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Nest Attendance Patterns in the American Alligator (*Alligator mississippiensis*)

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The behavioral variation in alligator nest attendance has characterized the species as iconic in common lore and perplexed biologists for decades. Here, we quantify patterns in nest attendance among mothers as well as variation in such patterns throughout two nesting seasons. We employed camera traps controlled by circuit boards to capture time-lapse photographs of alligator nest areas for the duration of each nesting season. Data revealed a bimodal pattern of nest attendance over time that significantly varied across incubation days in both 2011 and 2012, and also differed between years. Nest attendance also differed among hours in the diel cycle, and this pattern was the same for both years. Nest visits were frequent immediately after the eggs were laid, and attendance behavior attenuated rapidly after the first week of incubation. Nest visitation then increased near the end of the incubation period with the largest portion of visits recorded during hatching and the maternal movement of hatchlings away from nest sites. While the extent of this pattern varied between years, the pattern itself did not. The majority of attendance behavior occurred during night hours, with little visitation recorded between 1000 and 1600 hours. Our study is the first to document temporal variation in alligator nest attendances at daily, seasonal, and annual temporal scales, and our findings suggest nighttime visits during oviposition and hatching periods are consistent among years.

AMONG vertebrate classes, reptiles are mistakenly described as 'non-social' animals relative to birds and mammals (Doody et al., 2013). Contra to this notion, the social behaviors of courtship and associated aggregations, cooperative hunting, and other highly social behaviors are regularly observed among reptile lineages. Although parental care has not been widely documented among reptilian species, there are instances of brief maternal attendance by vipers (Greene et al., 2002; Hoss and Clark, 2014). Perhaps the most complex of all vertebrate social behavior is the myriad of social interactions observed in crocodilian reproduction, a lineage more closely related to birds than other reptiles but regarded as exhibiting less complex social behaviors than their sister group, Aves (Gans, 1996). Courtship displays and mating aggregations are followed by social hatching cues among neonates still within the calcified egg. Characterizing this sequence is one of the most iconic social behaviors among vertebrates: crocodilian parental care (Doody et al., 2013).

American Alligator (*Alligator mississippiensis*) reproduction begins in spring with mating typically occurring during April and May (Lance, 1989). Common among vertebrates, male alligators court females and engage in combative behavior for opportunities to reproduce with females (Joanen and McNease, 1980). Male alligators use a series of bellows and head movements to persuade the female to copulate (Vliet, 1989). Post copulation, nest site selection begins around late May to mid-June (Joanen and McNease, 1989) depending on seasonal thermal patterns. Female alligators select areas near the water on raised ground to construct a nest (Joanen, 1969), typically in an area with an abundance of vegetation for mound nest construction and cover. Common plant species in Gulf Coast alligator nests include roseau cane (*Phragmites* sp.), Sturdy Bulrush (*Scirpus robustus*), Three-corner Grass (*Scirpus olneyi*), Smooth Cordgrass (*Spartina patens*), and Hog Cane (*Spartina alterniflora*; Joanen, 1969). Nest construction can take multiple days to complete (Joanen, 1969) with nests reaching one to two meters in diameter and nearly one-meter high (Goodwin and Marion, 1978; Murray et al., 2013). Mother alligators excavate nest cavities in which an average of 30–35 eggs are deposited, with some nests containing more than 50 (Deitz and Hines, 1980; Joanen and McNease, 1989). The female then covers the exposed eggs with more plant litter (Joanen, 1969). Incubation duration averages 65 days, and females are limited to one clutch per season (McIlhenny, 1935).

Throughout the entire reproductive process, the behavior of nest defense against potential predators has become an iconic behavior for the American Alligator (McIlhenny, 1935; Neill, 1971; Kushlan, 1973; Kushlan and Kushlan, 1980). However, nesting defense frequencies vary widely in different areas and habitats. For instance, Hunt and Ogden (1991) reported 69% of alligators defending nests in Okefenokee Swamp, Georgia, while Deitz and Hines (1980) reported only 14.9% defense of 111 alligator nests in north-central Florida. Nest defense, defined here as active aggression in an attempt to fend off perceived nest predators, comprises one aspect of alligator nest attendance.

