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Climate change increases the production of female hatchlings at a northern sea turtle rookery

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Abstract. The most recent climate change projections show a global increase in temperatures, along with major adjustments to precipitation, throughout the 21st century. Species exhibiting temperature-dependent sex determination are highly susceptible to such changes since the incubation environment influences critical offspring characteristics such as survival and sex ratio. Here we show that the mean incubation duration of loggerhead sea turtle (*Caretta caretta*) nests from a high-density nesting beach on Bald Head Island, North Carolina, USA has decreased significantly over the past 25 yr. This decrease in incubation duration is significantly positively correlated with mean air temperature and negatively correlated with mean precipitation during the nesting season. Additionally, although no change in hatching success was detected during this same period, a potentially detrimental consequence of shorter incubation durations is that they lead to the production of primarily female offspring. Given that global temperatures are predicted to increase by as much as 4°C over the next century, the mass feminization of sea turtle hatchlings is a high-priority concern. While presently limited in number, studies using long-term data sets to examine the temporal correlation between offspring characteristics and climatic trends are essential for understanding the scope and direction of climate change effects on species persistence.

Key words: *climate change; hatching success; incubation duration; precipitation; sea turtle; sex ratio; temperature.*

INTRODUCTION

Anthropogenically induced climate change is projected to increase the global mean surface temperature by 0.3–4.8°C over the next century (IPCC 2014), with concomitant variation in levels of precipitation. In egg-laying species, such as sea turtles, incubation environment can influence offspring performance, survival, and sex (Ackerman 1997). High temperatures in the nest have been shown to increase hatchling mortality as well as the proportion of female hatchlings produced (Matsuzawa et al. 2002, Santidrian-Tomillo et al. 2015). High levels of precipitation, in turn, have been shown to lower nest incubation temperatures and enhance egg development but also cause egg suffocation (Kraemer and Bell 1980, Santidrian-Tomillo et al. 2015).

In sea turtles, sex is determined by the temperature during the middle third of incubation, with females produced

at higher temperatures, and males at lower temperatures within a thermal tolerance range of 25–35°C (Ackerman 1997, Howard et al. 2014). The pivotal temperature, which results in the production of a 1:1 ratio of male to female hatchlings is 29°C for loggerheads (*Caretta caretta*) in the United States (Mrosovsky 1988), with a narrow 2–3°C window surrounding the pivotal temperature in which both sexes are produced (Ackerman 1997). Moreover, the temperatures experienced during incubation (Standora and Spotila 1985) determine the number of days a nest incubates, as embryonic development proceeds quicker under high incubation temperatures (i.e., short incubation durations) and vice versa (Deeming and Ferguson 1991, Matsuzawa et al. 2002). As such, short incubation durations lead to the production of more female hatchlings (warmer than pivotal temperatures) and long durations produce more male hatchlings (cooler than pivotal temperatures).

Our goal was to evaluate whether changes in climatic conditions over the past 25 yr influenced either reproductive output or incubation duration of nests in a population of loggerhead sea turtles, a species currently listed as threatened by the IUCN. This population is located at

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high latitude in the Northern Hemisphere, within the northernmost range of the Northwest Atlantic Ocean Distinct Population Segment of *C. caretta*. Many of the sex ratio studies published to date focus on limited temporal scales, which is inadequate to accurately understand the variability in offspring sex ratios over multiple nesting seasons (Marcovaldi et al. 2014). Only recently have a few studies examined offspring sex ratios of the loggerhead over longer temporal scales (Fuller et al. 2013, Marcovaldi et al. 2016). Moreover, given that the sex ratios of loggerhead nests are already highly significantly female biased for populations studied across the species' range (3:1 female to male ratio; reviewed in (Hays et al. 2014), it is essential to understand the impacts of climate change at a

northern rookery where sand temperatures are relatively cooler and an abundance of male offspring are thought to be produced (Hawkes et al. 2007), offsetting the deficit of males produced elsewhere.

