



# Thermal conditions of green turtle (*Chelonia mydas*) nests in the largest rookery in the eastern Mediterranean

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**ABSTRACT:** Climate change impacts on vertebrates have many implications. The thermal conditions of vertebrates during incubation are known to influence morphological, physiological, and behavioral traits. Thus, incubation temperatures have consequences for ecological and evolutionary processes, and for certain reptiles can determine sex. For oviparous reptiles, information on the thermal environment of nests is often used to estimate sex ratio, metabolic heat, and their effects on hatching success. This critical baseline information is not always available for all species in all regions, hampering our ability to design analyses that could direct future management and conservation actions. Such is the case for green turtles in the Mediterranean, which nest at many different sites but few of which have had their thermal environment documented in detail. We recorded temperature in 225 green turtle nests (between 2009 and 2013) and 12 control sites in the sand (15, 30, and 45 m distance from high tide line between 2010 and 2013) at 75 cm depth at Akyatan beach, Turkey. The mean temperature of the nests ranged from 28.4 to 33.5°C, and those experiencing high temperatures exhibited low hatching success. The observed thermal environment within the nests exhibited a narrow range relative to the control sites, with daily temperature fluctuations in nests ranging from 0.1°C up to 4.5°C. The nest temperature was strongly negatively correlated with incubation duration, while metabolic heating was highest in the last third of the incubation duration, and was significantly correlated to clutch size.

**KEY WORDS:** Temperature-dependent sex · *Chelonia mydas* · Climate change · Metabolic heating

## 1. INTRODUCTION

The thermal environment during the incubation period is known to influence morphological, physiological, and behavioral traits, some of which have significant consequences for many ecological and evolutionary processes of reptiles (While et al. 2018). For instance, in many reptile species, the sexual

differentiation of gonads is driven by incubation temperatures during a critical period of embryonic development (Pieau 1996), while thermal conditions in the nest can impact offspring phenotype and survival (Noble et al. 2018). High incubation temperatures tend to produce smaller hatchlings with slower crawling and swimming speeds (Booth & Astill 2001, Booth et al. 2004, Booth & Evans 2011), which may

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affect fitness in the long term (Noble et al. 2018). High incubation temperatures and prolonged exposure to extreme thermal conditions can also result in death (Howard et al. 2014, Hays et al. 2017). Based on a literature review of extant sea turtles, the maximum thermal tolerance of sea turtle embryos ranges from 33 to 35°C (Howard et al. 2014). Recent work provided evidence that sea turtle embryos may show some resilience to extreme incubation temperatures when the extremes are relatively short in duration (Türkozan et al. 2021).

All marine turtles exhibit temperature-dependent sex determination (TSD), with the middle third of embryonic development being the thermosensitive period (Girondot et al. 2018). Higher temperatures produce more females, while cooler temperatures produce more males. The constant incubation temperature where a balanced (1:1) hatchling sex ratio occurs is called pivotal temperature and has been estimated to be close to 29°C, for nearly all species and populations of sea turtles (Yntema & Mrosovsky 1980, Miller & Limpus 1981, Ackerman 1997). While ideal for a 1:1 sex ratio, the pivotal temperature varies year to year and among populations/species. The range of temperatures that produce both sexes is termed the transitional range of temperatures (TRT) (Mrosovsky & Pieau 1991). Estimates of the sex ratio of hatchlings from different populations in different years range from nearly balanced to extreme female biases (Mrosovsky 1994, Hays et al. 2014). However, male-biased hatchlings are exceptions (Steckenreuter et al. 2010, Lolavar & Wyneken 2017). Estimates of sex ratios in sea turtle populations are generally based on empirical or computational techniques such as gonadal histology (Kaska et al. 1998, Wyneken et al. 2007, Kılıç & Candan 2014, Candan & Kolonkaya 2016, Tezak et al. 2020), by considering the length of incubation duration—with longer duration producing more males (Candan & Kolonkaya 2016)—and by relating the mean temperature during the middle third of incubation to sex ratio data generated by laboratory data (Kaska et al. 2006). However, since pivotal temperature and TRT are defined for constant incubation temperatures, mean incubation temperature cannot be considered reliable for sex ratio prediction when the temperature fluctuates. In other words, a more biologically relevant proxy must be used to predict the sex ratio of natural clutches (Fuentes et al. 2017)

For animals with TSD, unbalanced sex ratios could be intensified by ongoing climate change, which in turn would increase the risk of reproductive failure (Miller et al. 2003, Lasala et al. 2018). Recently,

