Herpetology Notes 19: 655–664, published on 12 August 2026

Embryonic development and deformations in unhatched eggs from Carolina Diamondback Terrapins, *Malaclemys terrapin* (Schoepff, 1793), on Skidaway Island, Georgia

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Carolina Diamondback Terrapins (DBTs), *Malaclemys terrapin* (Schoepff, 1793), are a species of turtle that inhabit North American salt marshes, ranging from Cape Cod, Massachusetts to Corpus Christi, Texas (Roosenberg et. al., 2019). These terrapins have one of the widest longitudinal ranges of a brackish water, temperate turtle species (Ernst and Lovich, 2009). This range exposes the terrapins to variable climates and temperatures. It is likely that each population has adapted to their local environment (Lovich et al., 2018). Terrapins were historically a popular choice for turtle soup in the first half of the 20th century, and they were commercially exploited throughout the Eastern seaboard (Brennessel, 2021). Now conservationists, researchers, and citizen scientists work together to help them recover (Kennedy, 2018).

Carolina Diamondback Terrapin populations experience ongoing anthropogenic threats from drowning in blue crab traps (Bishop, 1983; Roosenberg et al., 1997; Butler and Heinrich, 2007; Grosse et al., 2009, 2011; Harden and Willard, 2012), injury from boat propellers (Lester et al., 2013), and injury or death from cars when crossing coastal roads while attempting to nest (Grosse et al., 2011; Lovich et al., 2018; Williamson et al., 2024). DBTs start nesting in late spring and into summer. Nest sites may contain loose, sandy soil (for efficient gas exchange) and various amounts of vegetation (Burger and Montevecchi, 1975; Roosenberg, 1994). Nests are usually in close proximity to the salt marshes that will provide critical developmental habitat (Butler et al., 2022). Diamondback terrapins are sexually dimorphic, females reach sexual maturity in 4–8 years, depending on the availability of food, males mature in 3-4 years. Females produce 2–3 clutches of eggs per year, with a mean of 9.6 eggs (Ernst and Lovich, 2009; Lovich et al., 2018). Maintaining current levels of fecundity is vital to population stability.

Studies in New York suggested that most DBT eggs are viable, and nest failure is usually due to the incubation environment (Butler et al., 2018). It is important to understand the patterns of incubation, development, and common deformities or malformations terrapins may exhibit. In a comparable species, the European Pond Turtle (*Emys orbicularis*), lower genetic diversity and inbreeding were predictors of scute abnormalities (Velo-Antón et al., 2011). It is possible that declining populations of Carolina Diamondback Terrapin are experiencing low levels of genetic diversity. This could lead to a higher frequency of malformations.

Skidaway Island in Chatham County, Georgia is surrounded by extensive salt marshes. One terrapin population that inhabits Skidaway Island lays their eggs in the sand traps of the Terrapin Point Golf Course ([TPGC] Fig. 1). Volunteers from the Skidaway Audubon (non-profit, citizen scientists) collect the eggs and relocate them to one of four nest boxes in the terrapin hatchery (hatchlings are released into the surrounding salt marshes). Every year, less than 10% of the total eggs fail to hatch. This terrapin population nesting at the TPGC could be a good reference point for the health status of other terrapin populations because of the relatively high hatch success. Not much is known about the embryonic stages of DBTs, and in the past, the embryos were compared to the stages of the Common Snapping Turtle (*Chelydra serpentina*) (Brenessel, 2021). Carolina Diamondback Terrapin deformities have not been extensively studied and documented since the 1930's when Hildebrand (1930)

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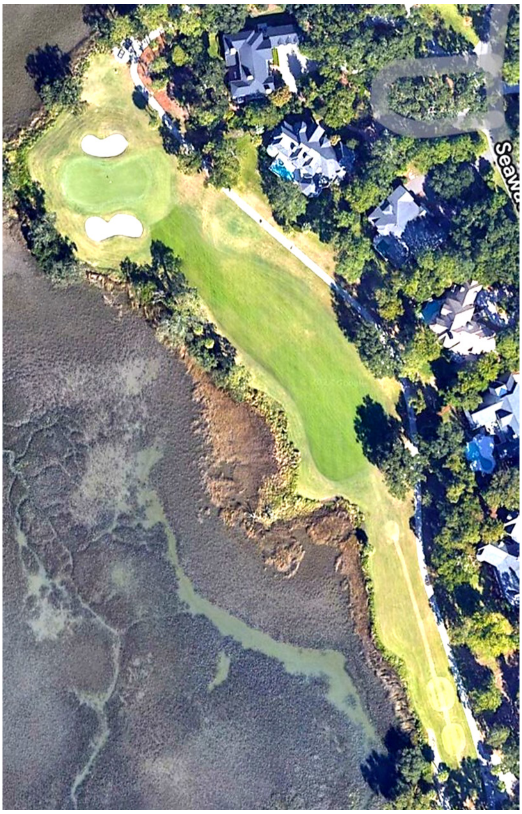