MATERIALS AND METHODS

Fieldwork

Fieldwork was conducted between May and October at Bald Head Island (BHI), North Carolina, USA (33.86° N, 78.00° W; Fig. 1a) by a monitoring program managed by the Bald Head Island Conservancy, beginning in 1991 and continuing to the present. BHI, a

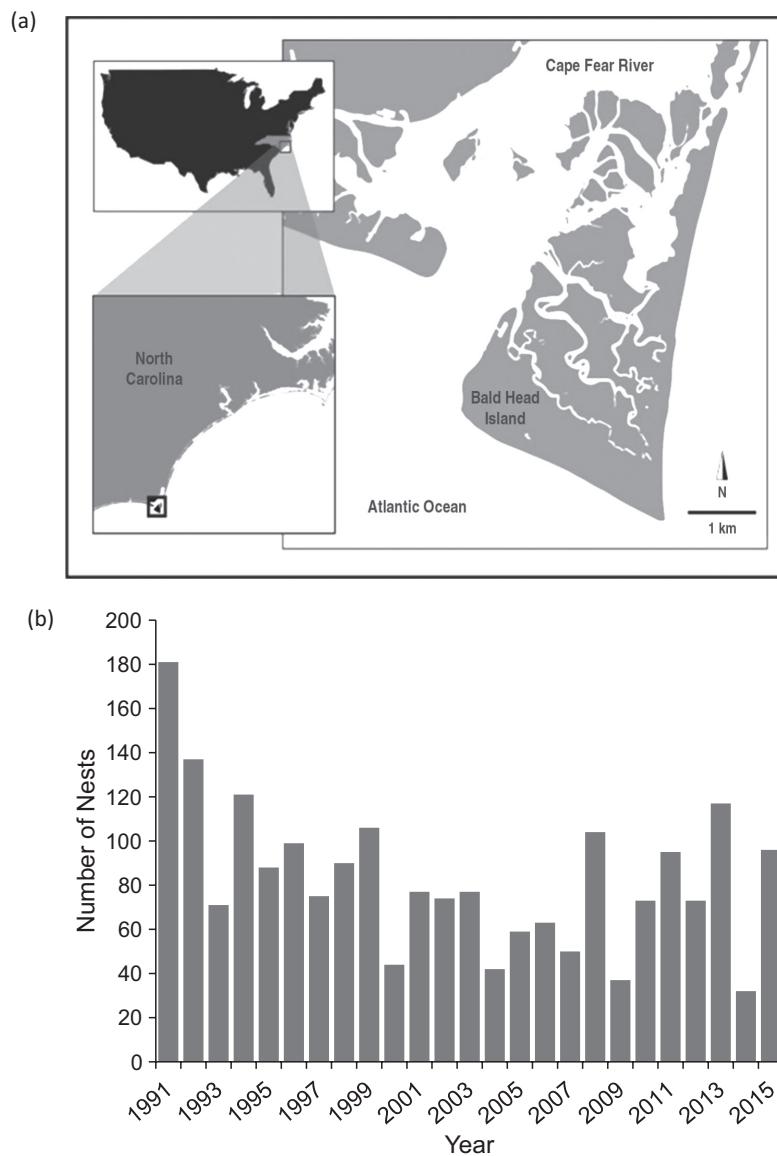


FIG. 1. (a) Map of Bald Head Island, North Carolina, USA. (b) Number of loggerhead sea turtle nests recorded yearly from 1991–2015 on Bald Head Island.

high-density nesting beach, supports an average of 83 ± 6.7 loggerhead nests per year (Fig. 1b). During the nesting season, trained teams patrol the beaches nightly from 21:00–06:00 to identify nests. All identified nests were protected from predators such as the red fox (*Vulpes vulpes*), coyote (*Canis latrans*), and raccoon (*Procyon lotor*) by metal cages. Nests were excavated three days post hatching to determine the number of hatched and unhatched eggs.

Data collection

We obtained historical monthly air temperatures and precipitation records from the National Centers for Environmental Information (NOAA) for a weather station located in Southport, North Carolina (33.92° N, 78.02° W) from 1991 to 2015 (data available online).² We calculated incubation duration as the period extending from the night of egg deposition to the night of first emergence of hatchlings, and used the incubation duration of each nest to calculate percentage of female hatchlings (Mrosovsky et al. 1999). We calculated hatching success as the number of hatched eggs divided by the total number of eggs in the nest. We estimated a mean seasonal (June–August) incubation duration, sex ratio, and hatching success and excluded nests that were eroded or predated from the analyses.