In a recent allometry study in southeast Texas, cursory observations revealed that nesting female alligators rarely defended their nests (Merchant and Murray, unpubl. obs.). Researchers did not observe females at most nest sites after extensive surveying during both day and night. All nests, however, contained viable eggs and most appeared to be opened to aid in hatching at the end of the incubation period. Therefore, it became apparent that many nests were attended during the 65-day incubation period, but not defended. The present study employed motion-sensitive infrared cameras to detect patterns of nest attendance by alligators. Interval-set camera traps were used to compile data on temporal regiments of nest mound visitation, excluding active defense or attendance behaviors that took place in nearby water or vegetation. The goal of this study was to document patterns of nest attendance in an effort to quantify

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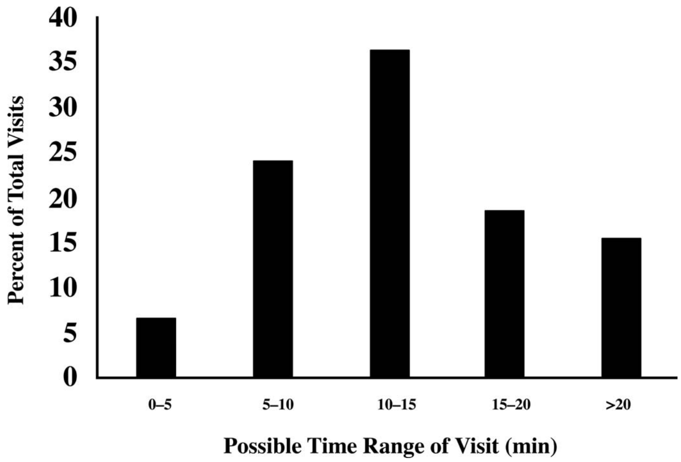

Fig. 1. Minimum length of visits to nests, based on the number of photos in which the alligators were captured. Photos were captured every five minutes, and time ranges were based on the number of consecutive photos in which the alligators were captured.

alligator behavior as well as provide aid to researchers who need to capture female alligators for other studies in which data from mother alligators is required.

MATERIALS AND METHODS

The initiation of alligator nesting in southwest Louisiana and southeast Texas occurs over a three-week period, starting in early-mid June and is dictated by ambient temperatures during March–June (Joanen and McNease, 1992). All eggs are typically deposited during the month of June. During the 2011 and 2012 alligator-nesting season, we surveyed the marshes every day for two weeks, starting on 1 June, looking for fresh alligator nests. When a new nest construction site was found, we placed a camera trap at the site to record the initial date of egg deposition and alligator visitation data during the duration of the incubation period. Camera traps were fitted with a circuit board that contained a timer linked to an infrared LED flash that was equipped to elicit a photograph from the camera trap sensor every five minutes (Merchant et al., 2013a). Photos were collected from 5 June 2011 to 29 August 2011 and from 9 June 2012 to 7 September 2012. Cameras were checked once per week to minimize disturbance of the nest site. During each visit, the SD cards were collected and replaced with fresh cards.

All images were carefully analyzed for the presence of alligators. More than 300,000 photos were compiled for 16 nests during the 2011 nesting season, and more than 170,000 for nine nests during the 2012 season, and each photo was searched for the presence of an alligator in the frame. Photos in which alligators were observed in the background away from the nest or water were scored as visits. The average time length (m) of attendance visits was calculated to assess potential bias caused by visits that occurred within the five-minute window between photographs. The number of consecutive frames in which alligators were captured during the same visit were summed, and a frequency distribution was created to illustrate the distribution of visit times.