Figure 1. Aerial image of TPGC Hole 10 sand traps with the surrounding marsh and residential land use. Skidaway Island, Chatham County, GA. Photo by Lisa Isenhour.

examined thousands of embryos from a diamondback terrapin hatchery in North Carolina during the height of turtle soup popularity. He was particularly interested in two headed embryos and hatchlings; however, other notations were made, including eye malformations and supernumerary scutes.

Climate change related temperature shifts are likely to have multiple impacts on different aspects of DBT life, from reproduction to the quality within their food web (Lovich et al., 2018; Lamont et al., 2025). Incubation temperatures could rise within the nest chamber to reach heights that have been shown to result in embryo deformation and death (Telemeco et al., 2013; Bladow and Milton, 2019; Valenzuela et al., 2019; Czaja et al., 2020). Environmental quality (presence of teratogens/toxins) has also been shown to affect the development of embryos and hatchling health (Outerbridge, 2016). Adult female terrapins spend more time in habitats that put them at higher risk of contaminant exposure than males (Williamson et al., 2024). This also puts their eggs at risk of exposure to contamination through maternal offloading of pollutants into the yolks before eggs are laid (Holliday et al., 2008, 2018; Williamson et al., 2024). DBTs could be used as a sentinel species in the salt marsh ecosystem (Holliday et al., 2018; Lamont, 2025). Having reliable standards with which to measure physical as well as chemical changes resulting from environmental influences will provide more evidence to support future investigations.

Due to the dearth of DBT records regarding embryonic deformities, we relied on sea turtle literature as a reference point. According to the studies surrounding sea turtle embryos, the majority of fully incubated unhatched eggs were fertilised, but did not complete incubation for some reason. The cause of embryo failure can vary, but most of the time, eggs stop developing within the first 10 days (Miller et al., 2003, 2017; Craven et al., 2019).

The goals of this study were to 1) identify the stage of egg failure, 2) identify the physical embryo, and 3) examine embryos for defects. Providing descriptions of the embryology and deformities found in a robust population should provide a solid baseline with which to compare populations that face environmental challenges.

Materials and Methods

Skidaway Audubon volunteers monitored sand traps within TPGC from April 15 – August 15 in 2021 and 2022 (Fig. 1, Sand traps at Hole 10), and DBT eggs were collected and relocated within six hours of deposition into nest boxes that were purposely built around the golf course (Fig. 2A). These nest boxes (Fig. 2B) were screened and protected from predation until eggs hatched naturally in approximately 45–60 days. Data were gathered by the volunteers during all aspects of the egg monitoring (Table 1).

Unhatched eggs were collected from the 2021 (n = 222) and 2022 (n = 305) nesting seasons and preserved in 70% ethanol before transportation to the laboratory. During evaluation in the lab, eggs were opened with stainless steel scissors and forceps. A small window was cut from the shell and used to search for embryos that might have attached to the inside surface of the shell. Larger sections of the shell were then opened, and the contents of the egg were searched for signs of development, including metabolised yolk, visible eyes, or cellular structures that stayed together when sprayed with ethanol (e.g., embryonic disc). Embryos