Jensen et al. (2018) suggested that a green turtle (*Chelonia mydas*) population of the Great Barrier Reef is likely to contain few or no males within the coming decades due to climate change, while Hays et al. (2017) predicted that increasing nest temperatures would cause decreasing hatching success in all sea turtle species. Therefore, high incubation temperatures are thought to be an essential driver of extinction for TSD species such as sea turtles (Janzen 1994, Boyle et al. 2014). However, phylogenetic reconstructions of ancestral states of the sex determination system indicate that many TSD taxa have survived during climatic fluctuations (Valenzuela & Lance 2004). Recent work proved that the *Mauremys reevesii* embryos move within an egg to select an optimal thermal regime to buffer ambient extremes and ameliorate impacts of climate change on offspring sex ratios (Ye et al. 2019). Furthermore, producing female hatchlings at higher temperatures to compensate for egg and hatchling mortality and increasing fecundity may be an excellent solution to overcome climate-related threats, meaning TSD provides resilience under climate change (Santidrián Tomillo & Spotila 2020). However, if the current rate of climate change is too rapid, there is a likelihood that turtles would not be able to adapt in time.

Precise information on incubation temperatures of sea turtle eggs may provide a foundation for many fields of research such as the predicted impact of climate change (Hawkes et al. 2007), evolutionary dynamics (Girondot et al. 2004), or variation in temperature-dependent sex mechanism (Pezaro et al. 2017). At the same time, an update of critical thermal thresholds (e.g. pivotal temperature) could facilitate more realistic models for deriving sex ratio patterns and projecting sex ratios under different climate change scenarios. These data may also help elucidate how sea turtles have adapted to changing temperatures over evolutionary time so that we can better understand long-term impacts and consequences on turtle populations.

Metabolic heat generated by incubating eggs within the nest is another critical parameter because it can have an impact on the sex ratio (Broderick et al. 2001, Jensen et al. 2018) or may cause embryonic mortality if the sand temperature nears the critical limit. Nevertheless, there remain data gaps in regional assessments for these critical parameters related to thermal nest conditions, despite previously published observations. For example, the Mediterranean Sea hosts 2 distinct populations of sea turtles, and assessments on the thermal conditions of incubation, derived from systematic sampling of nests from

the region, are established from studies based on a limited number of nests ( $n < 25$ ) for loggerhead (Godley et al. 2001) and green turtles (Broderick et al. 2000, Candan & Kolonkaya 2016, Yalçın-Özdilek et al. 2016).

Additional nest environmental parameters such as grain size, gas exchange and moisture also play an essential role in the thermal conditions of the nests and thus of hatchling sex ratios (Ackerman 1997). For instance, high rainfall and high-moisture concentrations in the nests decrease nest temperature and can indirectly alter hatchling sex ratios (Lolavar & Wyneken 2015, 2017, Matthews et al. 2021).

Green turtle nesting in the Mediterranean is limited to the eastern region of the basin, with major nesting colonies in Turkey and Cyprus (Türkozan & Kaska 2010), and with the mean annual nest number for the whole Mediterranean ranging from 685 to 1005 nests (Casale et al. 2018). Previous studies focusing on the sex ratio of hatchling green turtles provide evidence of solid female biases in the region (Kaska et al. 1998, Broderick et al. 2000, Kılıç & Candan 2014, Candan & Kolonkaya 2016, Yalçın-Özdilek et al. 2016). However, the scale of each of these studies is limited in terms of either sample size and/or number of seasons of study. Both larger sample sizes and longer time-series datasets are needed to fully understand spatiotemporal trends in hatchling sex ratio production and help contextualize predicted climate change impacts (Fuller et al. 2013).

Akyatan beach, Turkey, is one of the most important nesting sites for green turtles in the Mediterranean and accounts for almost 25% of all Mediterranean green turtle reproductive effort, with an average 362 nests annually between 2006 and 2011 (Türkozan & Kaska 2010, Yılmaz et al. 2015). Given its importance relative to the larger Mediterranean population, Casale et al. (2000) conducted research on beach temperatures over 2 decades ago. In that original study, temperature probes were used to measure sand temperatures near the surface and at nest depth during the nesting season, offering insight into the expected hatchling sex ratio (Casale et al. 2000). The nest temperature was estimated to range between 29 and 31.2°C at the nests studied, suggesting a female-biased hatchling sex ratio. The present study provides the outputs of a 5 yr study on thermal conditions of this same nesting beach. Over this period, temperature data loggers were deployed in nests and sand at nest depth. Nest and sand temperatures were compared to various incubation metrics (duration, success, etc.). Concurrently, metabolic heat and its potential contribution to incubation temperatures

that could surpass the lethal limit for successful embryonic development were explored. Our results contribute to the ongoing discussions concerning the thermal conditions of sea turtle nesting sites, provide baseline data related to green turtle nests in the Mediterranean, and add to a broader discussion of how rapidly changing climate may impact these species and others.

