

Communal nesting behaviour of female American Alligators, *Alligator mississippiensis* (Daudin, 1801) in southeastern Oklahoma, USA

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Animal reproduction incurs various costs to the parent, including metabolic, time, and resource investments. Selection can lead to differences in reproductive strategies that reduce costs in response to varying environmental pressures. The raising of young near other conspecific broods (communal breeding) occurs in a wide variety of animals, including various insects, amphibians, reptiles, birds, and mammals (Hayes, 2000; Baden et al., 2013; Riehl, 2013; Costa, 2018; Escobedo-Galvan et al., 2019; Fischer, 2023) and can confer evolutionary advantages, such as improved defence, vigilance, sharing of information, or access to key resources (Doody et al., 2009; Rubenstein and Alcock, 2018). Communal breeding is especially widespread among bird species when benefits (e.g., improved foraging success) outweigh risks (e.g., potential intraspecific conflict and higher risk of disease or parasitism) (Doody et al., 2009; Rubenstein and Alcock, 2018).

The deposition of eggs in close proximity to those of conspecifics (i.e., communal nesting) is typically viewed as a competitive behaviour (Espinoza and Lobo, 1996; Swanepoel et al., 2000; Doody et al., 2009; Cunha et al., 2016; Rodrigues et al., 2021; Pierini et al., 2022).

Communal nesting can place substantial costs on participants, such as increased risk of disease and parasites, resource competition, and injury (Brown and Brown, 1996; Cheetham et al., 2011), but it can also confer evolutionary advantages, including thermoregulation, enhanced protection, and predator satiation (Radder and Shine, 2007; Sousa and Freire, 2010; Oliveira et al., 2014; Rodrigues et al., 2021). When suitable nesting habitat is scarce, communal nesting may result from competition rather than a cooperative strategy (Cott, 1961; Kofron, 1989; Pooley, 1969; Pooley and Gans 1976; Webb and Smith, 1987; Webb et al., 1987; Swanepoel et al., 2000). Among crocodylians, the construction of nests close to conspecifics has been observed in some species, but such cases are generally regarded as competitive responses (Swanepoel et al., 2000; Rodrigues et al., 2021).

The American Alligator, *Alligator mississippiensis*, is a large crocodylian species ranging from tropical to subtropical and into temperate waters. Female *A. mississippiensis* construct nest mounds from sticks, mud, and vegetation and will guard nests and young from predators. Aside from a single observation by Enge et al. (2000), who reported two *A. mississippiensis* egg clutches in a single nest mound but offered no further details about eggs or female behaviour, female *A. mississippiensis* are typically understood to be solitary in their parental duties. Although nests can sometimes be constructed quite close to one another (e.g., Davis et al., 2001), we are unaware of previous reports of cooperative maternal care. Here, we report the first detailed account of communal nesting and the first report of potential cooperative behaviour by adult female *A. mississippiensis* in southeastern Oklahoma, USA.

Materials and Methods

Study area. Southeastern Oklahoma represents the northwestern range limit of *A. mississippiensis*. The only confirmed and documented reproduction by alligators within Oklahoma occurs at Red Slough Wildlife

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Management Area (RSWMA; 33.7214°N, 94.6424°W; Arbour and Bastarache, 2006). The number of nesting females and young observed at RSWMA has increased in recent years (unpublished data).

Field observations. We observed two separate events during the 2021 season that appear to provide evidence for communal nesting by *A. mississippiensis*. The first observation occurred on 28 July 2021 when we observed simultaneous guarding behaviour by two adult female alligators at a nest mound. As we approached the nest, two nearby adult females emerged and positioned themselves defensively at the nest site. The first female climbed onto the nest and assumed a protective posture at the centre of the mound. The second female came to the base of the nest – approximately 2 m from the first – and faced the observers with her mouth gaping. On 3 August 2021, we removed the top layer of vegetation from the nest to look for evidence of multiple egg clutches. To increase safety and minimize stress for the animals, we placed a visual barrier between the female observed nearby and the nest during data collection.

The second observation occurred on 5–6 September 2021 when a game camera at another nest mound captured an adult female *A. mississippiensis* opening an egg chamber, removing hatchlings, and carrying them to the water. Multiple game camera and direct

observations had previously been made of a different female guarding the same nest, including earlier in the day on 5 September. The female we observed guarding the nest was missing her left front leg but the female that opened the nest and removed the hatchlings was slightly larger and had four intact legs. We were not able to confirm if this was a case of communal nesting but camera footage and egg fragments around the nest suggest clutch size and offspring number consistent with a single nesting female.

Data analysis. We obtained egg lengths, widths, and calcification band widths (to the nearest 0.1 mm), reported as means \pm standard error. We then compared these values for different egg chambers using Student's *t*-tests with Cohen's *d* to assess effect size, using Paleontological Statistics v4.1 software (Hammer et al., 2001).