Nest attendance was measured across a hierarchy of three temporal scales, including yearly, daily, and hourly. The years 2011 and 2012 were treated independently, and the number of nests visited standardized by the total number of nests observed per year (i.e., proportion of nests visited) was calculated both per day during the duration of incubation and per diel cycle hour (i.e., a mother was marked as attending the nest during a given incubation day or diel hour across all incubation days if a photo captured her at the nest one or more times during that day or hour), and proportion of nests visited served as the response variable in two sets of analyses. First, the proportion of nests visited was regressed against time measured in continuous days since egg deposition (i.e., daily scale) using a generalized additive model (GAM; Wood, 2017). Year (i.e., 2011 or 2012) was added to the model as a factor to test for differences in nest attendance among years (i.e., annual scale). Next, the proportion of visited nests during each hour of the diel period was combined across days within a season and years to assess timing of daily visitations (i.e., hourly scale) using a GAM. Analysis with GAMs was necessary in this study because data did not fit a normal distribution, variances were heterogeneous, and relationships were non-linear. Fitting GAMs involves the use of splines in which a moving window with a subset of observations slides across the predictor variable and regression coefficients are constructed in a piecewise manner to yield a non-linear, smoothed relationship between a predictor variable (here: time) and a response variable (here: nest attendance; Wood, 2017). For both GAMs, an autocorrelation function was included because time-series data lack complete independence across temporal units (i.e., day or hour), smoothing parameters were optimized using cross validation, and a binomial error term was employed because data were binomial (not attended = 0; attended = 1). All statistical analyses were performed in program R (R Core Team, 2017) using the 'mgcv' package.

RESULTS

Three nests in 2011 and five nests in 2012 were either mock nests or fell to predation, and these nests were excluded from analysis. Of the remaining nests, all 25 (16 in 2011 and 9 in 2012) were characterized by at least one instance of maternal attendance. Further, the duration of individual visits for both nesting seasons typically lasted longer than five minutes. The majority (93.6%) of alligators were captured in at least two consecutive photos during visits, while only 6.4% of visits were only captured in one photo (Fig. 1).

At the annual temporal scale, daily nest attendances differed between 2011 and 2012 according to the initial GAM ($Z = 2.343$, $P = 0.019$), and independent GAMs were run for 2011 ($\chi^2 = 64.31$, $r^2 = 0.07$, $P < 0.01$) and 2012 ($\chi^2 = 56.98$, $r^2 = 0.13$, $P < 0.01$). Across both years, daily alligator nest attendance was frequent just after oviposition, declined rapidly during the first weeks of incubation, and then remained low until close to the end of the incubation period, when activity spiked again during both field seasons. The magnitude of attendance at the end of the incubation period was lower in 2011 (Fig. 2A) compared to 2012 (Fig. 2B). Attendance activity across the diel cycle period did not vary between years ($Z = 0.178$, $P = 0.86$), and years were combined in a single GAM. Attendance did, however, vary across the diel period within years ($\chi^2 = 72.52$, $r^2 = 0.14$, $P < 0.01$). During the nesting season, the majority of nest visitations occurred between hour 1600 and hour 1000 (4 pm–10 am; Fig. 2C). Daytime visits were noted in association with hatching when females assisted their hatchlings to escape from the nest to avoid predation.