## 2. MATERIALS AND METHODS

The present study was carried out during the 2009 to 2013 nesting seasons on Akyatan beach, Turkey (Fig. 1). During each nesting season (1 June to 15 September), nesting activity at the beach was monitored on a daily basis by on foot patrols conducted by 3 biology students trained previously in sea turtle monitoring. The exact locations of freshly laid nests were identified with a metal probe and marked with a numbered stick. For nests used in this study, temperature data loggers ('Tinytalk' data loggers model 2, Orion Components; resolution = 0.01°C, accuracy =  $\pm 0.5^\circ\text{C}$ ) were placed in the center of clutches of eggs within 12 h of laying, to avoid detrimental effects of egg handling on hatchling survival (Abella et al. 2007). When inserting the data loggers, care was taken to minimize egg rotation and returning them into the clutch, because the delicate embryonic membranes are easily torn if the eggs are rotated or jarred (Mortimer 1999). Each data logger recorded temperatures at 5 min intervals in 225 nests. Temperature data were collected during the breeding season from 1 June 2009 until 15 September 2013, temporally encompassing 95% of all nesting and hatching events. We applied a Mann-Whitney test to compare the hatching success of nests with and without data loggers and found no statistically significant impact on hatching success due to the manipulation of the clutch (Mann-Whitney  $U = 75738$ ,  $p = 0.134$ ), similar to what has been reported by other studies (Özdemir & Türkozan 2006, Tuttle & Rostal 2010). We also calculated the daily variation of the temperature in the nests.

During the 5 yr of this study, a total of 1590 nests were laid of which 14% were included. The temporal distribution of the studied nests within the season was limited to those laid in June (103 nests) and July (122 nests) during the course of the study because almost all nests on Akyatan beach are laid during these 2 months (see Fig. 2 in Yılmaz et al. 2015). After hatchling emergence, nest contents were examined, and loggers were retrieved. In addition to counting

