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Abstract. – **Miniature temperature loggers were used to better understand the incubation temperatures, patterns in metabolic heating, and potential implications for sex determination of relocated and in situ loggerhead sea turtle clutches near the northern extent of their nesting range. All sea turtles display temperature-dependent sex determination, with cooler nests producing males and warmer nests producing females. Analysis of the factors that affect incubation temperatures provides insight into variation in hatchling sex ratios over temporal and spatial scales and may help to guide management measures for the imperiled loggerhead sea turtle. Although no temperature difference was detected between relocated and in situ clutches during the thermal sensitive period, relocated nests hatched more quickly and incubated at warmer temperatures than in situ clutches for the entire incubation period. Metabolic heating was apparent in all clutches, beginning during the middle third of incubation, with the greatest gradient between nest temperature and surrounding sand temperatures ($\bar{x} = 1.5 \pm 0.05°C$) that occur during the final third of incubation. The magnitude of metabolic heating was not different between relocated and in situ clutches. Diel temperature fluctuations within nests were significantly less pronounced than in adjacent sand, which implies a degree of thermal buffering within the nest chamber. During the thermosensitive period, all nests incubated at a mean temperature above that of the estimated pivotal temperature (29.2°C), which implies a strongly female-biased hatchling sex ratio during the portion of the nesting season monitored. Potential impacts on incubation temperature and resultant sex ratios should be considered and explored on a beach-by-beach basis before adopting nest relocation as a conservation measure.**

Key Words. – **Reptilia; Testudines; Cheloniidae; *Caretta caretta*; loggerhead turtle; nest relocation; thermal buffering; temperature sex determination; North Carolina; climate change**

Many sea turtle monitoring programs rely on clutch relocation, in which a threatened nest is moved either to a safer part of a beach or into a hatchery, as a tool to increase the number of hatchlings produced. Because of habitat degradation and loss (Eckert and Eckert 1990), predators (Fowler 1979), or poaching by humans (Garcia et al. 2003), clutch relocation may be necessary on some nesting beaches; however, clutch relocation may decrease hatching success (Eckert and Eckert 1990; Marcovaldi and Laurent 1996; Pintus et al. 2009). Furthermore, relocation of clutches may distort gene pools by relaxing selection pressure (Mrosovsky 2006). Recently, concern has arisen that relocation may have detrimental effects on sea turtle populations because of the likely thermal changes that result from moving nests to drier and hotter microclimates (Standora and Spotila 1985; Hawkes et al. 2009; Fuentes et al. 2010).

Incubation temperatures within nests impact incubation duration and hatching success as well as hatchling size, behavior, and sex (reviewed in Ackerman 1997). In all sea turtle species, sexual differentiation is determined by incubation temperature (Yntema and Mrosovsky 1980; Morreale et al. 1982; McCoy et al. 1983), a phenomenon known as temperature-dependent sex determination. For marine turtles, cooler incubation temperatures produce predominantly male hatchlings, whereas warmer temperatures produce high proportions of females (Ewert et al. 1994), with a particular temperature, called the pivotal temperature, producing a 1:1 sex ratio (Mrosovsky 1994). The range of incubation temperatures at which both sexes are produced, known as the transitional range of temperatures (TRT), is often narrow in sea turtles (2°–3°C) and straddles the pivotal temperature (Mrosovsky 1994). The thermosensitive period, when sex is determined, occurs during the middle third of incubation (Yntema and Mrosovsky 1982). Furthermore, within the course of development, clutches produce progressively greater amounts of metabolic heat (e.g., Maxwell et al. 1988; Godfrey et al. 1997; Kaska et al. 1998; Broderick et al. 2001). This heat, depending upon its magnitude and timing, may have consequences for hatchling sex determination (Godfrey et al. 1997; Hanson et al. 1998). The degree to which metabolic heating is affected by clutch relocation has yet to be investigated.