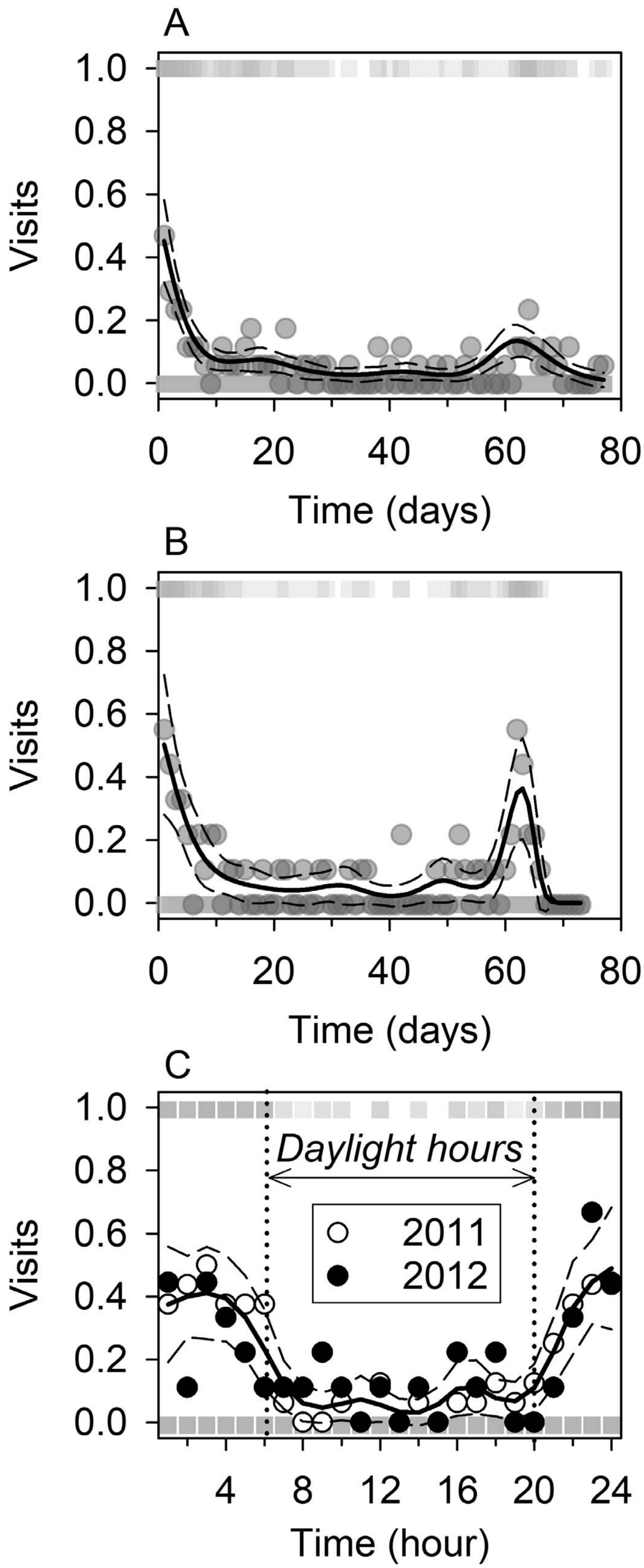

Fig. 2. Generalized additive model (GAM) analysis of alligator nest visitation varying over the incubation period in 2011 (A; $\chi^2 = 64.31$, $r^2 = 0.07$, $P < 0.01$) and 2012 (B; $\chi^2 = 56.98$, $r^2 = 0.13$, $P < 0.01$). Nests with an alligator present (1) or absent (0) are shown as binary classes (boxes) with darker shading indicating higher densities of observations. Binary data were used to calculate the proportion of nests with visits (circles). Nest attendance declined rapidly during the first weeks, remained low for the majority of incubation, and increased during hatching. This pattern was not different between years. For all panels, the solid line depicts the mean and broken lines depict 95% confidence interval. Further, GAM analysis depicting variation in nest attendance during the diel cycle in 2011 (white circles) and 2012 (black circles) (C; $\chi^2 = 72.52$, $r^2 = 0.14$, $P < 0.01$). The majority of nests visits by females occurred during the nighttime (2000–0600 hrs) for both seasons during this study. The unbroken line depicts the mean and dotted lines depict 95% confidence intervals. One GAM is fit to both years in (C) because results revealed no differences between 2011 and 2012 (see text).

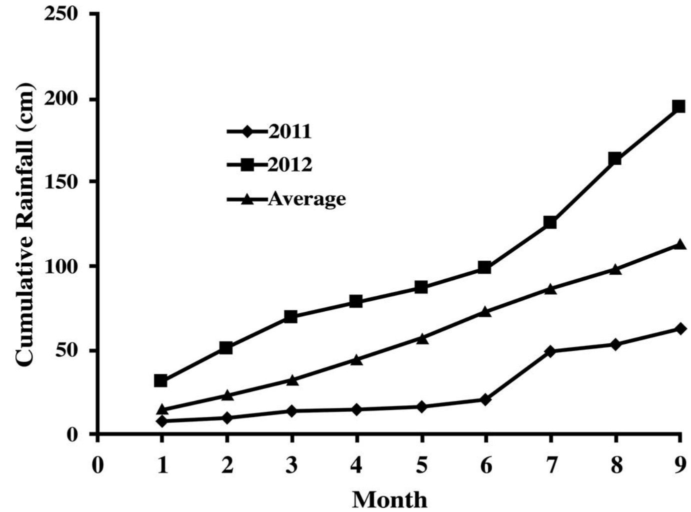

Fig. 3. Cumulative rainfall for coastal southeast Texas. Note that the 2011 field season experienced only 54.8% of the normal rainfall through the first nine months of the year, while the 2012 season has much higher rainfall (71% above normal). This time frame covers the entire breeding, nesting, and incubation periods for alligators, and nest attendance patterns were not different between years despite drastic difference in climatic conditions.