Validation of sex ratio estimation

Incubation duration has long been considered an effective proxy for estimating offspring sex ratios instead of invasive gonadal sexing techniques, which are otherwise required since loggerheads lack sexual dimorphic characteristics as hatchlings (Mrosovsky et al. 1999, Marcovaldi et al. 2014). Long incubation durations often correspond to lower incubation temperatures resulting in the production of more male hatchlings, while the reverse is true for shorter incubation durations (e.g., Mrosovsky et al. 1999; but see Wyneken and Lolavar [2015] for laboratory data reporting male hatchlings produced from eggs with shorter than predicted incubation durations). Several studies have highlighted the importance of considering temperature variations during the thermosensitive period for sexual differentiation (Georges 1989, Georges et al. 1994), and fluctuations have been shown to be substantial in freshwater turtles, which lay shallow nests (Georges 1989). However, a combination of thermal buffering and deeper egg chambers in sea turtle nests tend to lessen the effects of temperature fluctuations (DeGregorio and Williard 2011, Lolavar and Wyneken 2015). Moreover, multiple laboratory and field studies have since validated the use of incubation duration as an appropriate estimation for hatchling sex ratios, and have been

conducted on loggerhead populations nesting in the United States, Brazil, Greece and Cyprus (Godfrey and Mrosovsky 1997, Mrosovsky et al. 1999, 2002, Godley et al. 2001, Fuller et al. 2013). Sex ratio estimation curves in these studies were generated from measured incubation durations and corresponding hatchling sexes (validated through gonad dissection). Curves represent in situ field measurements as well as predicted curves from laboratory incubations. To account for possible variation in the estimated nest sex ratios, we used the incubation duration of each nest to calculate the percentage of female hatchlings, repeating the calculation using all available curves ($n = 7$). We then averaged all seven estimates to obtain a mean sex ratio for each nest.

Statistical analyses

We used linear regression to test how climate variables and nest characteristics changed over the course of our study. We used univariate and multivariate mixed models to determine the influence of temperature and precipitation on our three response variables: incubation duration, mean estimated sex ratio, and hatching success. Nest sex ratio and hatching success were logit-transformed to meet assumptions of normality, and year was included as a random effect in all models. We used the corrected Akaike information criterion (AIC_c) to select the best model. We also used linear regression to test the relationship between date of first nesting and (1) year and (2) mean April air temperatures to determine whether changes in nesting phenology had occurred. Data are reported as mean \pm SE; all analyses were done using JMP Pro 11 (SAS, Cary, North Carolina, USA).

RESULTS

While there was variation among the curves in pivotal incubation duration (the day at which 50% of each sex are produced) and the transitional range of incubation durations (TRI, time interval that produced mixed-sex clutches; Fig. 2a), the resulting sex ratio estimates were similar (Table 1; Fig. 2b). Using data on climate variables and nest characteristics collected from 1347 *C. caretta* nests over a 25-yr period (Table 2), we found that mean temperatures during the peak nesting season (June–August) significantly increased over the study period ($r^2 = 0.47$, $P = 0.0001$; Fig. 3a), while total monthly precipitation significantly decreased ($r^2 = 0.38$, $P = 0.001$; Fig. 3b). We also found that incubation durations significantly decreased over the study period when using the full data set (all nests included, $r^2 = 0.12$, $P < 0.0001$), as well as seasonal means (June–August, $r^2 = 0.37$, $P = 0.0013$; Fig. 3c); declining from 59.2 ± 0.4 d in 1991 to 52.5 ± 0.5 d in 2015. As a result, the proportion of female hatchlings produced on BHI significantly increased (all nests, $r^2 = 0.13$, $P < 0.0001$;