Patterns in hatchling sex ratio production at particular rookeries or across geographic regions are a topic of concern in light of global climate change predictions (e.g., Mrosovsky et al. 1984a; Broderick et al. 2001; Godley et al. 2002). Overwhelmingly female-skewed sex ratios (>90%) have been estimated for many beaches and for several species of sea turtles (Mrosovsky and Provancha 1992; Binckley et al. 1998; Hanson et al. 1998; Godfrey and Mrosovsky 1999; Broderick et al. 2001). Primary sex ratios that differ substantially from the 1:1 ratio predicted by evolutionary theory (Fisher 1930) may have serious demographic impacts for sea turtle populations by decreasing their reproductive potential and genetic diversity (Charnov and Bull 1989; Lovich 1996). Predicted future global climate change scenarios have the potential to exacerbate these concerns, with the possibility of increasing feminization or pushing nests into lethal incubation temperatures (reviewed in Hawkes et al. 2009). As rookeries in central portions of the species' geographic distribution become impacted by these changes, rookeries near the periphery may become critically important for producing male hatchlings (Hawkes et al. 2007). As such, management actions that influence incubation temperatures (i.e., clutch relocation) may alter hatchling sex ratios (Pintus et al. 2009) and subsequently impact sea turtle populations (Morreale et al. 1982; Yntema and Mrosovsky 1982; Dutton et al. 1985). Relatively few studies have investigated incubation temperatures at regionally important northern loggerhead rookeries in North Carolina (Mrosovsky et al. 1984a; Hawkes et al. 2007), and none have focused on the impacts of relocation on incubation temperatures and metabolic heating of northern nests.

By placing miniature temperature data loggers within clutches and at control points adjacent to each nest, we were able to monitor the incubation temperature of each clutch in relation to temperatures in the surrounding sand. Our objectives were to 1) quantify the timing and magnitude of metabolic heating within relocated and in situ loggerhead sea turtle nests in North Carolina, 2) compare incubation temperatures and metabolic heating of relocated and in situ clutches, and 3) gain insight into sex ratios produced at this understudied portion of the loggerhead's geographic range based on nest temperatures and published pivotal temperatures and TRTs (Mrosovsky 1988).

METHODS

Study Site. — Bald Head Island (BHI) is a forested barrier island located in southeastern North Carolina at the confluence of the Cape Fear River and the Atlantic Ocean. Available nesting habitat consists of 15.3 km of sandy beach on the west, south, and east sides of the island. Sea turtle monitoring and nest protection have been ongoing on BHI since 1983, with a mean of 89 ± 8.2 standard error (SE) (range, 36–198; 1983–2009) loggerhead nests deposited yearly on BHI.

Nest Location and Monitoring. — From 15 May to 15 August 2009, beaches were patrolled nightly on an hourly basis from 2100 hours to 0600 hours, whereas, from 16 August to 1 October 2009, the beach was patrolled once each morning. All-terrain vehicles equipped with red headlights were used for beach patrols. Nesting turtles were measured and equipped with 2 passive integrated transponder tags and Inconel flipper tags on the trailing edge of each flipper. After egg deposition, each nest's location was recorded with a handheld global positioning satellite unit (Garmin III Plus, Garmin Corp, Olathe, KS), and a wire cage (40 cm × 40 cm × 60 cm dimensions, 2.5 cm × 5 cm mesh size) was placed around each nest to exclude predators. Large mesh and thin wire sizes were selected to minimize shading of nests.

If a nest was deemed in immediate danger from tidal inundation or erosion, then it was relocated. Relocation took place immediately after the turtle covered the nest. The eggs were removed by investigators who were wearing latex gloves, and the eggs were placed in a rigid cooler lined with moist sand collected from the egg chamber. The eggs were carefully placed within the cooler in rows and columns, maintaining axial orientation and oviposition order. When clutches were removed from the egg chamber, nest depth and width were measured, and an egg chamber of equivalent proportions was dug by hand. Relocation sites were below the dune vegetation line but high enough on the beach to avoid tidal inundation or erosion, usually several meters above the spring high tide line. The eggs were transported by foot to the relocation site and placed, by hand, into the new egg chamber in approximately the same order in which they were laid. Sand removed from the original nest was used to cover the constructed egg chamber. Relocated nests were then covered with wire cages. Clutch relocation always took place at night and lasted less than 60 minutes.