DISCUSSION

Here, we present patterns of nest visitation by mother alligators during the incubation period of her eggs. The frequency of maternal visitation varied over the course of incubation, peaking immediately after oviposition and again at the end of incubation, during hatching. The number of nests visited at the end of incubation was greater in 2012 compared to 2011 (Fig. 2A, B). Additionally, nest visitation varied over the diel cycle, characterized by a bimodal pattern with little attendance occurring during midday hours. This pattern of diel nest visitation was maintained across field seasons. Intuitively, however, we acknowledge low explanatory power of our GAM analyses. Time alone predicts patterns of attendance in our model, but other factors that correlate with time (e.g., hormones associated with parental care) are likely the driving mechanisms.

Nest attendance occurred at similar frequencies following oviposition during both years, with high attendance rates during the first and last weeks of incubation, and much lower rates during the middle 50 days (Fig. 2). Attendance frequencies at hatching were higher in 2012 than 2011, resulting in a statistical difference in the generalized additive model. During the first nine months of the 2011 calendar year, the J. D. Murphree Wildlife Management Area experienced severe drought conditions. The total rainfall for this period was 62.2 cm. In contrast, this same area experienced heavy rainfall (194.3 cm) during the same period in 2012

Fig. 4. An alligator confronts a wild hog in a nest defense behavior. The eggs were deposited in the nest on 10 June 2011, and thus this photo was captured on the second day after egg deposition. This was the only photo captured in the sequence. There was no damage to the nest, and no hair or blood was found at the nest site; thus, we assume that this confrontation resulted in a successful nest defense for the alligator.

(Fig. 3). Although the two alligator nesting seasons varied dramatically in rainfall, the same nest visitation patterns were observed across the incubation period, although the magnitude varied between years. In addition, nest visitation frequency varied among individual females.

Higher initial rate of nest attendance may be due to higher rates of predation immediately after oviposition. Unpublished data collected by author MM showed that nests are highly vulnerable to predation during the first three days after the eggs are laid. This elevated susceptibility to predation may be due to fresh scents emitted with oviposition. Eggs quickly dry after the first three days, potentially decreasing the chance of detection by predators. Further, the nest attendance remained low for the middle seven weeks of incubation and then increased dramatically during the last week of incubation during both field seasons (Fig. 2A, B). The nest attendance by female alligators during the last portion of incubation was likely primarily to assist hatchlings to the

