93:87–94
- Hays GC, Broderick AC, Glen F, Godley BJ (2003) Climate change and sea turtles: a 150-year reconstruction of incubation temperatures at a major marine turtle rookery. *Glob Change Biol* 9:642–646
- Houghton JDR, Hays GC (2001) Asynchronous emergence by loggerhead turtle (*Caretta caretta*) hatchlings. *Naturwissenschaften* 88:133–136
- Hulin V, Delmas V, Girondot M, Godfrey MH, Guillon JM (2009) Temperature-dependent sex determination and global change: are some species at greater risk? *Oecologia* 160:493–506
- IPCC (2000) Emissions scenarios. Cambridge University Press, Cambridge
- IPCC (2007) Contribution of working groups I, II and III to the fourth assessment report of the intergovernmental panel on climate change. Climate change 2007 synthesis report, IPCC, Geneva
- Janzen FJ (1994) Climate change and temperature-dependent sex determination in reptiles. *Proc Natl Acad Sci USA* 91:7487–7490
- Kaska Y, Downie R, Tippett R, Furness RW (1998) Natural temperature regimes for loggerhead and green turtle nests in the eastern Mediterranean. *Can J Zool* 76:723–729
- Kaska Y, Ilgaz C, Özdemir A, Baskale E, Türkozan O, Baran I, Stachowitsch M (2006) Sex ratio estimations of loggerhead sea turtle hatchlings by histological examination and nest temperatures at Fethiye beach, Turkey. *Naturwissenschaften* 93:338–343
- LeBlanc AM, Drake KK, Williams KL, Frick MG, Wibbels T, Rostal DC (2012) Nest temperatures and hatchling sex ratios from loggerhead turtle nests incubated under natural field conditions in Georgia, United States. *Chelonian Conserv Biol* 11:108–116
- Limpus CJ, Reed PC, Miller JD (1985) Temperature dependent sex determination in Queensland sea turtles: intraspecific variation in *Caretta caretta*. In: Grigg G, Shine R, Ehmann H (eds) *Biology of Australasian frogs and reptiles*. Royal Society of New South Wales, Sydney, p 342–351
- Marcovaldi MA, Godfrey MH, Mrosovsky N (1997) Estimating sex ratios of loggerhead turtles in Brazil from pivotal incubation durations. *Can J Zool* 75:755–770
- Margaritoulis D, Argano R, Baran I, Bentavegna F and others (2003) Loggerhead turtles in the Mediterranean Sea: present knowledge and conservation perspectives. In: Bolten AB, Witherington BE (eds) *Loggerhead sea turtles*. Smithsonian Books, Washington, DC, p 175–198
- Mrosovsky N (1988) Pivotal temperatures for loggerhead turtles from northern and southern nesting beaches. *Can J Zool* 66:661–669
- Mrosovsky N (1994) Sex ratios of sea turtles. *J Exp Zool* 270:16–27
- Mrosovsky N, Godfrey M (2010) Thoughts on climate change and sex ratio of sea turtles. *Mar Turtle Newsl* 128:7–11
- Mrosovsky N, Provanca J (1992) Sex ratio of hatchling loggerhead sea turtles: data and estimates from 5-year study. *Can J Zool* 70:530–538
- Mrosovsky N, Baptistotte C, Godfrey MH (1999) Validation of incubation duration as an index of sex ratio of hatchling sea turtles. *Can J Zool* 77:831–835
- Mrosovsky N, Kamel S, Rees AF, Margaritoulis D (2002) Pivotal temperatures for loggerhead turtles (*Caretta caretta*) from Kyparissia Bay, Greece. *Can J Zool* 80:2118–2124
- Öz M, Erdo an A, Kaska Y, Dü en S and others (2004) Nest temperatures and sex-ratio estimates of loggerhead turtles at Patara beach on the southwestern coast of Turkey. *Can J Zool* 82:94–101
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37:637–669
- Parmesan C, Ryrholm N, Stefanescu C, Hill JK and others (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583
- Patino-Martinez J, Marco A, Quinones L, Hawkes L (2012) A potential tool to mitigate the impacts of climate change to the Caribbean leatherback sea turtle. *Glob Change Biol* 18:401–411
- Rees A, Margaritoulis D (2004) Beach temperatures, incubation durations and estimated hatchling sex ratio for loggerhead sea turtle nests in southern Kyparissia Bay, Greece. *Testudo* 6:23–36
- Robinson RA, Crick HQP, Learmonth JA, Maclean IMD and others (2009) Travelling through a warming world: climate change and migratory species. *Endang Species Res* 7:87–99
- Shaver DJ (1996) Head-started Kemp's Ridley turtles nest in Texas. *Mar Turtle Newsl* 74:5–7
- Thomas CD, Thomas A, Cameron RE, and others (2004) Extinction risk from climate change. *Nature* 427:145–148
- Vogt RC (1994) Temperature controlled sex determination as a tool for turtle conservation. *Chelonian Conserv Biol* 1:159–162
- Walther GR, Post E, Convey P, Menzal A and others (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Warner DA, Shine R (2008) The adaptive significance of temperature-dependent sex determination in a reptile. *Nature* 451:566–568
- Weishampel JF, Bagley DA, Ehrhart LM (2004) Earlier nesting by loggerhead sea turtles following sea surface warming. *Glob Change Biol* 10:1424–1427
- Witt MJ, Hawkes LA, Godfrey MH, Godley BJ, Broderick AC (2010) Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. *J Exp Biol* 213:901–911
- Wright LI, Stokes KL, Fuller WJ, Godley BJ and others (2012a) Turtle mating patterns buffer against disruptive effects of climate change. *Proc R Soc Lond B* 279:2122–2127
- Wright L, Fuller WJ, Godley BJ, McGowan A, Trengenza T, Broderick AC (2012b) Reconstruction of parental genotypes over multiple breeding seasons reveals male green turtles do not breed annually. *Mol Ecol* 21:3625–3635
- Yntema CL, Mrosovsky N (1980) Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. *Herpetologica* 36:33–36
- Zbinden JA, Margaritoulis D, Arlettaz R (2006) Metabolic heating in Mediterranean loggerhead sea turtle clutches. *J Exp Mar Biol Ecol* 334:151–157
- Zbinden JA, Davy C, Margaritoulis D, Arlettaz R (2007) Large spatial variation and female bias in the sex ratio of loggerhead sea turtle hatchlings of a Mediterranean rookery. *Endang Species Res* 3:305–312