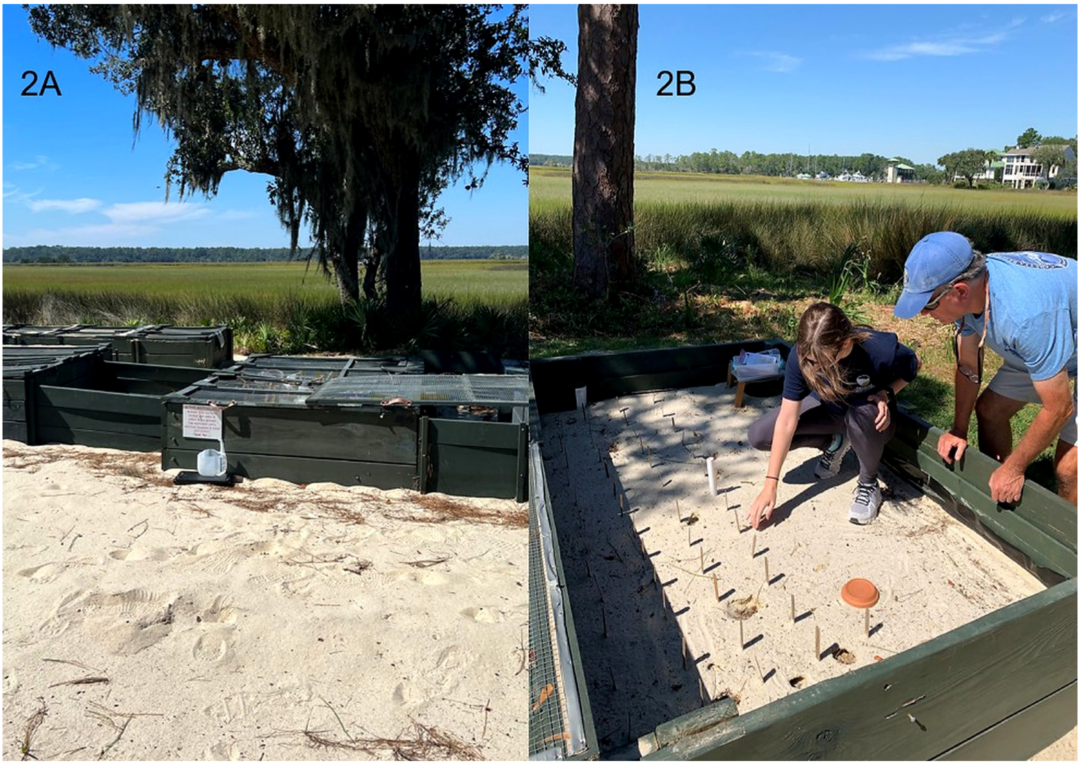

Figure 2. Nest boxes at TPGC Hole 10. (A) Nest boxes with screened lids. (B) Jim Olson and Ashleigh Feltman clearing out end of season nest boxes. Photos by Kathryn Craven.

were examined using a dissecting microscope with illumination (4–400x total magnification). Embryos were classified by measuring the length of the embryo using a vernier calliper and classified as early, mid, or late development (Craven et al., 2019). The two measurements that were used for this study were total length (TL, head to tail) and straight-line carapace length (SCL, when the carapace was visible, nuchal scute to pygal scute). If no embryo was found but there were positive signs of yolk metabolism, then it was considered that the egg failed at a stage before visible embryonic development (NVE = non-visible embryo). Early-embryo development (EED) was less or equal to 10.0 mm in total length; mid-embryo development (MED) was between 10.1–20.0 mm long (SCL); late embryo development (LED) was greater than 20.1 mm in length (SCL). Size was used to estimate the age at which embryo failure occurred during incubation (Miller, 2017). Notes were taken of any deformities that embryos displayed.

Table 1. Nest statistics from the TPGC hatchery. Over six years, the total number of recorded terrapins and nests has increased. Hatch success has remained the same. Asterisks indicate the nesting years sampled for this study.

Year	Total eggs	Hatched	Unhatched	Hatch success (%)
2020	3459	3151	308	91.1
2021*	3697	3440	257	93.0
2022*	4088	3786	302	92.6
2023	4823	4489	325	93.1
2024	6387	5781	606	90.5
2025	7298	6711	587	92.0

A Chi-Square analysis with four groupings (no embryo visible vs. early-, mid-, and late-stage) was used to test whether all eggs had an equal chance of failing in any condition (NVE, EED, MED, LED). Data did not meet the conditions for normality (see Results). Multiple Nonparametric One-Sample Signed Rank Tests were used to test whether the median number of malformations was significantly different from zero within the three embryonic stage groups. A Kruskal-Wallis One-Way ANOVA on Ranks was used to test whether each stage had significantly different rates of malformations. A Dunn's All Pairwise Multiple Comparison was used to determine where the median number of malformations were significantly different between the embryonic stage groups (Boslaugh and Watters, 2008).

