

Alligator Nest Temperatures and Hatchling Sex Ratios in Coastal South Carolina

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Abstract: The relation between natural nest temperatures and hatchling sex ratios of American alligator (*Alligator mississippiensis*) has not been determined adequately. The few studies to date have been limited by study design, low sample size, and inadequate equipment. We investigated this relationship in 20 nests in impoundment habitat in South Carolina during 1995. Actual sex ratios were highly correlated ($r = 0.971$, $P < 0.001$) with sex ratios predicted from laboratory results, on the basis of mean nest temperatures between days 30–45 of incubation (temperature-sensitive period (TSP)). Mean nest temperatures during the TSP ranged between 29.1 to 33.8 C, with daily fluctuations within a nest ranging from 0.4 to 1.9 C. Rainfall appeared to have the greatest effect on nest temperatures. While nest temperatures provided a useful estimate of hatchling sex ratios, we recommend that researchers monitor hatchling sex ratios directly. Nest temperatures provide other relevant indicators for alligator management.

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Sex determination in all crocodylians, including American alligators, is dependent on egg incubation temperature prior to hatching (Ferguson and Joanen 1982, Lang and Andrews 1994). Over the range of viable incubation temperatures (28–35 C), the temperature-dependent sex determination (TSD) pattern for alligators is female-male-female. Temperatures ≤ 31.5 C and ≥ 35.0 C produce exclusively females, whereas temperatures from 32.5–33.0 C yield 100% males. Varying ratios of males and females are produced at transitional temperatures. The thermo-sensitive period (TSP) for alligators occurs during days 30–45 of incubation (Lang and Andrews 1994).

Incubation environment in the nest has a profound effect on hatchling sex for alligators. Crocodylian nest temperatures are affected by habitat, rainfall, air temperature, and metabolic embryo heat (Webb et al. 1977, 1983; Magnusson 1979; Ferguson and Joanen 1983; Hutton 1987; Hayes 1990; Schulte and Chabreck 1990; Campos 1993), but how these variables affect hatchling sex ratios is unknown. Some studies

have only utilized spot measurements to record alligator nest temperatures (Dietz and Hines 1980, Klause 1984, Platt 1990, Platt et al. 1995). Other studies (Joanen 1969, Chabreck 1973, Ferguson and Joanen 1983, Hayes 1990, Schulte and Chabreck 1990) have recorded nest temperatures over the incubation period but report equipment malfunctions or were limited by small sample sizes. Thus, the relationship between temperatures from naturally-incubated alligator nests and hatchling sex ratios remains poorly understood.

New temperature recording technology, information about pattern and timing of TSD in alligators (Land and Andrews 1994), and a new technique for sexing live hatchlings (Allsteadt and Lang 1995b) prompted us to attempt a thorough study of nest temperature and hatchling sex ratios correlations. Therefore, our objective was to describe the relationship between nest temperatures and naturally-incubated hatchling sex ratios in coastal South Carolina.

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Methods

The study, which was part of long-term study initiated in 1994, was conducted during 1995 along the north-central coast of South Carolina on the 10,118-ha Santee Coastal Reserve in Charleston County. The 1,421-ha mainland portion of managed impoundments known as the Cape served as the principal study site. The primary vegetative species within the impoundments were giant cordgrass (*Spartina cynosuroides*), saltmarsh bulrush (*Scirpus robustus*), and wigeongrass (*Ruppia maritima*). Trees and shrubs were sparse, except on dikes. Surrounding wetlands were tidal and subject to extreme salinity variation (0 to 35 ppt) from periodic discharges into the Santee River from the Santee-Cooper lakes (Rhodes and Lang 1995).

Mean annual and seasonal temperatures were normal (< 1 C deviation) and annual rainfall was 6% above normal during 1995. The June-August rainfall was 43% above normal. However, nearly 50% of the three-month rainfall was a result of a tropical storm during a 5-day span in late August. This storm occurred after the TSP for nests located on the study area.