² <http://www.ncdc.noaa.gov/data-access/land-based-station-data>

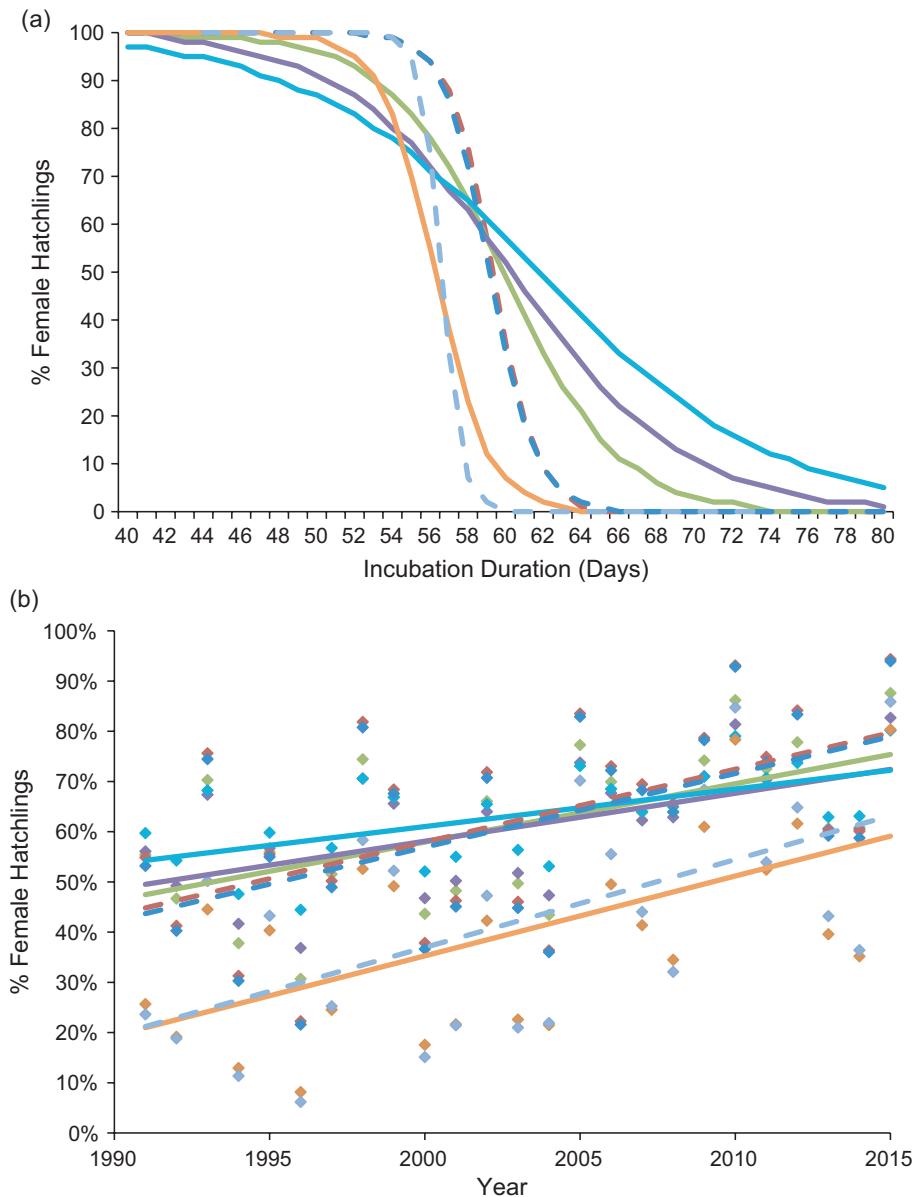


FIG. 2. (a) Incubation duration vs. offspring sex ratio. Curves were redrawn from published studies comparing actual offspring sex ratio and incubation durations. Solid lines represent field studies (blue, United States [Godley et al. 2001]; purple, United States [Godfrey and Mrosovsky 1997]; green, Brazil [Mrosovsky et al. 1999]; orange, Cyprus [Fuller et al. 2013]). Dashed lines represent laboratory studies (light blue, Greece [Mrosovsky et al. 2002]; dark blue, Brazil [Godley et al. 2001]; red, Brazil [Mrosovsky et al. 1999]). (b) Regression lines for mean percentage of female hatchlings produced using the seven estimation curves. Regression analyses on all curves were significant with r^2 values between 0.35 and 0.37 and $P < 0.01$. These results were similar to those obtained when using the mean sex ratio estimate from all seven curves.

seasonal means, $r^2 = 0.36$, $P = 0.0016$; Figs. 2b and 3d). We found no significant change in either hatching success (all nests, $r^2 = 0.003$, $P = 0.05$; seasonal means, $r^2 = 0.01$, $P = 0.70$; Fig. 3e) or date of first nesting ($r^2 = 0.05$, $P = 0.27$; Fig. 3f) over time. Finally, there was no significant correlation between mean April air temperature and date of first nesting ($r^2 = 0.11$, $P = 0.12$).

Our univariate models show that temperature had a significant effect on incubation duration and percentage of female offspring ($F_{1,23} = 59.94$, $P < 0.0001$ and $F_{1,23} = 58.21$, $P < 0.0001$, respectively), but no effect on the hatching success of nests ($F_{1,23} = 0.0001$, $P = 0.99$; Table 3). Precipitation had a marginally significant effect on hatching success (Table 3). In our multivariate models, temperature explained the most variation in

TABLE 1. Estimated pivotal incubation durations (PID), percentage of female hatchlings, and transitional range of incubation durations (TRI) for loggerhead turtles across the species range.