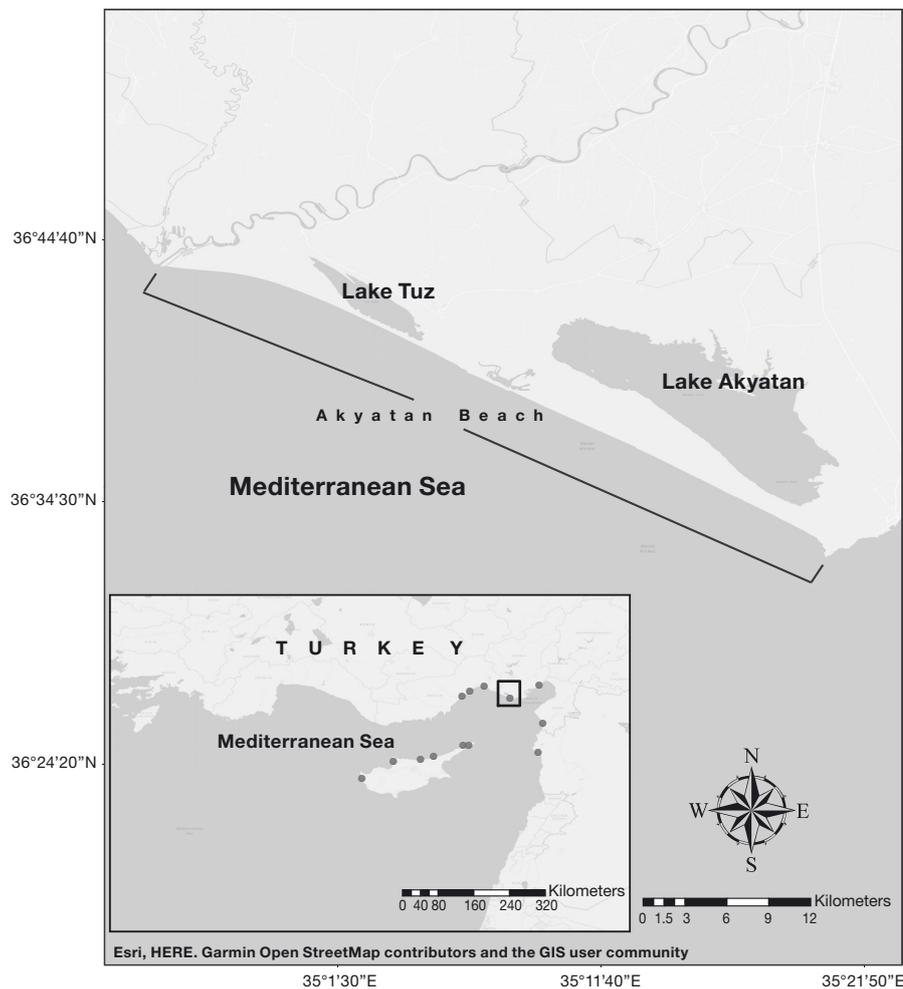


Fig. 1. Location of the study site on Akyatan beach, Turkey. The inset map shows major green turtle nesting sites in the Mediterranean (Casale et al. 2018)

empty eggshells, we classified contents of unhatched eggs as embryos (containing visible embryos or blood) or no visible embryos. We calculated the clutch size and hatching success (percentage of eggs in the clutch that successfully produced hatchlings) for each nest (Miller 1999). Incubation duration was calculated as the number of days which elapsed between the night of laying and the day of first hatchling emergence. The incubation temperature was assessed during each trimester of incubation duration (first third, middle third, and last third).

Data loggers were also placed in 3 randomly selected control sites at 15, 30, and 45 m perpendicular distance from high tide line on the study beach. These data loggers were placed at a depth of 75 cm, the mean depth of green turtle clutches at this site (Yılmaz et al. 2015). These data loggers recorded temperatures synchronously at intervals of 2 h,

starting on 1 June each season. The sand temperature control points were selected randomly from a section of the beach where the nests were concentrated, based on GPS coordinates collected since 2006 (Yılmaz et al. 2015), and marked carefully to collect sand temperature data from the exact locations each year.

All data loggers were calibrated with a mercury thermometer of known accuracy. Because data loggers require time to equilibrate with the surrounding sand, we excluded the readings taken within the first 24 h of deployment from our analyses.

To calculate metabolic heat, we collected sand temperature data from data loggers placed at 4 different stations each year at 45 m from the high tide line (the average distance of nests for Akyatan beach). For each station, we calculated the daily temperature average during the season. For study nests,

Table 1. Descriptive statistics of nest temperatures ( $^{\circ}\text{C}$ ,  $\pm\text{SD}$ )

Year	Entire incubation duration			Middle third of incubation			Daily variation		
	N	Mean	Range	N	Mean	Range	N	Mean	Range
2009	20	30.3 $\pm$ 0.9	28.5–31.4	19	30.0 $\pm$ 0.9	28.5–31.1	20	0.2 $\pm$ 0.04	0.02–1.1
2010	39	30.7 $\pm$ 0.7	29.1–31.9	37	30.2 $\pm$ 0.8	29.0–32.0	39	0.1 $\pm$ 0.04	0.0–1.3
2011	57	32.0 $\pm$ 0.8	29.6–33.5	52	32.0 $\pm$ 0.9	29.5–33.6	57	0.2 $\pm$ 0.05	0.01–2.3
2012	57	30.9 $\pm$ 0.8	29.6–33.4	56	30.7 $\pm$ 0.9	29.0–33.5	57	0.2 $\pm$ 0.04	0.0–1.7
2013	53	31.1 $\pm$ 0.6	29.7–33.0	52	30.8 $\pm$ 0.6	29.7–32.5	53	0.2 $\pm$ 0.09	0.01–4.5

we calculated the daily average nest temperature during incubation. Finally, we subtracted the mean daily sand temperature from the mean daily nest temperature to calculate the metabolic heat (Zbinden et al. 2006). Metabolic heat was estimated as an average for each trimester of incubation.

All data were analyzed using STATISTICA software version 12, and the mean was expressed as  $\pm\text{SD}$ . All data were tested for normality before proceeding with parametric or nonparametric tests. ANOVA was used for multiple comparison of groups, *t*-test was used for dual comparisons between groups of data. Relationships between variables were tested using linear regression. The non-linear association between mean nest temperature and hatching success was assessed by applying generalized additive models (GAM) with smooth functions generated by penalized regression splines and identity link function, using the *mgcv* 1.8-34 package in R 4.0.3 (Wood 2011). Metabolic heating was further analyzed using linear multilevel models. For the models developed, 'years' was used as crossed random effects, with the state of the incubation period (i.e. first, middle and last third of incubation period) used as a fixed effect term. Linear multilevel models were fitted using restricted maximum likelihood.