To locate alligator nests, an aerial survey was conducted on 13 July 1995 as described by Rhodes and Lang (1995). Nest locations were plotted on an aerial photograph (scale 1 cm = 158.4 m). Immediately following aerial survey, these nests were located on the ground. Nesting habitat features recorded are defined in Rhodes and Lang (1995). Either a Hobo® or Optic Stowaway® temperature recorder (Onset Computer Co., Pocasset, Mass.), programmed to log temperature, date, and time every hour or half hour, respectively, was placed adjacent to eggs in the chamber center for each active nest. Accuracy for temperature recorders was ± 0.2 C.

To estimate oviposition date and TSP, 1 banded egg from each clutch was collected and preserved in 10% formalin (Webb and Manolis 1987). Preserved embryos

were later staged according to Ferguson (1987), and embryo age (in days) at collection was determined by relating stage and initial nest temperature (Table 1). From age, we estimated oviposition date and the TSP (30–45 days of incubation) by back- and forward-dating, respectively.

Because Lang and Andrews (1994) found that the thermosensitive period (i.e., the period of time when incubation temperature determines sex) occurs during the middle third of development, eggs were collected during the last trimester (12 and 13 Aug. 1995). During egg collection, temperature recorders were removed and clutch size (+1 for sacrificed egg) was noted. Egg measurements taken and incubation techniques for the period following egg collection are outlined in Rhodes and Lang (1995).

Once hatching was complete, hatchlings, by clutch, were removed to separate 0.6 × 0.6-m open-air raceways containing water and basking areas (Rhodes and Lang 1995). All unhatched eggs were opened, and late-stage embryos and dead hatchlings were sexed by internal gonad examination. Live hatchlings were sexed (Allsteadt and Lang 1995*b*); and for each individual, total and snout-vent lengths (nearest 1.0 mm) and weight (nearest 0.1 g) was recorded. All hatchlings were released at original nest sites in early September.

Lang and Andrews (1994) determined alligator sex ratios at constant incubation temperatures. For any given temperature, there is an expected sex ratio based on interpolation of values in Table 1. Using this relationship, we predicted an expected hatchling sex ratio for each naturally-incubated nest on the basis of mean nest temperature for 3 time periods; i.e., 25–45 days, 30–45 days, and 35–45 days. The relationship between actual live hatchling sex ratios and the 3 predicted values were described using simple correlation (Zar 1996:371–374), and the best match was selected. We

Table 1. Approximate age (in days) for representative developmental stages in the American alligator at constant incubation temperatures of 29–35 C (top). Expected time to hatch (in days) and sex ratios (% male) for alligator embryos incubated at 29–35 C in 0.5 C increments (bottom) (adapted from Lang and Andrews 1994).

Stage	Incubation Temperature													
	29	29.5	30	30.5	31	31.5	32	32.5	33	33.5	34	34.5	35	
14	20		17		16		14		14		14		14	
15	24		20		19		17		16		15		15	
16	28		21		20		18		17		16		16	
17	30		23		22		21		18		17		17	
18	32		25		24		22		20		19		19	
19	34		27		26		24		22		21		21	
20	38		30		28		26		24		23		23	
21	42		34		33		31		29		28		28	
22	48		40		38		35		34		33		33	
25	64		54		50		50		48		46		46	
Hatch (days)	84	80	77	73	71	68	66	64	63	62	61	61	60	
% ♂♂	0	0	0	0	0	0	66	100	100	84	35	7	0	
range (% ♂♂)							13–100			100–40		70–0		20–0

then compared the expected sex ratio on the basis of nest temperature for 30–45 days with the actual sex ratio using the chi-squared distribution to test for a significant difference. Our expectation was that the actual versus expected sex ratios would not differ ($P > 0.05$).

Results

We located 24 nests (1 nest/59 ha) during an aerial survey, including 20 active nests and 3 false nests; 1 nest was not located during ground search. Average clutch size was 45.0 eggs (range = 25–57), and a total of 872 eggs were collected. Hatching success, defined as total eggs divided by total eggs hatched, was 79.8%. All 20 nests hatched ≥ 13 eggs, and a total of 648 young were subsequently released.