Results

Since 2020, the hatching success for rescued terrapin eggs from the TPGC has been greater than 90% (Table 1). The number of females nesting has increased from less than 200 to over 350 (there may be some increase attributed to increases in effort and experience for the citizen scientists). During the same period (2020–2025) the number of total nests laid increased from less than 4000 to over 7000 per season. The number of unhatched eggs varied between 0–100% of each clutch, with an overall total of 7–9% of eggs failing per year. Between 2020 and 2022 the mean clutch size was 8.55 eggs, consistent with the mean for the species (Lovich et al., 2018). In comparison to populations in decline, Terrapin Point has a robust, stable nesting aggregation with good hatch success (Table 1).

During the course of the study, 527 unhatched eggs were examined (2021 n = 222 and 2022 n = 302). Of those, 362 unhatched eggs (n = 141 in 2021, n = 221 in 2022) were considered in the study as they were not punctured or torn. Spacer eggs (formed with albumin but no yolk, Fig. 3) were excluded from this study as they were much smaller than a typical non-spacer egg.

Of the 362 eggs that were examined, 65 were found to have visible embryos with malformations. A total of 20 different types of malformations were recorded (Table 2), either found alone or in combination with other malformations. In this analysis, 11% of eggs with embryos had one deformity, 28% of eggs with embryos had multiple deformities, and 61% of eggs had normal embryos.

Embryos were separated into three size categories as an indication of the age of the embryo when it stopped development (Fig. 4). The combined data is shown in Figure 5, however, in 2021 (n = 141), there were 119 non-visible embryos, six EEDs, 12 MEDs, and four LEDs. In 2022 (n = 221), there were 178 non-visible embryos, 17 EEDs, 16 MEDs, and 10 LEDs.

The Chi-Square (Fig. 6) indicated that terrapin eggs from the TPGC sample were significantly more likely to fail (X^2 = 629.36, p < 0.00001) very early in development (the first 10 days, Miller, 2003) before a visible embryo could form. Data distribution failed the

Figure 3. Side by side comparison of a typical egg (Left) and a spacer egg (Right). Spacer eggs only contained albumen and are unable to support embryonic development. Photo by Kathryn Craven.

Table 2. Count of eggs, embryonic stages, and malformation types per embryonic stage. Early (EED) embryos are 0–10 mm, Mid (MED) embryos are 11–20 mm, Late (LED) embryos are > 21 mm. NVE = Non-visible embryo (fertile, but less than 10 days of development.

Values	Early	Mid	Late	NVE	Grand total
Count of egg	23	28	14	297	362
Microcephaly		1			1
Megacephaly		1			1
Skull abnormality		1	3		4
Bicephaly	1				1
No skull		2			2
Abnormal nostrils			1		1
Abnormal jaw shape	1		3		4
Underhung jaw		1	2		3
No underjaw		1			1
Cleft beak		1			1
Anophthalmia		1	1		2
Cyclops			1		1
Abnormal scute count		4	6		10
Abnormal shell shape	1	4	4		9
Left front limb		2	2		4
Right front limb		2	1		3
Left rear limb	1	3	2		6
Right rear limb	1	2	2		5
Abnormal tail			1		1
Hypomelanism			1		1
Abnormal skeleton		4	1		5
Exposed organs		3			3