Location	Estimated female hatchlings (%)				Source
	Estimated PID (d)	At 59 d, in 1991	At 52 d, in 2015	Estimated TRI (d)	
Laboratory					
Brazil	59.3	57	100	53–64	Mrosovsky et al. (1999)
Brazil	59.3	53	100	53–65	Godley et al. (2001)
Greece	56.6	2	100	54–59	Mrosovsky et al. (2002)
Field					
United States	60.2	57	87	42–80	Godfrey and Mrosovsky (1997)
Brazil	59.9	57	93	43–73	Mrosovsky et al. (1999)
United States	61.7	61	83	40–80	Godley et al. (2001)
Cyprus	56.3	12	95	48–63	Fuller et al. (2013)

TABLE 2. Five-year means of climate conditions and nest characteristics over 25 yr (1991–2015) at Bald Head Island, North Carolina, USA.

Date range	Temperature (°C)	Precipitation (mm)	Incubation duration (d)	Female offspring (%)	Hatching success (%)
1991–1995	25.8	162.8	59.7	53.1	78.9
1996–2000	25.5	174.9	59.4	53.7	78.8
2001–2005	26.2	150.4	58.7	56.9	81.1
2006–2010	27.6	70.3	56.2	71.5	79.3
2011–2015	26.9	98.2	55.8	71.9	77.3

incubation duration and percentage of female offspring ($F_{1,22} = 38.35$, $P < 0.0001$ and $F_{1,22} = 37.63$, $P < 0.0001$, respectively), while precipitation was the most significant predictor of nest hatching success ($F_{1,22} = 10.03$, $P = 0.005$; Table 3).

DISCUSSION

The successful production of sea turtle hatchlings remains a critical conservation priority, particularly in the face of rapid environmental change (Hawkes et al. 2007, IPCC 2014). We found that temperatures significantly increased and precipitation levels significantly decreased over a 25-yr period at the BHI loggerhead rookery. Although increasing temperatures did not affect the hatching success of nests, we found that nests tended to have lower hatch rates when rainfall was higher. Given that BHI is not subjected to periods of prolonged drought, it is likely the high levels of precipitation caused egg suffocation and thus clutch failure (McGehee 1990). This raises potential longer-term concerns for the continued production of hatchlings as the most recent climate change projections predict increases in intensity and frequent rainfall events (IPCC 2014).

Temperature did, however, significantly affect incubation duration, where we found an average decrease of seven incubation days over our study period, and a concomitant increase in the estimated percentage of female

hatchlings produced, from a mean of 55% in 1991 to a mean of 88% in 2015 (see Table 1 for ranges). While hatchling sex ratios have been estimated using various methods (Witt et al. 2010), the pelagic lifestyle of juvenile and adult sea turtles makes it difficult to assess operational sex ratios (OSR; i.e., ratio of total breeding males vs. females) in the wild (Delgado et al. 2010, Hays et al. 2010). Recently, the OSR for a loggerhead population in the Mediterranean was found to be less female biased (50:50 female to male) than the hatchling sex ratio (70:30 female to male), as males return to breed with numerous females (Hays et al. 2010). However, despite the potentially mitigating effect of male mating behaviors on skewed sex ratios, rapid warming and near complete feminization of hatchlings will inevitably lead to a reduction of viable male mates (Hays et al. 2010). Highly female-biased OSRs have been shown to markedly decrease female fecundity (Milner-Gulland et al. 2003) and will ultimately lead to low fertilization success and egg production as sperm becomes limited (Rankin and Kokko 2007).

Adaptations in response to climate change have already been documented in many plants, birds, and small mammals in the form of range expansions and shifts (Hughes 2000), though evidence for this behavior in turtles is limited (Janzen 1994). Indeed, sea turtles exhibit a high degree of nest site fidelity, repeatedly returning to the same beach within and across nesting seasons (Webster and Cook 2001). Adjustment of nesting phenology has also been suggested as a potential