Egg chamber temperature was monitored in each nest; and a summary of relevant parameters for each nest are shown in Table 2. Egg laying was estimated to have occurred over a 15-day period between 14–28 June, and the period of sex determination (i.e., thermo-sensitive period; TSP) occurred between 14 July and 12 August for all nests. Mean temperatures during the TSP (as indicated in Table 2) for each nest ranged from 29.1 to 33.8 C ($N = 384$ –768), with 27.1 and 35.6 C the lowest and highest, respectively, nest temperatures recorded. The overall mean nest temperature for the 20 nests was 31.9 C. The overall mean daily fluctuation (= difference between daily maximum and minimum temperatures) for the TSP was 1.0 C ($N = 20$), with mean daily temperatures fluctuating as little as 0.4 C and as much as 1.9 C within a nest during the TSP. Mean air and water temperatures during the TSP were 27.0 and 30.9 C, respectively.

Actual hatchling sex ratio was highly correlated with the expected sex ratio predicted by the mean nest temperature during the TSP of sex determination ($r = 0.971$, $P < 0.001$, $N = 20$; Table 2). Although the best match between actual and predicted sex ratios was based on mean nest temperature during days 30–45, extending or shortening the time period used to calculate mean nest temperature resulted in correlation values of $r = 0.880$ for 25–45 days and $r = 0.861$ for 35–45 days ($P < 0.001$). Based on mean nest temperatures during days 30–45, there was a significant difference between actual versus predicted sex ratios for the 20 nests ($X^2 = 124.34$, $df = 19$, $P < 0.001$); however, the difference could be attributed to 4 nests.

Mean nest temperatures during TSP in nests No. 7, 9, 10, and 17 predicted sex ratios of 100%, 100%, 93%, and 54% males, respectively, whereas the actual sex ratios were 36%, 56%, 41%, and 85% males, respectively. Mean TSP nest temperature for nests No. 10 and 17 occurred in pivotal temperature ranges, spreads where sex ratios may vary between 13%–100% males (Table 1). Thus, the large disparity between actual versus predicted sex ratios for these 2 nests was not unexpected. For the other 2 nests (No. 7 and 9), mean TSP nest temperatures occurred in the male-producing range. However, No. 7 had an increasing temperature trend throughout the TSP only to be reduced twice by rainfall, and temperatures for No. 9 remained mostly on either side of the male range during the TSP. Consequently, by averaging temperatures, both nests were classified as male-producing nests when, in fact, nest tempera-

Table 2. Nesting parameters, nest temperatures, and predicted and actual sex ratios for alligator nests, Santee Coastal Reserve, South Carolina, 1995.

Nest No.	Clutch size	Julian date laid	Julian date TSP	Mean TSP nest temperature (range)	Mean daily TSP nest temperature fluctuation	No. sexed	Predicted sex ratio (% ♂♂)	Actual sex ratio (% ♂♂)
17	43	167	195-210	33.8 (28.6-34.9)	1.0	13	54	85
6	57	167	197-212	33.6 (32.3-34.6)	0.8	44	74	80
20	45	170	200-215	33.5 (32.0-34.6)	1.0	42	84	74
1	43	168	198-213	33.0 (28.7-35.3)	1.2	40	100	73
5	25	166	196-211	33.0 (31.9-33.8)	0.5	17	100	76
9	49	165	195-210	32.8 (29.9-35.2)	1.0	36	100	56
15	51	166	196-211	32.7 (31.3-34.1)	1.0	46	100	85
14	50	165	195-210	32.6 (31.5-34.6)	0.6	47	100	98
7	45	169	200-215	32.6 (30.8-34.3)	0.6	39	100	36
10	40	165	195-210	32.4 (30.7-33.2)	0.5	32	93	41
16	41	175	205-220	32.3 (27.7-33.7)	1.1	15	86	73
12	48	175	205-220	31.9 (28.1-34.6)	1.9	26	53	35
18	47	170	200-215	31.4 (27.9-32.8)	0.8	40	0	0
19	39	174	204-219	31.0 (29.9-32.2)	0.4	35	0	0
2	46	168	198-213	30.9 (28.9-32.1)	1.1	39	0	0
11	47	175	205-220	30.9 (27.6-32.5)	1.1	42	0	5
4	46	170	200-215	30.5 (27.5-33.5)	1.9	31	0	3
8	40	179	209-224	30.3 (27.3-32.3)	1.2	23	0	0
13	48	168	198-213	29.8 (28.0-31.3)	1.5	17	0	0
3	45	167	197-212	29.1 (27.1-30.7)	1.5	24	0	0

tures during the TSP rarely occurred in the male range. When nests 7, 9, 10, and 17 were excluded from the analysis, there was no significant difference between actual versus predicted sex ratios for the other 16 nests ($X^2 = 17.14$, $df = 15$, $P = 0.32$).