### 3. RESULTS

#### 3.1. Nest temperatures

The nest temperatures during the entire incubation ranged from 28.5 to 33.5 $^{\circ}\text{C}$  with a mean value of 31.1  $\pm$  0.9 $^{\circ}\text{C}$  ( $N = 226$ ) (Table 1). During the same period, the mean daily nest temperature variation was 0.2  $\pm$  0.06 $^{\circ}\text{C}$  ( $N = 226$ , range = 0.1 to 4.5). However, the daily range of some individual nests increased up to 4.5 $^{\circ}\text{C}$  (Table 1). The mean temperature during the middle third of incubation was lower than the average recorded over the entire

incubation period (*t*-test,  $t = 2.55$ ,  $df = 440$ ,  $p < 0.05$ ) with a mean of 30.9  $\pm$  1.04 $^{\circ}\text{C}$ . The year of data logger deployment accounted for 42% ( $=0.3941/0.9389$ ) of the variation in mean nest temperature. Overall, mean nest temperatures were higher during the 2011 nesting season and lower during the 2009 and 2010 nesting season. The mean temperatures during the whole period of incubation (ANOVA,  $p < 0.001$ ), the middle third of incubation (ANOVA,  $p < 0.001$ ), and daily temperature variations (ANOVA,  $p < 0.001$ ) differed significantly in terms of the year studied (Table 1).

We found a strong significant correlation between nest temperature and incubation duration ( $r^2 = 0.48$ ,  $p < 0.001$ ) (Fig. 2). The GAM model suggested a significant effect of mean nest temperature upon hatching success (adjusted  $r^2 = 0.18$ ,  $p < 0.001$ ) (Fig. 3), further revealing reduced hatching success when the temperature approached 32 $^{\circ}\text{C}$ . There was a significantly positive relationship between mean temperature of nests and distance from the high tide line ( $r^2 = 0.050$ ,  $p < 0.001$ ).

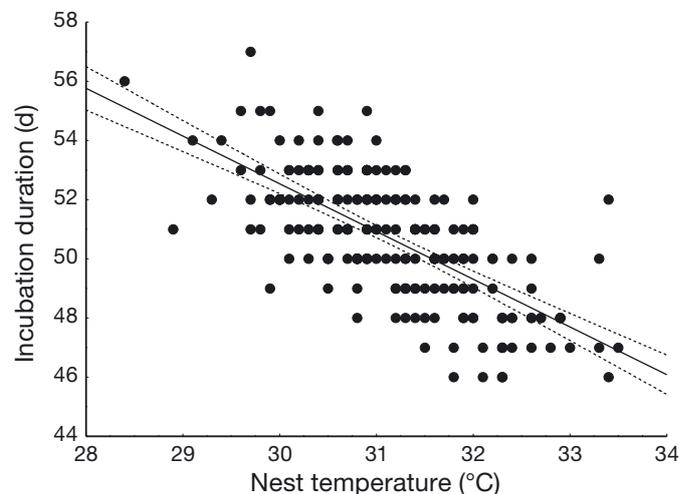


Fig. 2. Relationship between nest temperature and incubation duration (incubation duration = 100.94 – 1.613 nest temperature). Dashed lines show the 95% confidence interval for the prediction of the linear model

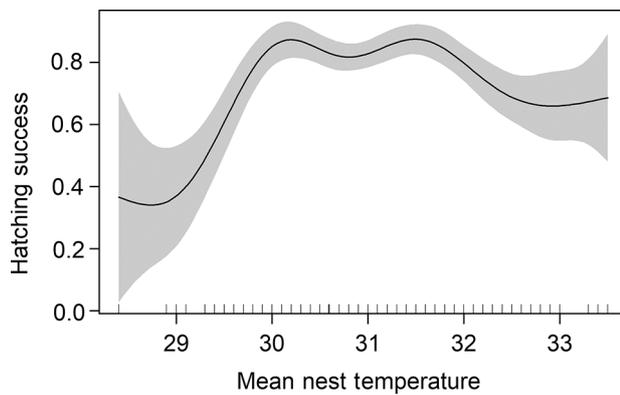


Fig. 3. Relationship, derived from the generalized additive model, which illustrates the response between smoothed components of hatching success against mean nest temperature. Shaded gray area indicates 95 % confidence intervals

### 3.2. Thermal profile at nest depth

Nest temperature and sand temperature at nest depth were strongly correlated ( $r^2 = 0.69$ ,  $F_{1,10419} = 22909$ ,  $p < 0.001$ ) (nest temperature =  $-25.09 + 1.8721$  sand temperature) through the season. Sand temperatures during the reproductive season were characterized by a sharp increase from the start of the nesting season, followed by a slight decline at the end of the egg incubation period (Fig. 4). This pattern was observed at all control sites regardless of the distance from the high tide line. The sand temperatures rose above the pivotal temperature in July and August and cooled in September but remained above the pivotal temperature (Fig. 4). When all data