Results

We found two distinct incubation chambers in the nest mound where cooperative guarding appeared to be occurring (Fig. 1). Incubation chambers were designated as “north” and “south” based on their positions. The south egg chamber contained 44 eggs with length of 66.1 ± 0.4 and width of 41.2 ± 0.6 (Table 1).



Figure 1. Photograph of an American Alligator, *Alligator mississippiensis*, nest at Red Slough Wildlife Management Area (RSWMA) in Oklahoma, USA, with the vegetation layer removed from the top. Two separate clutches in distinct nest chambers are visible. The “north” chamber is on the left and the “south” chamber on the right. Photo by Jake A. Pruett.

Table 1. *Alligator mississippiensis* egg clutch data from a shared nest at Red Slough Wildlife Management Area (RSWMA) in Oklahoma, USA, with additional data for Rockefeller Refuge in Louisiana, USA and the St. John's River watershed in Florida, USA. Only egg numbers are provided for the two RSWMA nests, but other values are means with egg numbers range provided where available.

Locality	n	Eggs per Nest	Length (mm)	Width (mm)	Weight (g)	Band Width (mm)
RSWMA (south chamber)		44	66.1	41.2	—	29.1
RSWMA (north chamber)		43	63.9	39.8	—	30.3
Rockefeller Refuge (Allsteadt et al., 1995)	3	47 (45–51)	—	—	76	—
Rockefeller Refuge (Davis et al., 2001)	22	38 (19–51)	—	—	—	—
Rockefeller Refuge (Lance et al., 2009)	92	35 (17–48)	—	—	—	—
St. John's (Milnes et al., 2001)	51	40	—	—	80	—

The north chamber contained 43 eggs with length of 63.9 ± 0.7 and width of 39.8 ± 0.4 . We observed opaque calcification bands around the eggs with mean band width of 29.1 ± 1.0 for eggs in the south chamber and 30.2 ± 0.7 for eggs in the north chamber. Some eggs did not have calcification bands (8 of 44 in the south chamber and 16 of 43 in the north chamber). We noted that some eggs appeared deformed and oblong (Fig. 2). These eggs (one from the south chamber, two from the north chamber) were identified as outliers and removed from the data set prior to statistical comparisons. We found two distinct egg chambers with significant differences in mean egg length ($t = 5.41, p < 0.001$) and width ($t = 4.16, p < 0.001$). We did not find a significant difference in calcification band width ($t = 0.81, p = 0.42$). Effect sizes as measured by Cohen's d were 0.54 for comparisons of egg length and 0.42 for egg width. We found a significant difference between the two chambers in the number of eggs with calcification bands ($\chi^2 = 5.82, df = 1, p = 0.01$).



Figure 2. Photograph of a deformed alligator egg (top) beside a normally formed egg (bottom). Deformed eggs were present in both egg chambers and excluded from statistical analysis. Photo by Jake A. Pruett.

Discussion

Among crocodylians, communal nesting is more often reported in species that are hole-nesting compared to species that build mound-type nests (Murray et al., 2020). Nest-sharing among mound-nesting species is currently interpreted as a response to the limited availability of appropriate nest site locations (Swanepoel et al., 2000). The number of nesting females at RSWMA is low due to the small population size (unpublished data), and we find it unlikely that the limited availability of nest site locations is driving the apparent cooperative guarding behaviour.

Mound nest construction is typically followed by prolonged nest attendance and defence. Nest-guarding females may have less access to food and need to leave the nest to forage, although they opportunistically feed on approaching prey (Barão-Nóbrega et al., 2016). While we documented one observation of simultaneous guarding of a shared nest mound, we observed guarding by a single female on multiple occasions. Thus, shared guarding among conspecific females may provide fitness-related benefits from enhanced predator deterrence and increased foraging time (while the nest is guarded by the other female). Observations of a non-attendant female investing time and energy in opening and removing hatchlings from an egg chamber which had been guarded by a different female may be the result of maternal drive in response to chemical cues or vocalizations on the young (Passek and Gillingham, 1999).

In oviparous reptiles, eggs within a single clutch can vary in length but egg width is typically more uniform, possibly influenced by the mother's pelvic aperture (Congdon and Gibbons, 1985, Werner, 1988, Thorbjarnarson, 1994). We found significant differences between north and south chambers in egg length, width, and proportion of eggs with calcification bands. Furthermore, the numbers of eggs in each of the two incubation chambers aligned with expected single clutch sizes for *A. mississippiensis* nests (Table 1). These results suggest that the eggs in these two chambers were laid by two different females. We did not find a difference in calcification band width, which is dictated by the rate of embryonic development (Ferguson, 1982). These results suggest that the two clutches were oviposited in close temporal proximity. Although we were not able to determine whether or how both females contributed to the construction of the nest, we propose that our observations may be the result of a cooperative strategy rather than a competitive effect. Though previous research has not shown a

correlation between genetic relatedness of hatchlings and nest mound proximity (Davis et al., 2001), genetic analyses would be required to rule out relatedness as a potential explanation for the behaviour we describe.

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