Daily mean nest temperatures throughout the measurement period for 4 representative nests are shown in Fig. 1, together with daily mean air and water temperatures and rainfall. Differences among nests were consistent, resulting in relatively uniform temperatures within a particular nest from one day to the next. For example, the top traces in Fig. 1b and 1c were warm nests (No. 6 and 20, respectively) that produced 80% and 74% males, respectively. In contrast, the bottom traces in Fig. 1b and 1c were cool nests (No. 3 and 18, respectively) that produced exclusively females. These differences persisted whether the TSP occurred relatively early (Fig. 1b) or late (Fig. 1c).

During the measurement period, ambient air and water temperature increased gradually. In general, nest temperatures were considerably warmer (2–6 C) than air temperatures, but approximated (± 2 C) water temperature (Fig. 1a). Rainfall, particularly heavy precipitation, often resulted in sharp, but transitory drops in nest temperatures. Mean daily nest temperatures fell as much as 3.2 C before rapidly recovering within 24 hours.

Discussion

In our field study, warm nest temperatures (> 31.5 C) produced varying proportions of males whereas females were produced in cool nests (< 31.5 C). When alligator eggs are incubated at constant temperatures (± 0.1 C) under experimental conditions, the range of viable temperatures (from 29.0–35.0, Table 1) closely parallels the range of temperatures in the nests we monitored (Table 2). In the lab, the resultant pattern of sex determination at low to high incubation temperatures is female-male-female, with substantial clutch-dependent variability in sex ratio at transitional temperatures (between 31.5–32.5, and between 33.0–35 C; Table 1). A similar female-male-female pattern of sex determination was evident over the range of mean nest temperatures (28.9–33.8 C) in our study (Table 2).

Congruence of the present study with recent laboratory investigations indicates that the predicted pattern of (TSD) is operable in the field. While earlier studies (Ferguson and Joanen 1982, 1983) demonstrated that sex ratio biases in natural nests were related to nest temperatures, the production of female-biased sex ratios at high nest temperatures (> 33 C) in the present study is consistent with the revised pattern of TSD in alligators (Lang and Andrews 1994). In 2 recent field studies of alligator nesting (Schulte 1989, Hayes 1990), warm nests produced some females, contrary to earlier reports. Furthermore, a TSP of 30–45 days based on recent lab studies (Lang and Andrews 1994) is supported by our field results, in contrast to previous reports of an earlier TSP (7–21 days; Ferguson and Joanen 1982). Thus, the salient feature of the TSD phenomenon in alligators, i.e., the TSD pattern in relation to temperature and the timing of the TSP (Lang and Andrews 1994), is applicable under natural as well as experimental conditions.