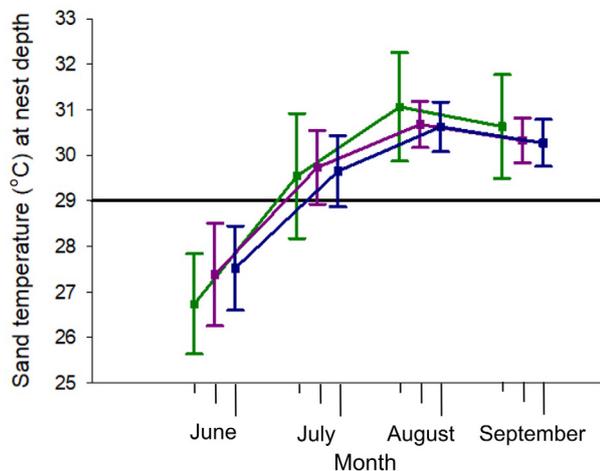


Fig. 4. Relationship between pivotal temperature (horizontal black line) and mean sand temperatures ( $\pm$ SD) over the main nesting season during 2010 to 2013 at 15 m (green), 30 m (purple) and 45 m (blue) perpendicular distance from high tide line. All temperatures are for 75 cm depth.

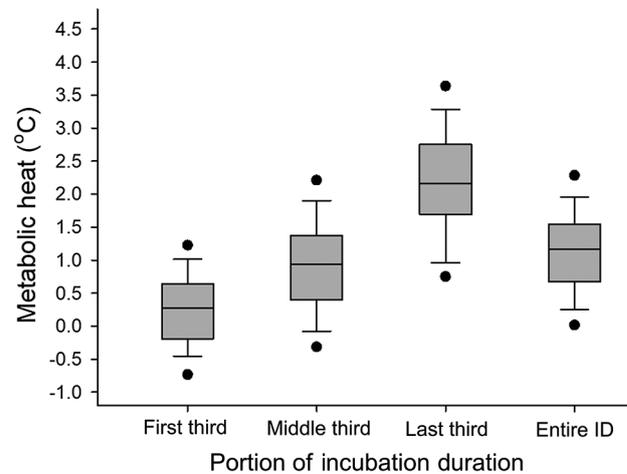


Fig. 5. Mean metabolic heat throughout the first third, the middle third, the last third and the entire incubation duration (ID) over the main nesting season during 2010 to 2013. Black lines within each bar represent median values, the upper and lower boundaries of the box represent the 75th and 25th percentiles, the vertical lines the 10th and 90th percentiles and the dots the 5th and 95th percentiles, respectively

were pooled, temperature at the control sites ranged from 21.1 to 34.4°C and generally increased with distance from the high tide line.

### 3.3. Metabolic heat

The pooled mean metabolic heat across all years was estimated as  $1.1 \pm 0.7^\circ\text{C}$  ( $N = 204$ , range from  $-0.8$  to  $3.2^\circ\text{C}$ ) throughout incubation. The multilevel linear showed that only 5% ( $=0.027/0.567$ ) of the variation was related to the year at which data were collected, with relatively lower in-nest temperatures obtained in 2010. After accounting for the contribution of the fixed effects, nest temperatures differed with a positive effect of the increased duration of incubation period; overall, metabolic heating was 9 times higher during the last third of the incubation period over the first one, and about 3 times higher over the second third (Fig. 5). There was a positive but weak, correlation between clutch size and metabolic heat ( $r^2 = 0.049$ ,  $p < 0.001$ ) (Fig. 6).

## 4. DISCUSSION

To enhance our ability to protect species under the Earth's rapidly changing climate, we need updated information on critical parameters and their underlying trends of ectotherms. The present study provides