Temperature Loggers. — Miniature temperature data loggers (Thermochron iButtons product DS1922L-F51, Dallas Semiconductor, Dallas, TX; 5.9 mm × 17.4 mm, 3.12 g) were used to record clutch and sand temperatures. Temperature data loggers have a resolution of 0.2°C, an accuracy of 0.5°C, and store up to 2048 recordings. Temperature loggers were coated in 2 layers of plastic tool dip (Plasti-Dip International, Circle Pines, MN) to prevent damage from water and salt. Before deployment, the instruments were calibrated according to procedures recommended by Wibbels (2003). Temperature loggers were placed alongside a thermometer traceable to the National Institute of Standards and Technology in a controlled water bath. Temperatures were recorded at 15°C, 25°C, and 35°C, and linear regression was used to describe the relationship between temperature logger output and the National Institute of Standards and Technology traceable thermometer readings. When necessary, appropriate correction factors were applied to each individual temperature logger.

The temperature loggers were programmed to record temperature at 1-hour intervals and were placed in the approximate center of each nest's egg chamber as the female loggerhead oviposited. The depth from the

Table 1. Nest characteristics of 12 loggerhead sea turtle (*Caretta caretta*) nests monitored with temperature data loggers on Bald Head Island, NC, during the 2009 nesting season.

Nest no.	Lay date	Emergence date	Relocated?	Hatching success	Mean metabolic heating third trimester (°C)
1	30 Jun	21 Aug	Yes	0.90	1.6
2	1 Jul	20 Aug	Yes	0.69	1.9
3	3 Jul	26 Aug	Yes	0.48	0.6
4	21 Jul	15 Aug	Yes	0.00	1.1
5	8 Jul	NA	Yes	0.97	NA
6	12 Jul	3 Sep	Yes	0.60	2.3
7	15 Jul	6 Sep	No	0.77	2.0
8	17 Jul	16 Sep	No	0.99	1.5
9	22 Jul	15 Sep	No	0.88	1.7
10	22 Jul	15 Sep	No	0.97	0.6
11	22 Jul	19 Sep	No	0.86	1.5
12	8 Jul	2 Sep	No	0.95	1.8

temperature logger to the top of the nest then was measured. At the conclusion of the nesting process, a control temperature logger was buried at an equivalent depth 1 m adjacent to the nest (i.e., control site) at the same distance from the water line as the egg chamber. The nests were monitored nightly as the expected hatching date approached so that exact time of hatchling emergence could be recorded. Three days after hatchling emergence, each nest was excavated, and clutch size and hatching success (number of successfully hatched eggs per total number of eggs laid) were determined. Temperature loggers were retrieved at this time, and the data were downloaded by using Embedded Data Systems and the OneWire Viewer computer program.

Data Analysis. — Metabolic heating was determined as the difference between nest temperature and mean control temperature at any point during incubation, minus the minimum observed difference between the 2 values (Broderick et al. 2001). Levene's test was used to compare variance between nest temperatures and control-site temperatures during the temperature sensitive period (TSP) (middle third of incubation) and entire incubation duration. Welch's t-tests were used to compare temperatures between nest and control sites. To test whether incubation temperatures of relocated and in situ nests were different, we used generalized linear mixed models (GLMM) with Poisson error distributions and assessed differences with Wald statistics. GLMMs compared temperatures during the entire incubation period and during the TSP between relocated and in situ clutches while controlling for the random factors of temperature logger depth, lay date, and clutch size.

Incubation periods were broken into trimesters by dividing the entire incubation period from egg deposition until hatchling emergence by three. A GLMM with repeated measures was used to compare levels of heating between the first, second, and final third of incubation, while controlling for depth, lay date, and clutch size as covariates. All statistical analyses were performed by using SPSS 15.0 (SPSS Inc, Chicago, IL). All means are reported ± 1 SE.

RESULTS

Fifteen pairs of temperature loggers (one in clutch and one at control site 1 m away) were placed in loggerhead nests between 30 June and 2 August 2009. Data loggers were successfully retrieved from 12 nests (6 in situ, 6 relocated) because 3 clutches were fatally inundated during Tropical Storm Bill in late August (Table 1). Another control temperature logger was lost during excavation, which limited our calculations of metabolic heating to 11 clutches.