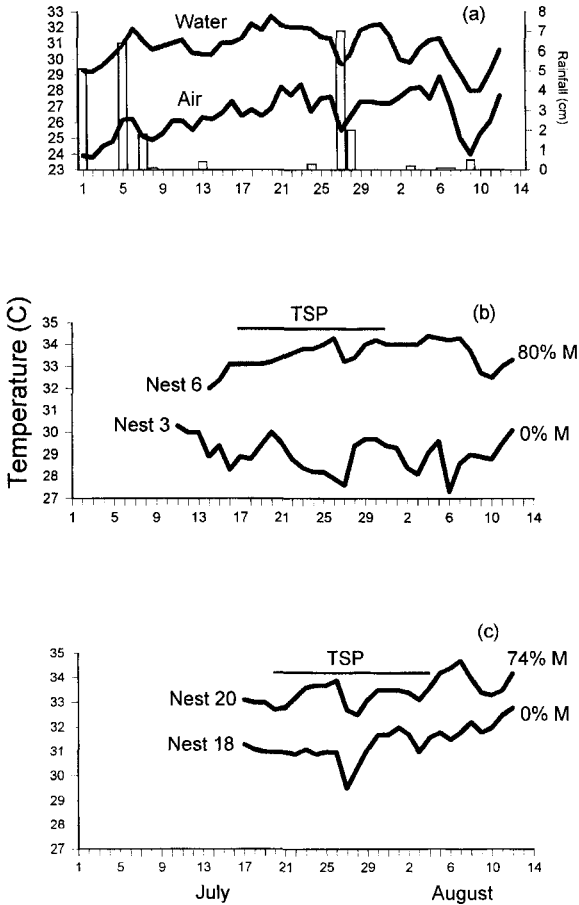


Figure 1. (a) Daily records of ambient water (at 1.5m depth) and air (shaded; at ground level) temperatures (C) on the Santee Coastal Reserve, South Carolina, July–August 1995. Rainfall (cm, right axis) is shown as daily totals.

(b) Daily record of mean egg chamber temperature (C) in a warm alligator nest (No. 6) versus a cool nest (No. 3). Sex ratio (% male) of each nest is indicated at right of each trace, and the thermo-sensitive period (TSP; denoted with a solid black line) is shown for days 30–45 of incubation.

(c) Another warm alligator nest (No. 20) versus a cool nest (No. 18) with the TSP starting 2 days later than in (b); otherwise legend as in (b) above.

Many factors affect nest temperatures. Insolation, rainfall, air temperature, metabolic heat, heat of decomposition, nest composition, habitat, and time of nesting have been shown to influence crocodilian nest temperatures (Chabreck 1973; Webb et al. 1977, 1983; Magnusson 1979; Ferguson and Joanen 1983; Hutton 1987; Lang et al. 1989; Hayes 1990; Schulte and Chabreck 1990; Campos 1993). The complexity of these factors and their interactions argue against simple associations between a single factor and resultant sex ratios. For example, previous studies on alligators attempted to establish an association between nest location and the production of a particular sex. Hot levee nests reportedly produced males, whereas cool marsh nests resulted in females (Ferguson and Joanen 1982, 1983). In similar habitats, Schulte and Chabreck (1990) reported warm marsh nests that produced males, and a cool levee nest of exclusively females. Hayes (1990) concluded that TSD in wild alligator nests studied at 2 locations in Texas is complex, and not easily predicted by nest type or location. In addition, because seasonal climate potentially has a major impact on alligator nest temperatures, Rhodes and Lang (1995) suggested that hatchling sex ratios are likely to vary from year to year within the same habitat.

In the present study, time of nesting had minimal effect on the differences we observed in nest temperatures and sex ratios because of synchronous nesting (Table 2). Rather, specific nest features presumably contributed to the observed differences, as evidenced by warm versus cool nests in the same habitat subject to the same climatic regime (Fig. 1). Thus, nest characteristics seem to be key factors resulting in the observed sex ratio differences.

Most alligator nesting in South Carolina occurs in wetland impoundments (Wilkinson and Rhodes 1992) on interior remnant dikes and berms and marsh areas characterized by giant cordgrass (*Spartina cynosuroides*) (Rhodes, unpubl. data). Seventeen of 20 nests located were constructed primarily out of cordgrass, with the remaining 3 nests comprised of black needle rush (*Juncus spp.*). Chabreck (1973) felt that variation between nest temperatures resulted from nest materials. He hypothesized that nests constructed largely of green vegetation would have a higher temperature, as a result of decomposition, than nests having a higher ratio of partially decomposed vegetation or mineral soil. Our sample size was too small to draw any conclusions about vegetative differences.

In addition to nest type and construction, nest exposure (e.g., open versus shaded) has been implicated as a determinant of differences in nest temperatures and resultant sex ratios in other species (Lang et al. 1989, Campos 1993). However, in our study, all nests were exposed to overhead sunlight during the day. Metabolism of the eggs may contribute appreciable heat to the nest (Magnusson 1979, Magnusson et al. 1985, 1990), but embryonic metabolism peaks relatively late in incubation (i.e., during the last quarter; Whitehead 1987) after the period of sex determination. Therefore, such effects may accelerate development, but are not likely to influence sex ratios.