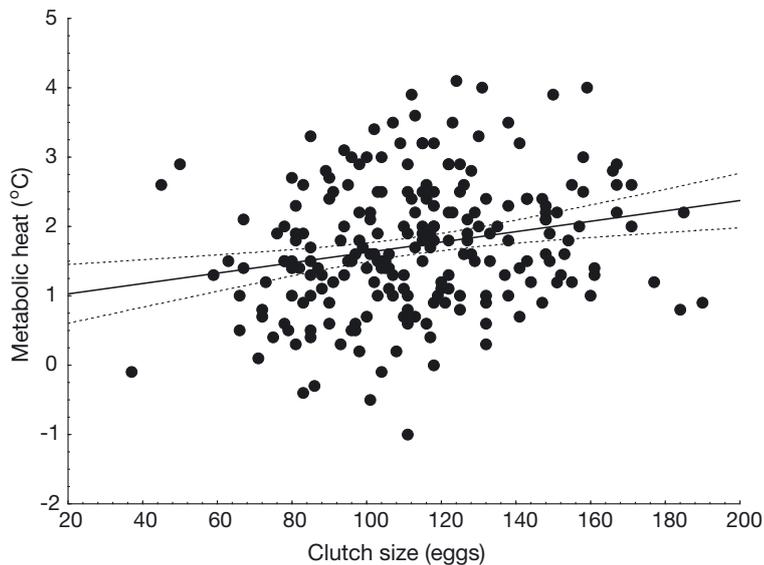


Fig. 6. Relationship between metabolic heating and clutch size (metabolic heat =  $0.878 + 0.0074$  clutch size). Dashed lines show the 95% confidence interval for the prediction of linear model

reference values for incubation temperatures of green turtles in the Mediterranean and demonstrates that high nest temperatures are linked to a reduction in population recruitment (Fig. 3; see also Türkozan et al. 2021). Reduction in hatching success highlights a growing threat associated with projected warming conditions in the Mediterranean and thus deserves more attention when defining research priorities and conservation actions.

The incubation temperature of nests carries great importance since it affects sex ratio in the nests (Mrosovsky 1994), offspring phenotype, survival (Hays et al. 2017, Noble et al. 2018), hatching success (Godley et al. 2001, Laloë et al. 2014, Hays et al. 2017) and locomotor performance of hatchlings (Ischer et al. 2009, Fisher et al. 2014, Kobayashi et al. 2018). Although some green turtle hatchlings may be produced successfully from eggs incubated at temperatures as high as 35°C over the entire incubation period (Howard et al. 2014), there is an increased failure rate of incubation at constant temperatures above 32°C (Miller 1985). In fact, there are reports of decreasing hatching success in response to mean incubation temperatures above 29°C (see Howard et al. 2014 and references within). While our results generally show hatching success decreased at mean temperatures above 32°C, this decline was not evident for all nests with high average incubation temperature. Conversely, some nests with mean temperatures below 30°C had low hatching success. It should be noted that the mean nest temperature reported here (31.1°C) is higher than those reported

for other nesting sites in the same region (eastern Mediterranean) some time ago, such as in Sugözü, Turkey, with a mean of 29.9°C (Candan & Kolonkaya 2016), in Samandağ, Turkey, with a mean of 29.9°C or Alagadi with a reported mean nest temperature of 30.9°C (Broderick et al. 2000). Therefore, considering the overall reduction in hatching success over increasing nest temperatures, we suggest that continued monitoring of these 2 key parameters is critical to guide any conservation action in the near future.

Many factors are likely to influence the temperatures of sea turtle nests. For example, the distance from the sea (Kılıç & Candan 2014), sand albedo (Hays et al. 1995, 2001), nest moisture (Lolavar & Wyneken 2015, 2017, Matthews et al. 2021) and sand grain particle size (Mortimer 1990, Ackerman 1997) could profoundly impact incubation conditions. In many conservation and monitoring studies, nests are consistently relocated to further distances from the high tide line. At our study site, the core nesting area has no shade and a homogeneous color, yet we could detect variations in thermal conditions related to the distance from the water. As evident in the present study, under this beach thermal variation, the relocation applied has resulted in higher nest temperatures that in turn could cause sex ratio alterations (Godfrey & Mrosovsky 1999) or jeopardize reproductive success (Türkozan et al. 2021). Undoubtedly, relocation of sea turtle nests which are at risk could offer many benefits; however, considering the multiple factors that drive hatching success, it is clear that this method should be used with caution (Türkozan & Yılmaz 2007, Lolavar & Wyneken 2017, Lockley & Eizaguirre 2021, Tanabe et al. 2021). In this context, we highlight that the application of relocation for conservation would be significantly enhanced by prior knowledge of beach temperature profiles, with an emphasis on minimizing thermal differences in incubation conditions between the original and the transferred nest location. Such practical suggestions on careful application of classic conservation practices become particularly pronounced considering that the Mediterranean region represents a climate change hotspot, with future projections predicting temperature increases at a higher rate compared to the global average, including significant reductions of precipitation, and the potential rise of prolonged heat waves (Lionello & Scarascia 2018)