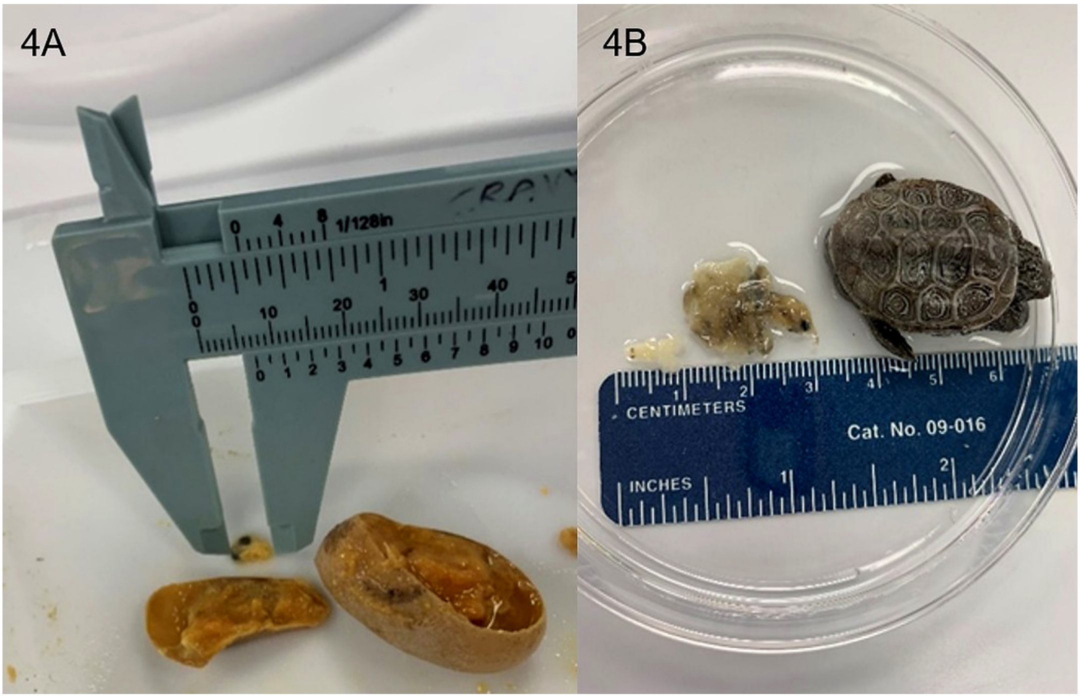

Figure 4. (A) Measuring early-stage embryo with callipers, using total length; (B) Examples of 3 different stages of embryos. Photos by Kathryn Craven.

Shapiro-Wilk test for normality ($p < 0.005$). Additional analysis using Non-Parametric One-Sample Signed Rank Tests indicated that the median number of malformations of the smallest visible embryos (EEDs) was not significantly different from zero ($z = 1.633$, $p = 0.250$). This could imply that malformations in this stage were statistically random. The MEDs and LEDs median number of malformations were significantly different

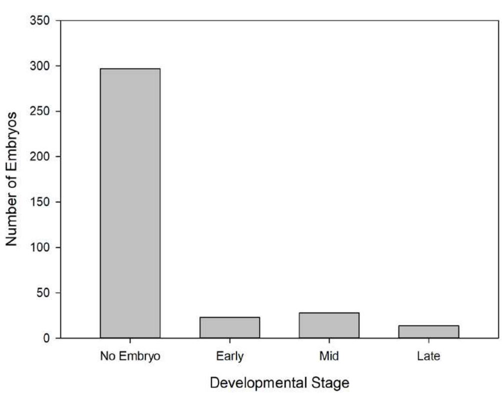

Figure 5. Count of embryo stages in 2021 and 2022 combined. Early (EED) embryos are 0–10 mm, Mid (MED) embryos are 11–20 mm, Late (LED) embryos are > 21 mm. NVE = Non-visible embryo (fertile, but less than 10 days of development).

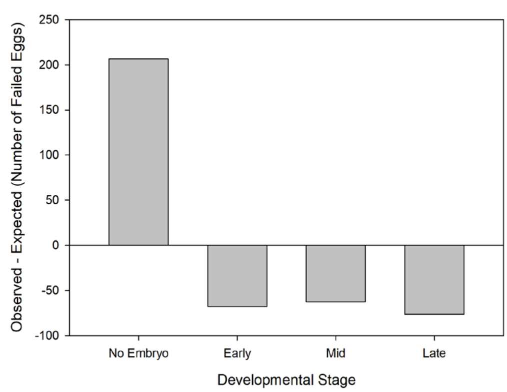

Figure 6. Chi-Square analysis indicating that eggs are more likely ($p < 0.00001$) to fail in the first 10 days, prior to visible embryo formation.

from zero ($z = 3.201$, $p < 0.001$ and $z = 2.689$, $p = 0.004$ respectively), and this implied that the malformations from the MEDs and LEDs were non-random.

There was a significant difference ($H = 12.749$, $p = 0.002$, Kruskal-Wallis One-Way ANOVA on Ranks) in the median number of malformations between early-, mid-, and late-stage embryos. Late-stage embryos were found to have significantly more malformations than early-stage embryos, but no other comparisons had significant differences (Dunn's All Pairwise Multiple Comparison, Fig. 7). Severe deformities were found in early and late-stage embryos (Fig. 8A, 8B respectively). Similarly, the lack of skeletal features (the skull, jaw, and other bones) was most noticeable in LEDs. However, some of the most remarkable conditions, including bicephaly (Fig. 9A, 9B), were visible very early.