Water depth and rainfall were found to initially affect moisture content in alligator nests, and nests made of the same species of vegetation exhibited differences in moisture content (Chabreck 1975). Further, Chabreck (1975) reported that nests rapidly reached a saturation point and then remained at that level through time, with

rainfall and water depth having little effect after saturation. We did not measure water level at the nest or the distance of nest from water. In a previous study in the same habitat, we noted that nests located at low elevations within impoundments were cooler and produced more females than those at high elevations (Rhodes and Lang 1995).

Although clear-cut differences in mean nest temperatures were observed during the TSP (29.1–33.8 C, Table 2), mean daily fluctuations within individual nests ranged from ± 0.2 to ± 1.0 C and were not predictably related to nest temperature (Table 2). We suggest that the differences in nest thermal characteristics in our study primarily resulted from differences in nest type and construction (i.e., material, size, and/or shape) and differences in nest moisture that were, in turn, related to location and height above the water table. Efforts are now underway to examine these features systematically and to quantify how they may relate to nest temperatures and resultant sex ratios. With the exception of transitory changes in nest temperatures related to periodic rainfall, the overall thermal consequences of the alligator mound nests in our study were to produce stable egg temperatures buffered from daily extremes and to promote elevated egg temperatures relative to ambient conditions while maintaining adequate moisture levels.

As noted earlier, seasonal climate has been identified as a major determinant of nest temperatures and sex ratio biases in alligators as well as other crocodylians (see reference cited above). Our findings with respect to hatchling sex ratios in a wet year (1994) (Rhodes and Lang 1995) versus a dry year (1995) in the same habitat support this contention. A wet climatic regime tended to produce cooler nests that resulted in a strong female-biased cohort of hatchlings with only 21% males (Rhodes and Lang 1995); whereas, a relatively dryer regime resulted in twice as many males (42%) (this study).

Management Implications

If it is important to estimate hatchling sex ratios, is it better to determine actual sex ratios directly or is it sufficient to monitor nest temperatures to predict hatchling sex ratios? We strongly recommend directly sexing hatchlings (as outlined in Rhodes and Lang 1995). Less detailed information regarding the pattern and timing of TSD as it relates to the species of interest is required, and fewer inferences are necessary to make reliable estimates. Furthermore, there is considerable variation in sex ratio outcome at transitional temperatures in the lab. And this variability adds uncertainty to predictions based solely on nest temperatures.

So why monitor nest temperatures? In certain circumstances, nest temperature may be a useful indication of which types of nesting habitats are suitable for the production of viable young of both sexes. For example, it has been suggested that certain vegetation used as nest material in Louisiana causes high nest temperatures that result in embryonic death (L. McNease and R. Elsey, La. Dep. Wildl. and Fish., pers. commun.). In other situations, manipulation in water levels may alter nest temperatures and resultant hatchling survivorship and/or sex ratios. Also, postulated long-

term changes in regional and/or global climate may have effects on nest temperatures with attendant consequences.

From a management viewpoint, a compelling reason to monitor alligator nest temperatures is that there are direct effects of incubation temperature on hatchlings other than sex determination. These effects, including available yolk reserves and hatchling size (Allsteadt and Lang 1995a), have been shown in alligators to ultimately influence juvenile survivorship, performance, and growth (Joanen et al. 1987). For example, many hatchlings from cool nests that hatch after lengthy incubations do not thrive in the weeks following hatching; mortality is likely higher on these offspring. Likewise, hatchlings from hot nests typically emerge quickly with large yolk reserves at small body sizes, and abnormalities and runts are frequent at high incubation temperatures (Rhodes and Lang, unpubl. data). Thus, not only sex, but hatchling "quality" is apparently related to the nest environment.

Our study indicates that the predicted TSD pattern from the lab is operable under natural conditions. However, natural nest temperatures vary even in similar habitat within the same season, and such variation indicates that the factors affecting nest temperatures are complex. Therefore, we suggest that information on hatchling sex ratios be obtained by directly sexing hatchlings as opposed to relying solely on predictions based on nest temperatures. Monitoring of nest temperatures is useful for management and natural history reasons.

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