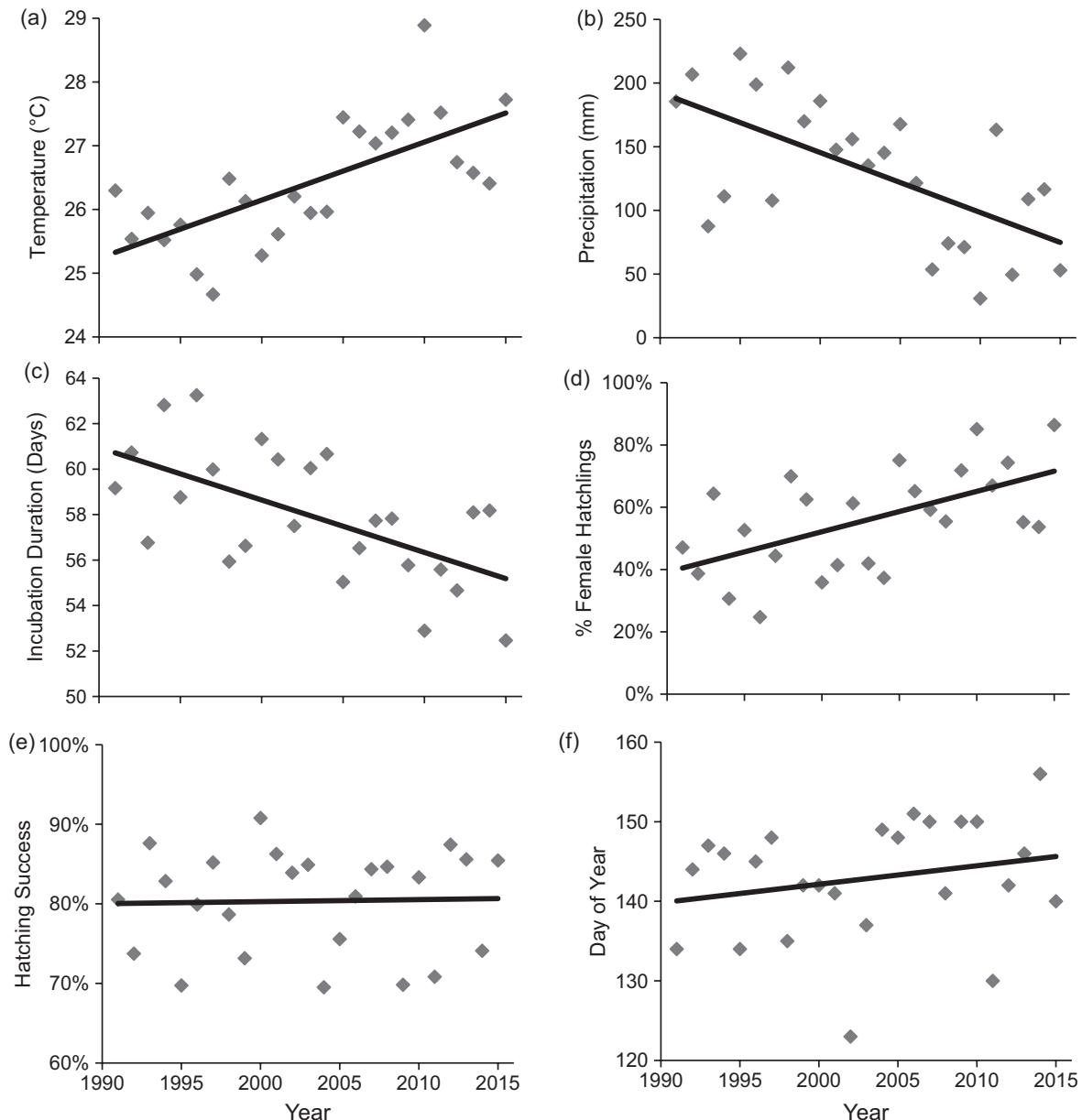


FIG. 3. Temporal changes in climatic conditions and nest characteristics over 25 yr (1991–2015) at Bald Head Island, North Carolina. Shown are regressions lines for (a) mean seasonal air temperatures ($r^2 = 0.47$, $P = 0.0001$), (b) mean seasonal precipitation ($r^2 = 0.38$, $P = 0.001$), (c) mean incubation durations ($r^2 = 0.37$, $P = 0.0013$), (d) mean percentage of female offspring produced ($r^2 = 0.36$, $P = 0.0016$), (e) mean nest hatching success ($r^2 = 0.01$, $P = 0.70$), and (f) date of first nesting ($r^2 = 0.05$, $P = 0.27$).

mechanism to offset an increase in seasonal temperatures (Hughes 2000). Sea turtles have been documented nesting earlier in the season during years of warmer sea surface temperatures (Weishampel et al. 2004, Hawkes et al. 2007) but more research is needed as only a few studies have observed shifts in nesting start date over longer timescales (e.g., decades; Mazaris et al. 2008).

Estimates of nest sex ratios derived from incubation durations predict that 97% of offspring will be female when incubation durations fall below 50 d. Nearly half of

the nests (45 out of 92) laid in the most recent nesting season at BHI incubated for 52 d or less, the shortest durations observed at this site to date. BHI has long been considered a rookery that exhibits more balanced sex ratios than its more southern counterparts, potentially providing males to breed with females from those highly female-biased rookeries. Here we show that a continued rise in global temperatures could play an increasingly important role in the future viability of the loggerhead turtle in the Western Atlantic. As such, we should

TABLE 3. Univariate and multivariate mixed-model analysis of the relationship between climate variables and various nest attributes.