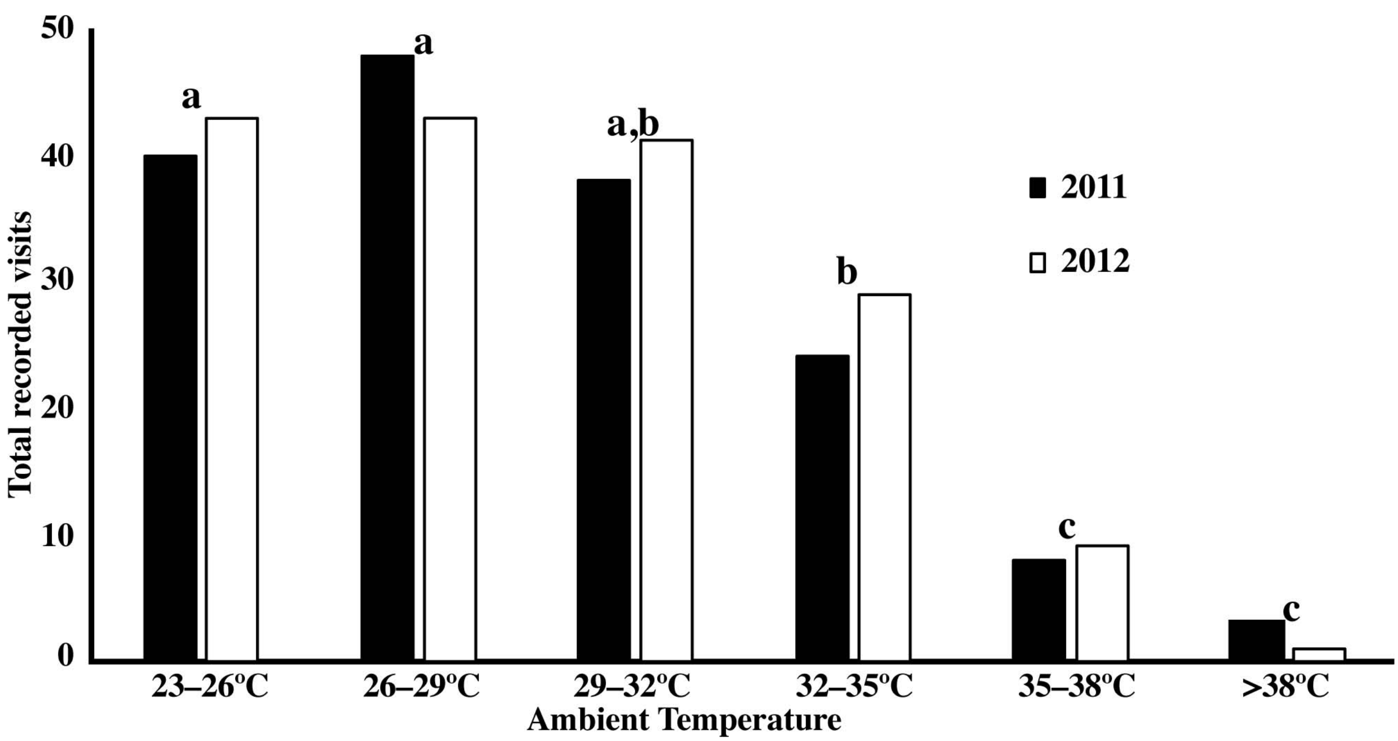

Fig. 5. Nest visits were temperature-dependent, as most of the visits occurred at night when temperatures were lower, or, observationally, during periods of cloudy weather with thunderstorms during the mid-morning hours of the 2012 season.

water where they are less susceptible to terrestrial predators. Recent data collected in our laboratory has shown that alligator nests attract a broad spectrum of diverse animals including birds, mammals, and other reptiles (Merchant et al., 2013b). Many of these animals, such as racoons, bobcats, foxes, and many large wading birds, can be potential predators of hatchlings. In addition, fire ants (*Solenopsis invicta*) are known to consume hatchling alligators (Allen et al., 1997). During both field seasons, alligators visited nest sites more during the nighttime hours than during the daytime (Fig. 2C). The main predators of alligator eggs, racoons (*Procyon lotor*) and wild hogs (*Sus scrofa*), tend to be nocturnal, and increased night attendance may be in response to the activity of terrestrial predators (Urban, 1970; Campbell and Long, 2010). Observations revealed that 73% of racoon predation and 86% of hog predation occurred at night; however, there were some photos captured of these predators during daylight hours, including the daytime photo of an alligator confronting a wild hog at a nest (Fig. 4). Previous studies have shown that alligator nest predation rates due to racoons can be as high as 52% (Joanen and McNease, 1989), and the increased distribution of feral hogs has been reported to be an increasing problem for the alligator ranching industry (Elsey et al., 2012).

Alternatively, alligators may visit nests at night as a result of preferred temperatures. Alligator nest attendance at temperatures below 26, 29, 32, and 35°C comprised 27.0, 59.5, 85.1, and 90.4% of visits respectively, during the 2011 season. Likewise, during the 2012 season, 25.9, 51.8, 76.5, and 94% of all visits occurred at ambient temperatures of the same regimen. This notion was observationally supported by an increase in nest visitation during mid-morning storms in 2011, when cloudy weather and rain decreased temperatures dramatically during this time period. Thermal data (Fig. 5) show that alligators attend nests primarily when ambient temperatures were below 35°C. Furthermore, 78.3% and 76.5% of visits occurred when the ambient temps were less than 32°C during the 2011 and 2012 nesting seasons, respectively. Many of the daytime visits occurred near the end of the incubation period when female alligators engaged in helping hatching and movement of hatchlings to the water and away from the nest site.

In conclusion, we quantify the maternal nest attendance pattern of the American Alligator (*Alligator mississippiensis*) across the nest incubation period. This iconic behavior appears more complex than initially perceived, being predominantly associated with predation risk and hatching aid. A cursory interpretation of these data reveals a highly efficient mechanism to maximize individual fitness, and further research is required to assess the variation in attendance patterns among populations, in association with relative maternal experience, relative to quantified fitness consequences and ecological trade-offs.

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