There was no effect of clutch relocation on temperature during the middle trimester of incubation (GLMM W = 0.11, $p = 0.74$) and no discernible effect of lay date (W = 2.15, $p = 0.14$), clutch size (W = 1.33, $p = 0.25$), or depth (W = 1.20, $p = 0.27$). However, relocated clutches did incubate at a higher mean temperature than in situ clutches over the entire incubation period (GLMM W = 9.07, $p = 0.05$). No effect from clutch size (W = 0.52, $p = 0.47$) or depth (W = 0.31, $p = 0.72$) was discernible, although lay date (W = 2.94, $p = 0.09$) had a minor, negatively correlated effect on the model. Furthermore, relocated clutches incubated for shorter durations ($\bar{x} = 53.0 \pm 0.8$ days) than clutches left in situ ($\bar{x} = 57.0 \pm 1.0$; $p = 0.016$). Mean temperature during the entire incubation period was not different between nest and control sites (t = −0.847, $p = 0.406$). All 12 of the monitored nests had a mean incubation temperature during the TSP (range of means, 29.4°–30.9°C) above that of the pivotal temperature (29.2°C) reported for this beach (Mrosovsky 1988; Fig. 1).

Temperatures recorded in clutches over the entire course of incubation ranged from 21.7°C to 34.2°C, with means that ranged from 29.0°C to 31.0°C (Table 2). Diel temperature fluctuated to a greater extent at control locations than within clutches (Fig. 2), with greater variance during both the TSP ($F_{2,12} = 0.019$, $p = 0.05$) and the entire incubation period ($F_{2,12} = 7.187$, $p = 0.01$). Standard deviations of temperatures were greater at control sites than at nest sites during the TSP

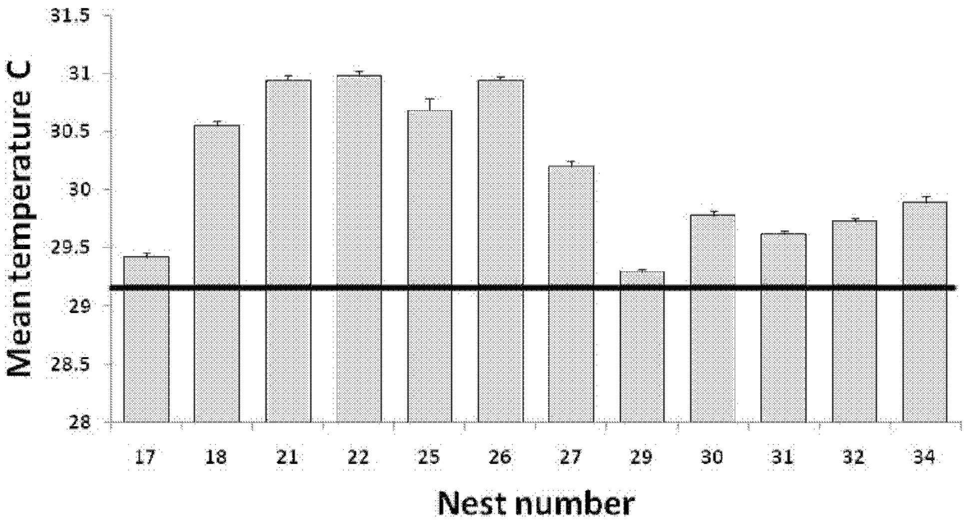

Figure 1. Mean temperatures (± 1 SE) during the middle third of incubation of 12 loggerhead sea turtle (*Caretta caretta*) clutches. The horizontal line represents the nearest reported pivotal temperature (29.2°C) for loggerheads (Mrosovsky 1988): clutches incubated below this temperature produce predominantly male hatchlings, clutches incubated above this temperature produce predominantly female hatchlings (Yntema and Mrosovsky 1980).

(t = −2.66, p = 0.001) and during the entire incubation period (t = −3.26, p = 0.001).

Metabolic heating was evident in all monitored clutches. Nest temperatures began to show a deviation from surrounding sand temperatures between days 24 and 37 of incubation (Fig. 2). Heating was evident during the TSP in each of the clutches, however, for all clutches, heating was greater during the final third of incubation ($F_{2,33}$ = 7.41, p = 0.03) compared with the first or the middle third (Fig. 3). There was no effect of clutch relocation on metabolic heating, with no discernible effect of clutch size (GLMM W = 0.49, p = 0.45), lay date (W = 0.17, p = 0.85), or depth (W = 0.34, p = 0.72). Intensity of heating ranged from 0.9°C to 0.88°C, with a mean of 0.52° ± 0.1°C, for the entire incubation duration, and ranged from 0.5°C to 2.3°C, with a mean of 1.5° ± 0.5°C (± S.E.) during the final third of incubation.