Model	Incubation duration			Percentage of female offspring			Hatching success		
	AIC	<i>P</i>	<i>R</i> ²	AIC	<i>P</i>	<i>R</i> ²	AIC	<i>P</i>	<i>R</i> ²
Univariate									
Temperature	100.5	<0.0001	0.7	50.5	<0.0001	0.7	45.9	0.9	3 × 10 ⁻⁶
Precipitation	129.4	0.3	0.4	79.1	0.3	0.4	47.9	0.1	0.3
Multivariate									
a. T/P	111.7		0.7	63.9		0.7	51.4		0.3
Temperature		<i><0.0001</i>			<i><0.0001</i>			0.10	
Precipitation		0.8			0.8			0.01	
b. T/P/T × P	122.6		0.7	76.9		0.73	66.0		0.3
Temperature		<i><0.0001</i>			<i><0.0001</i>			0.1	
Precipitation		0.7			0.7			0.01	
T × P		0.3			0.3			0.8	

Notes: Year is included as a random factor in all models. T, temperature; P, precipitation. The model with the lowest Akaike information criterion corrected for sample size (AIC_c) score is shown in boldface type and the significant effects (*P* < 0.05) are shown in italic type.

continue to incorporate these impacts into species assessments, with particular emphasis placed on maintaining suitable thermal nesting habitat for sea turtles in important male-producing regions.

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LITERATURE CITED

- Ackerman, R. A. 1997. The nest environment and the embryonic development of sea turtles. Pages 83–107 in P. L. Lutz and J. A. Musick, editors. *The biology of sea turtles*. CRC Publishing, Boca Raton, Florida, USA.
- Deeming, D. C., and M. W. J. Ferguson. 1991. Physiological effects of incubation temperature on embryonic development in reptiles and birds. Pages 147–172 in D. C. Deeming, and M. W. J. Ferguson, editors. *Egg incubation: its effects on embryonic development in birds and reptiles*. Cambridge University Press, Cambridge, UK.
- DeGregorio, B. A., and A. S. Williard. 2011. Incubation temperatures and metabolic heating of relocated and in situ loggerhead sea turtle (*Caretta caretta*) nests at a northern rookery. *Chelonian Conservation and Biology* 10:54–61.
- Delgado, C., A. V. M. Canario, and T. Dellinger. 2010. Sex ratios of loggerhead sea turtles *Caretta caretta* during the juvenile pelagic stage. *Marine Biology* 157:979–990.
- Fuller, W. J., B. J. Godley, D. J. Hodgson, S. E. Reece, M. J. Witt, and A. C. Broderick. 2013. Importance of spatio-temporal data for predicting the effects of climate change on marine turtle sex ratios. *Marine Ecology Progress Series* 488:267–274.
- Georges, A. 1989. Female turtles from hot nests: Is it duration of incubation or proportion of development at high temperatures that matters? *Oecologia* 81:323–328.
- Georges, A., C. Limpus, and R. Stoutjesdijk. 1994. Hatchling sex in the marine turtle, *Caretta caretta*, is determined by proportion of development at a temperature, not daily duration of exposure. *Journal of Experimental Zoology* 270:432–444.
- Godfrey, M. H., and N. Mrosovsky. 1997. Estimating the time between hatching of sea turtles and their emergence from the nest. *Chelonian Conservation and Biology* 2:581–585.
- Godley, B. J., A. C. Broderick, and N. Mrosovsky. 2001. Estimating hatchling sex ratios of loggerhead turtles in Cyprus from incubation durations. *Marine Ecology Progress Series* 210:195–201.
- Hawkes, L. A., A. C. Broderick, M. H. Godfrey, and B. J. Godley. 2007. Investigating the potential impacts of climate change on a marine turtle population. *Global Change Biology* 13:923–932.
- Hays, G. C., S. Fossette, K. A. Katselidis, G. Schofield, and M. B. Gravenor. 2010. Breeding periodicity for male sea turtles, operational sex ratios, and implications in the face of climate change. *Conservation Biology* 24:1636–1643.
- Hays, G. C., A. D. Mazaris, and G. Schofield. 2014. Different male vs. female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Frontiers in Marine Science* 1:1–9.
- Howard, R., I. Bell, and D. A. Pike. 2014. Thermal tolerances of sea turtle embryos: current understanding and future directions. *Endangered Species Research* 26:75–86.
- Hughes, L. 2000. Biological consequences of global warming: Is the signal already apparent? *Trends in Ecology and Evolution* 15:56–61.
- IPCC. 2014. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Page 151 in R.K. Pachauri, and L.A. Meyer, editors. *Climate Change 2014: Synthesis Report*. IPCC, Geneva, Switzerland.
- Janzen, F. J. 1994. Climate change and temperature-dependent sex determination in reptiles. *Proceedings of the National Academy of Sciences USA* 91:7487–7490.
- Kraemer, J. E., and R. Bell. 1980. Rain-induced mortality of eggs and hatchlings of loggerhead sea turtles (*Caretta caretta*) on the Georgia coast. *Herpetologica* 36:72–77.