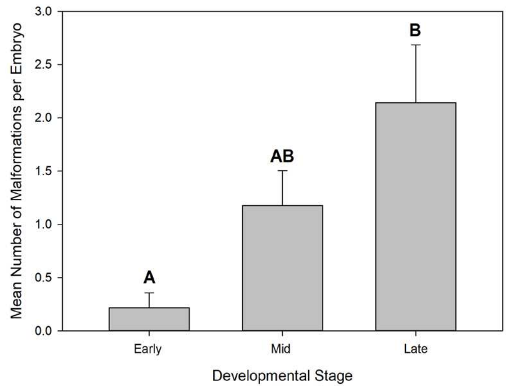

Figure 7. Dunn's All Pair Wise Multiple Comparison indicates that late-stage embryos (LEDs) were significantly more likely to have malformations than early-stage embryos (EEDs). Mid stage embryos (MEDs) did not have a significantly different rate than either EEDs or LEDs.

Discussion

Unhatched terrapin eggs were most often found with non-visible embryos (NVE, Fig. 5). Following the pattern of chelonian development (Miller et al., 2003), this indicated embryonic arrest prior to 10 days of development. Embryos are more sensitive to environmental factors at the beginning and the end of incubation (Craven et al., 2019), and it would be useful in future studies of this population to explore them. The eggs could have encountered problems during translocation, sudden variations in temperature or oxygen levels in early incubation, or other environmental conditions such as those suggested by Hildebrand (1930). Records of hatching success in artificially incubated (translocated) nests ranged from 32% (Herlands et al., 2004) up to 100% depending on the initial condition of the eggs (Roosenberg and Kelly, 1996). In situ nest hatching success averaged 63–88% (Roosenberg et al., 2014) with even lower success rates in populations with heavy predation (Butler et al., 2018). Movement of turtle eggs within the sensitive first 12 hours of incubation can tear embryonic membranes that have attached to the inside of the eggshell (Ferguson et al., 1985). Extreme heat can cause direct mortality in

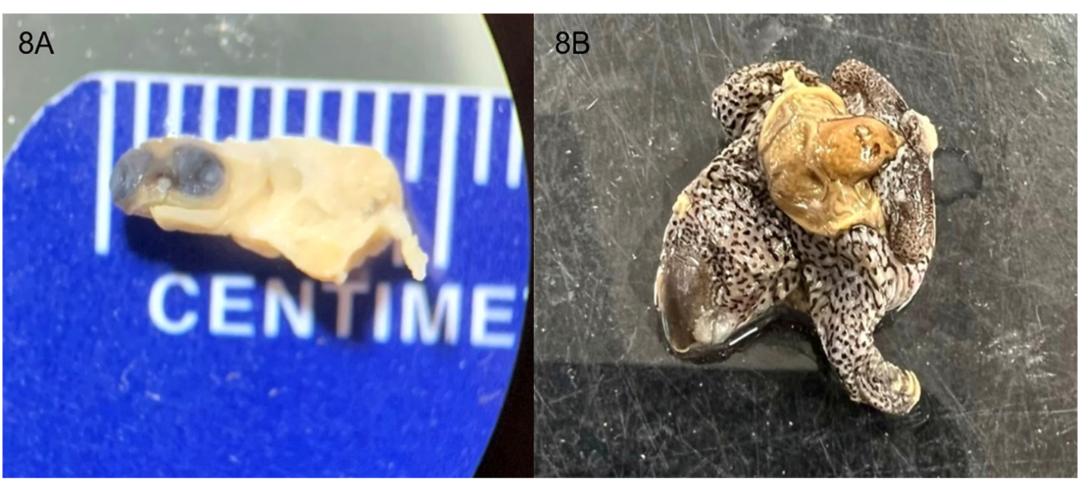

Figure 8. (A) Example of an early-stage embryo with an abnormal jaw formation. (B) Late-stage embryo with major malformations. This embryo displayed obvious shell, limb, and skeletal deformities. Photos by Kathryn Craven.