DISCUSSION

The use of paired temperature loggers provided useful insight into the incubation temperatures of loggerhead clutches in comparison with adjacent sand at a regionally important northern rookery. Most importantly, although we provided evidence that relocated clutches had higher mean incubation temperatures (30.4° ± 0.3°C) and incubated for shorter durations (54 ± 0.8 days) than those left in situ (29.4° ± 0.2°C and 57 ± 1.0 days), we detected no difference in incubation temperatures during the TSP. Our results agree with those of the study by Pinuts et al. (2009) in which relocated clutches of Green Turtles (*Chelonia mydas*) did not incubate at different temperatures than in situ clutches. Understanding changes in incubation temperatures caused by relocation has direct conservation implications, as concern rises over increas-

Table 2. Incubation temperatures (± 1 SE) from 12 loggerhead sea turtle (*Caretta caretta*) nests monitored with temperature data loggers on Bald Head Island, NC, during the 2009 nesting season. Statistics are given for the entire incubation duration of the clutch and for the thermosensitive period, the middle third of incubation when hatchling sex is determined.

			Entire incubation period				Thermosensitive period			
Nest no.	Incubation duration (d)	Clutch size (eggs)	Mean temperature (°C)	SE	Minimum (°C)	Maximum (°C)	Mean temperature (°C)	SE	Minimum (°C)	Maximum (°C)
1	52	146	30.0	0.04	27.2	32.6	29.4	0.04	30.2	30.7
2	50	152	31.0	0.04	23.7	33.6	30.6	0.04	29.7	30.7
3	54	84	30.8	0.04	23.2	32.7	30.9	0.04	29.7	30.7
4	56	112	30.3	0.04	26.2	33.7	31.0	0.04	29.7	32.7
5	53	94	30.4	0.10	21.7	33.7	30.7	0.10	27.7	32.7
6	53	140	30.9	0.03	24.2	34.2	30.9	0.03	28.2	32.7
7	61	118	29.7	0.04	25.7	34.2	30.2	0.04	26.7	32.7
8	55	110	29.0	0.02	27.2	31.7	29.3	0.02	27.2	31.2
9	55	118	29.5	0.03	26.7	31.7	29.8	0.03	26.7	31.7
10	59	100	29.0	0.03	26.2	31.2	29.6	0.03	26.7	31.2
11	61	85	29.1	0.02	25.7	32.2	29.7	0.02	26.7	32.2
12	58	95	29.4	0.06	26.6	32.6	29.9	0.06	27.6	32.6

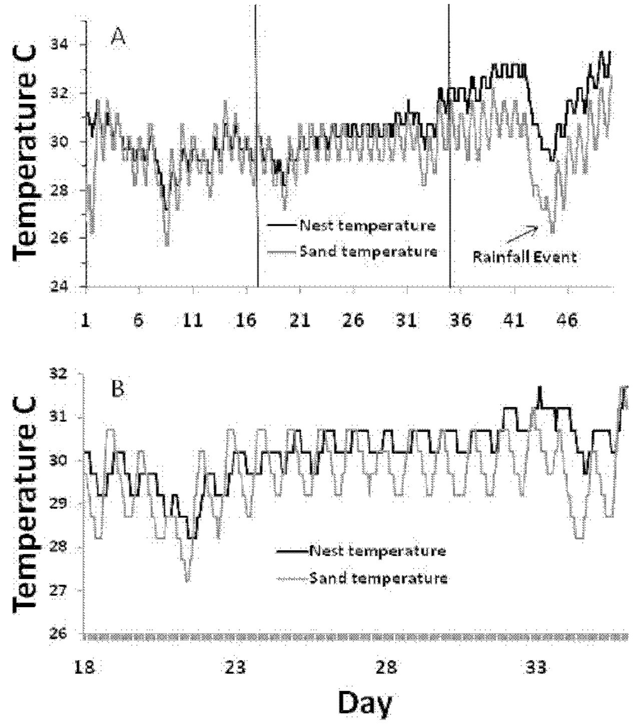

Figure 2. Temperature profile from the center of a loggerhead sea turtle (*Caretta caretta*) clutch and from a control site of equal depth 1 m adjacent to the nest. Vertical lines represent the middle third of incubation, referred to as the thermo-sensitive period, in which hatchling sex is determined. (A) the entire incubation duration of the clutch, and B) the thermo-sensitive period.