- Lolavar, A., and J. Wyneken. 2015. Effect of rainfall on loggerhead turtle nest temperatures, sand temperatures and hatchling sex. *Endangered Species Research* 28:235–247.
- Marcovaldi, M. A. G., A. J. B. Santos, A. S. Santos, L. S. Soares, G. G. Lopez, M. H. Godfrey, M. Lopez-Mendilaharsu, and M. M. P. B. Fuentes. 2014. Spatio-temporal variation in the incubation duration and sex ratio of hawksbill hatchlings: implication for future management. *Journal of Thermal Biology* 44:70–77.
- Marcovaldi, M. A. G., et al. 2016. Identification of loggerhead male producing beaches in the south Atlantic: implications for conservation. *Journal of Experimental Marine Biology and Ecology* 477:14–22.
- Matsuzawa, Y., K. Sato, W. Sakamoto, and K. A. Bjorndal. 2002. Seasonal fluctuations in sand temperature: effects on the incubation period and mortality of loggerhead sea turtle (*Caretta caretta*) pre-emergent hatchlings in Minabe, Japan. *Marine Biology* 140:639–646.
- Mazaris, A. D., A. S. Kallimanis, S. P. Sgardelis, and J. D. Pantis. 2008. Do long-term changes in sea surface temperature at the breeding areas affect the breeding dates and reproduction performance of Mediterranean loggerhead turtles? Implications for climate change. *Journal of Experimental Marine Biology and Ecology* 367:219–226.
- McGehee, M. A. 1990. Effects of moisture on eggs and hatchlings of loggerhead sea turtles (*Caretta caretta*). *Herpetologica* 1990:251–258.
- Milner-Gulland, E. J., O. M. Bukreeva, T. Coulson, A. A. Lushchekina, M. V. Kholodova, A. B. Bekenov, and I. A. Grachev. 2003. Reproductive collapse in saiga antelope herds. *Nature* 422:135.
- Mrosovsky, N. 1988. Pivotal temperatures for loggerhead turtles (*Caretta caretta*) from northern and southern nesting beaches. *Canadian Journal of Zoology* 66:661–669.
- Mrosovsky, N., C. Baptistotte, and M. H. Godfrey. 1999. Validation of incubation duration as an index of the sex ratio of hatchling sea turtles. *Canadian Journal of Zoology* 77: 831–835.
- Mrosovsky, N., S. Kamel, A. F. Rees, and D. Margaritoulis. 2002. Pivotal temperature for loggerhead turtles (*Caretta caretta*) from Kyparissia Bay, Greece. *Canadian Journal of Zoology* 80:2118–2124.
- Rankin, D. J., and H. Kokko. 2007. Do males matter? The role of males in population dynamics. *Oikos* 116:335–348.
- Santidrian-Tomillo, P., et al. 2015. Global analysis of the effect of local climate on the hatchling output of leatherback turtles. *Scientific Reports* 5:16789. DOI:10.1038/srep16789.
- Standora, E. A., and J. R. Spotila. 1985. Temperature dependent sex determination in sea turtles. *Copeia* 1985: 711–722.
- Webster, W. D., and K. A. Cook. 2001. Intraseasonal nesting activity of loggerhead sea turtles (*Caretta caretta*) in southeastern North Carolina. *American Midland Naturalist* 145:66–73.
- Weishampel, J. F., D. A. Bagley, and L. M. Ehrhart. 2004. Earlier nesting by loggerhead sea turtles following sea surface warming. *Global Change Biology* 10:1424–1427.
- Witt, M. J., L. A. Hawkes, M. H. Godfrey, B. J. Godley, and A. C. Broderick. 2010. Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. *Journal of Experimental Biology* 213: 901–911.
- Wyneken, J., and A. Lolavar. 2015. Loggerhead sea turtle environmental sex determination: implications of moisture and temperature for climate change based predictions for species survival. *Journal of Experimental Zoology Part B Molecular and Developmental Evolution* 324:295–314.