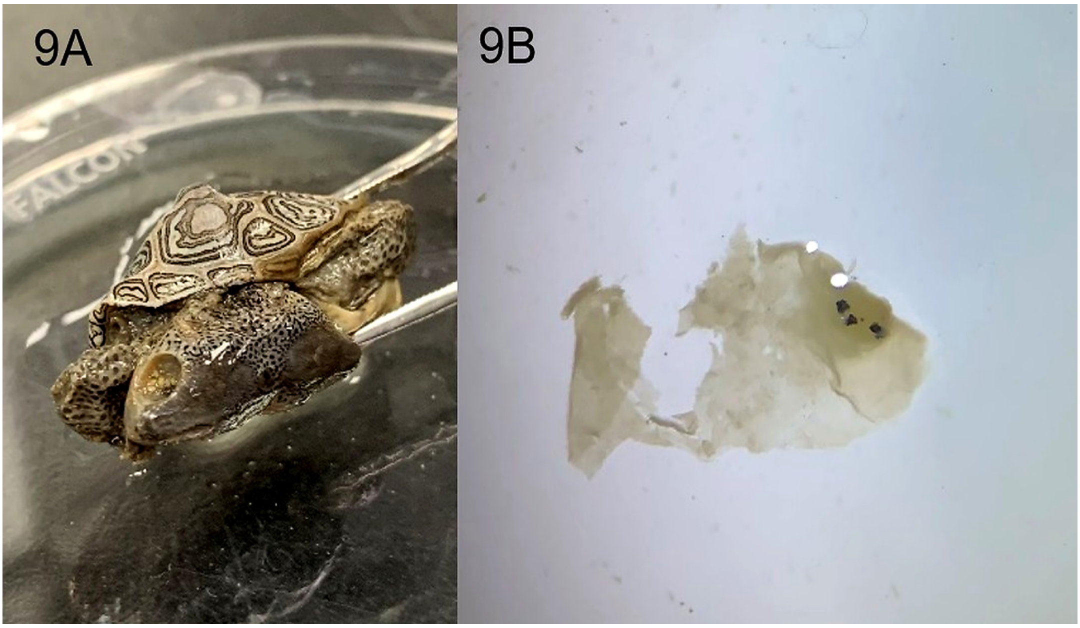

Figure 9. Example of late-stage (A, occipital skull fusion) and early-stage (B, two pairs of eyes) embryos displaying twinning. Photos by Kathryn Craven.

embryos, giving the appearance that the egg may not have developed (Rowe et al., 2020). In spite of this appearance, the eggs were fertile and early embryonic death can be distinguished.

When embryos were present in eggs, they were more likely to display malformations during late-stage, similar to what Bácenas-Ibarra et al. (2015) found in Hawksbill, Olive Ridley, and Green Sea Turtles. This could be attributed to the fact that the embryos have to be larger to show signs of some malformations. Using Miller et al. (2017) as a guide, the same major guideposts in development can be used to determine stages of growth. Both sea turtles and Carolina Diamondback Terrapins complete development in approximately 60 days. The first sign of pigmentation will take place in the eyes. The appearance of the scute pattern, scute/scale pigmentation and other defined external elements of the head and limbs do appear after the 30-day mark of incubation and qualify as features of the LED embryo. Early-stage and Mid-stage embryos (EED, MED) should not be ignored as they can display major malformations early in development, such as abnormal jaw formation (Fig. 8) or bicephaly (Fig. 9). The EED embryos were less than 10.0 mm in total length, and require detailed examination of egg contents. As climate change increases the chance of embryo mortality due to overheating, decreasing nest success could be an early warning sign. It is important for future studies to investigate DBT embryonic development further to improve the conservation of this species.

Carolina Diamondback Terrapins remain at risk of anthropogenic threats in spite of interventions (Maerz et al., 2018). Studies that identify potential threats such as embryonic failure are critical because they could help conservationists implement the best strategies to protect the most vulnerable populations. Terrapins are being threatened by climate change that can lead to overheating, habitat loss, competition for resources (road mortality, crab trap bycatch), and teratogens that can accumulate within their habitats and food sources (Outerbridge et al., 2016; Rowe et al., 2020).

Climate change is expected to increase global surface temperatures from 2–5 °C within the next century. This global temperature change will affect many taxa by increasing metabolic rates, increasing feeding requirements, and altering interactions within the environment (competition, resource availability, etc.) (Rowe et al., 2020; Fuentes et al., 2023). Reptile nests will be heavily affected since they are sensitive to temperature and humidity (Craven et al., 2019). Recent studies focusing on sea turtles have suggested that current nest temperatures are becoming closer to the embryonic upper thermal tolerance limits (Martín-del-Campo et al., 2021). Terrapin hatching success decreased as the mean incubation temperature increased, and hatching success was reduced by 33% at 34 compared to 31 °C, and it is clear that an increase in mortality at 34 °C represents the approximate thermal tolerance threshold (Rowe et al., 2020).