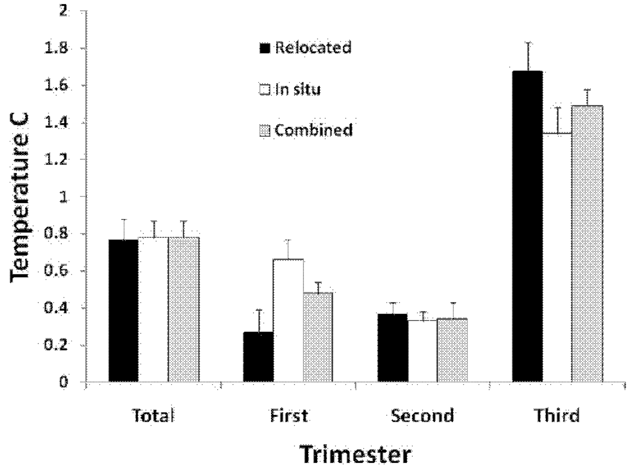

Figure 3. Estimated mean metabolic heat (± 1 SE) recorded within 12 loggerhead sea turtle (*Caretta caretta*) nests during the entire incubation period and during each third of the incubation period.

ingly female-biased sex ratios (Hawkes et al. 2009). Because temperature often varies between different zones of the beach (Standora and Spotila 1985; Fuentes et al. 2010), when a nest is relocated it is moved away from the tide line and closer to the dunes, a microenvironment that can be significantly hotter than environments closer to the tide line (Standora and Spotila 1985; Spotila 1987), which potentially leads to feminization of the hatchlings. Although numerous studies have documented decreased hatchling success, which resulted from relocation efforts (Eckert and Eckert 1990; Marcovaldi and Laurent 1996), few have examined the thermal impact of nest relocation (but see Pintus et al. 2009). Despite the limited scale and sample size of our study, we suggest that this is the first step toward gaining an understanding of the implications of this common management technique for loggerhead sea turtles near the northern extent of their nesting range.

To the best of our knowledge, this is the first study to investigate and compare metabolic heating in relocated relative to in situ clutches. Understanding the intensity and timing of metabolic heating has implications in the inference of sex ratios via sand or air temperatures (Maxwell et al. 1988; Hawkes et al. 2007). Although we observed heating in all of the nests monitored, we detected no difference between metabolic heating in relocated vs. in situ clutches during the entire incubation period or during the TSP (Fig. 3). As reported in previous studies, most heating occurs during the third trimester of incubation (e.g., Kaska et al. 1998; Broderick et al. 2001); however, some degree of heating ($\bar{x}$ = 0.49° ± 0.9°C) was apparent in 10 of 11 nests monitored in our study during the thermosensitive period. Some studies have documented enough metabolic heating in nests during the TSP to significantly alter hatchling sex ratios (Hanson et al. 1998; Broderick et al. 2001). Although the amount of heating is greater during the final third of incubation, the presence of metabolic heating during the TSP warrants attention and may add further error to studies that use indirect means of predicting sex ratios. Sex ratios predicted by monitoring air and sand temperature or incubation durations should use a correction for metabolic heating, as done in Hawkes et al. (2007) and Fuentes et al. (2010). Accurate estimation of nest temperatures will be most important for clutches that incubate near the pivotal temperatures or at rookeries, with many nests incubating near the pivotal temperature.