In addition to shading and nest depth, metabolic heat is considered to be one of the most influential factors affecting nest temperature (van de Merwe et al. 2006). Reported metabolic heat values range between 0.1 and 6°C for green turtles (Booth & Astill 2001). Our reported values for metabolic heat ( $1.1 \pm 0.7^\circ\text{C}$ ) are higher than previously published research in the Mediterranean, including the values of 0.8°C in Sugözü, Turkey (Önder & Candan 2016), and 0.7°C in Samandağ, Turkey (Sönmez 2018), but align with the highest values that were observed during the last third of incubation duration (1.6°C reported by Önder & Candan 2016, 1.7°C reported by Sönmez 2018). Metabolic heat is important because it can impact the female sex ratio from 5 to 30% when the sand temperatures at nest depth are near the pivotal temperature (Broderick et al. 2001, Önder & Candan 2016), thus influencing the primary sex ratio of a nesting population (Gammon et al. 2020). Furthermore, metabolic heat can influence the clutch adversely, especially when the sand temperatures approach lethal levels. In these cases, metabolic heat may drive nest temperatures above lethal levels or cause sublethal effects (Howard et al. 2014), leading to increased mortality and subnormal embryonic development. Additionally, greater metabolic heat is produced by larger clutches (Booth & Astill 2001, Broderick et al. 2001, the present study) and requires further attention for conservation planning. Even though we detected no clear temporal trend in nest temperature across years, the thermal conditions were above the pivotal temperature in July and August, with higher metabolic heat in the last third of the incubation duration. Considering that most of the nests are laid in June and July these conditions are likely to contribute to a female-biased hatchling sex ratio (~2:1 female:male, based on O. Türkozan unpubl. data).

Artificial manipulation of incubation temperature (e.g. enhancing shade over incubating eggs by planting trees behind nesting beaches) has been proposed as a potential strategy for mitigating the effects of increasing temperatures on sea turtles (e.g. Wood et al. 2014). In contrast, Girondot et al. (1998) recommended that conservation interventions should focus on improving the natural conditions of incubation by concentrating only on the protection of turtles, their habitats and nesting sites, rather than manipulating sex ratios. Many sea turtle nesting populations lack baseline information about sand and nest temperatures, which complicates conservation planning.

Another expected impact of climate change is highly female-biased sex ratios of hatchlings from the nesting beaches (Hays et al. 2003, Hawkes et al. 2007). In contrast to other scientific studies, Hays et al. (2017) suggested that highly female-biased hatchling sex ratios are not incompatible with balanced operational sex ratios. Paternity studies of green turtles in Northern Cyprus and Turkey (Wright et al. 2012, Türkozan et al. 2019) and loggerhead turtles from Australia (Tedeschi et al. 2014, Howe et al. 2018) showed almost 1:1 or male-biased operational sex ratios. Similarly, juvenile and adult sex ratios were found to be more balanced (51.5% female) in foraging grounds of loggerhead turtles in the Mediterranean (Casale et al. 2014). Acknowledging the impacts of climate change upon sea turtle population recruitment, there is ongoing scientific discussion on how to conserve populations. We propose that systematic monitoring programs should be developed at critical nesting sites, to detect how hatchling sex ratio, hatching success, and in-nest mortality are impacted. Using these solid background data, calculated projections at a given site could direct the attention of scientists and conservationists towards carefully reviewing local conditions prior to developing specific mitigation measures. The combination of information collected in the field with projected data is critical towards establishing an early warning system to direct management intervention (Almpanidou et al. 2018). In this context, decisions on actions towards cooling the nests, through planting vegetation, artificial shading, sprinkling water on the nests, etc. should be based on a critical evaluation of several components (climate dynamics) and documented local conditions. A recent modelling study showed that climate change scenarios do not call for immediate interventions, and some of the widely used conservation tools for cooling the nests may negatively impact sea turtle populations in the long term (Santidrián Tomillo et al. 2021). However, our study highlights high incubation temperatures at a key green turtle nesting site in the Mediterranean, suggesting that management intervention may be required to preserve this population in the near future.

*Acknowledgements.* The data of this study were collected under a protocol between the 7th District of Forest and Water Ministry of Turkey and WWF-Turkey. This project was supported by MAVA Foundation, Garanti Bank, UNDP-GEF Small Grant Programme (SGP), the Dutch Embassy in Turkey, and individual supporters of the Adopt a Marine Turtle Programme of WWF Turkey. The authors thank the reviewers and the editor for their constructive comments.

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Editorial responsibility: Paolo Casale,  
Pisa, Italy

Reviewed by: N. J. Pilcher, S. V. Madrak and 1 anonymous  
referee

Submitted: March 17, 2022

Accepted: November 29, 2022

Proofs received from author(s): January 30, 2023