Kobayashi et al. (2016) studied the survival rate of Loggerhead Sea Turtle nests that were incubated at varying temperatures. It was found that female-producing nests had a higher mortality rate at early embryonic stages compared to male-producing nests. Higher incubation temperatures also negatively affected the locomotor performance of the hatchlings. Kobayashi et al. (2016) concluded that female Loggerhead hatchlings would face lower survival rates compared to males if climate change were to continue. Incubation temperatures over 35 °C were also associated with the death of Olive Ridley Sea Turtle embryos (Valverde et al., 2010). If DBTs exhibit similar patterns, conservation efforts that mitigate the impact of pending global temperature increases should be implemented. However, terrapins are more likely to be affected by rising sea levels and altered sex ratios before the temperature rises enough to cause devastating embryonic mortality (Rowe et al., 2020).

The presence and concentration of various contaminants in the sediment of terrapin habitats, terrapin eggs, and prey have the potential to cause malformations and embryonic death. Petroleum hydrocarbons and trace metals, can be linked to developmental abnormalities of the gonads and other organs, endocrine interference, and immunological stress (Holliday et al., 2008). Insecticides and herbicides (which are used heavily at some golf courses) can lead to contaminants leaching into the environment. Terrapins excrete bioaccumulated hydrocarbons through egg yolk production, which can lead to chronic low-level embryonic exposure. In Bermuda, terrapin eggs had significantly higher concentrations of Cd, Cu, Pd, Zn, and Hg, as well as hydrocarbons compared to the benthic sediment samples. The highest levels of contaminants were found in the potential food for the terrapins (gastropods). Unhatched eggs were examined for abnormalities in development, though the sample size was small (n = 25 eggs). The eggs from Bermuda showed an increase in contaminants compared with previous studies (Outerbridge et al., 2016). Of the 25 eggs opened, 10 had non-visible embryos, and 10 showed early developmental arrest (EED). It is possible that maternal transfer of contaminants contributed to early embryonic arrest. Of the five that continued to incubate, one developed normally, and the others exhibited various deformities, including facial, limb, shell, scute, head, and eye malformations. Bermuda's hatch rate was low (19%) despite the absence of nest predation, which is a serious concern for the local population (Outerbridge et al., 2016).

Deformities were found in the Skidaway population in high diversity, but each malformation (with the exception of supernumery scutes) was low in frequency. Hildebrand (1930) had found that malformations were less common in terrapins than in freshwater turtles. Head malformations were the most common (Table 2), followed by carapace scute abnormalities. Observations in sea turtle embryos included the same types of abnormalities, along with hypomelanism (Velo Anton et al., 2011; Craven et al., 2019). Terrapin embryos examined in the current study did not display frequent pigment deficiencies. Only two albino terrapins had been reported previously (Hildebrand, 1930).

Hildebrand's observations were made before modern teratogens had entered the environment. Although herbicides are used on the Terrapin Point Golf Course, the nest boxes are made with sand brought in from off site and replaced annually. The nest boxes should provide a contaminant free environment.

Going forward, it will be important to investigate and understand causes contributing to population declines. Our findings indicate that terrapin eggs are most sensitive to developmental arrest during the first 10 days of incubation. Malformations were visible in all embryonic stages, but more complex malformations were most commonly seen in late-stage embryos. While the later stages (MEDs and LEDs) show visible malformations more easily, it is important to examine EEDs as they also can display major malformations. The TPGC has a healthy population of DBTs with over 90% hatch success. The examination of unhatched eggs, provides a baseline for future changes. As temperatures in the nesting environment and stress on the eggs increase, monitoring development can be used to guide management decisions and assist population recovery. Additional research on the embryonic development of DBTs, including those factors that influence hatching success is clearly needed. The population in the Skidaway Audubon provides hope that with proper management and community engagement, DBTs have a better chance at having robust species health in the future.

Acknowledgments. Thank you to the volunteers and organisers of Skidaway Audubon at the Landings, for collecting the eggs and the important data from the terrapins. This work was conducted under GA DNR scientific collecting permit #1000545218. Thank you to Georgia Southern University, the Honors College, and the Paulson Student Research Award for funding support.

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Accepted by Matthijs P. van den Burg