An interesting observation that resulted from this study was that diel temperature fluctuations were greater in sand than they were in egg chambers, although mean temperatures were not significantly different, which suggests that the egg chamber of a loggerhead sea turtle nest provides a degree of thermal buffering compared with adjacent sand at equivalent depth. Several studies reported extreme diel temperature fluctuations within loggerhead nests (Kaska et al. 1998; The Chu et al. 2008); however, we are unaware of any reports of the discrepancy between temperature fluctuations within and adjacent to nests. Hays et al. (2003) and Kaska et al. (1998) report very little diel fluctuation at the center of green turtle (*Chelonia mydas*) nests, possibly because of the deeper egg chambers of this species. Georges et al. (1994) suggested that, depending upon its magnitude, diel temperature fluctuations can have profound effects on sex determination, although exposure to short-duration spikes of extreme temperatures will not necessarily drive sexual differentiation toward a particular sex (Wibbels et al. 1991). The buffered thermal environment within the egg chamber may further ameliorate the effects of rapid environmental fluctuations on sexual differentiation. Further evidence of the dampening effect of temperature fluctuations came during the observation of an extended rainfall event (Fig. 2). This rainfall event resulted in a 5°C drop in temperature at the control site and only a concurrent 4°C drop in temperature within the adjacent nest. Rainfall, depending upon its extent and timing, may play a very important role in sex determination of hatchling turtles from a particular beach (e.g., Booth and Astill 2001; Houghton et al. 2007). Monitoring of ambient sand temperature alone may lead to further error by negating the dampening effect of the egg chamber reported in this study.

Studies that attempt to predict sex ratios for a beach must have data concerning the pivotal temperatures and the transitional range of temperatures that drive sexual differential for the species of concern (Wibbels 2003). Despite the fact that these thermal parameters can change among populations and species (Mrosovsky 1994), they often remain within a narrow range of temperatures (27.0°–31.0°C) (reviewed in Wibbels 2003). The temperature loggers used in this study (Thermochron ibuttons) had an accuracy of 0.5°C, which places limitations on our ability to draw conclusions regarding sex ratios produced at this rookery. Nevertheless, when using the pivotal temperature (29.2°C) and TRT (27.5°–0.4°C) reported for loggerheads on BHI (Mrosovsky 1988), it appears that, when assuming the maximum error associated with temperature recordings, most of the nests monitored (7 of 12) were female biased. Nearly half of the nests (5 of 12) had a mean temperature during the TSP above the upper limit of the TRT (30.4°C), which indicated that they likely produced 100% female hatchlings. None of the nests incubated below the pivotal temperature during the TSP, which meant that none of these nests were 100% male or male biased. Previous sex ratio estimations for this beach proposed a 58% production of female hatchlings (Hawkes et al. 2007). This discrepancy may be because of our limited sampling period, because we were unable to deploy temperature loggers until 30 June, which missed the opportunity to monitor nests deposited earlier in the season. These early nests likely experienced cooler incubation temperatures and, thus, may have produced greater proportions of males (Mrosovsky et al. 1984). Also, our study only presents data from one nesting season; hatchling production can vary from year to year, depending on meteorological factors such as mean temperatures and rainfall (Mrosovsky and Provancha 1992; Godfrey et al. 1996). We believe that future investigations into sex ratio production would benefit from a combination of the methodology used in this study (paired temperature loggers) and that used by Hawkes et al. (2007; large-scale remote inference based on meteorological data). Future studies that use temperature loggers would also benefit from placing multiple data loggers in different locations within the nest as both temperature and the degree of metabolic heating can vary spatially within an individual nest (Hanson et al. 1998; Houghton and Hays 2001). Our study placed temperature loggers only in the center of egg chambers, the area of the nest that experiences the greatest amount of metabolic heating and higher temperatures than lower regions of the nest (Kaska et al. 1998; Wallace et al. 2004). Metabolic heating rates reported in this study should be considered the maximum amount of heating for the nest, because heating likely decreases toward the peripheral portions of the egg chamber. Likewise, our estimates of hatchling sex ratio likely overlook cooler temperatures found in the bottom of the nest, which potentially produce male hatchlings (Kaska et al. 1998).

As global temperatures rise in parts of the world, feminization of turtle populations may increase on many beaches (Hawkes et al. 2009; Robinson et al. 2009). Relatively minor changes in air temperature (2°–3°C) could lead to the 100% feminization of nesting areas in the southern United States (Hawkes et al. 2007). As such, human intervention (i.e., nest relocation), which has the potential to exacerbate this issue, must be assessed on an evidence-based level. Although this study was unable to detect increased temperatures that resulted from relocation, this could vary on a site-by-site basis as relocation strategies differ. We urge caution in the use of relocation without first empirically testing the effects on the thermal environment of relocated clutches.

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