Condition and Coloration of Lingual Lures of Alligator Snapping Turtles

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Abstract - The lingual lures of *Macrochelys* (alligator snapping turtles) are believed to be the only prey-capturing lures within the mouths of modern reptiles. To date, no formal assessment of lure condition in *Macrochelys* has been published, and few researchers record lure data. Herein, we report damaged or missing lures from 25 *Macrochelys temminckii* (Alligator Snapping Turtle; 7 adults, 18 juveniles) from a sample of more than 2000 lure assessments in 4 states, indicating this is a rare occurrence. We also describe lingual lure color observed in these assessments and introduce standardized terminology and color categories. We suggest researchers record data on the condition and coloration of the lingual lure to further our understanding of this ecological and evolutionary adaptation.

Introduction

Macrochelys temminckii (Troost in Harlan) (Alligator Snapping Turtle) is the largest freshwater turtle in North America, with males known to exceed 90 kg (Johnston et al. 2023 [this issue], Pritchard 1989, Rosenbaum et al. 2023 [this issue]). It is a highly aquatic and long-lived species, exceeding 80 years old in captivity, with less known concerning lifespan of wild individuals (Ewert et al. 2006). Known from 14 states in the United States, the core range of the Alligator Snapping Turtle is located along the Lower Mississippi River (Pritchard 1989). Population declines have been noted throughout much of its range, with overharvesting for domestic and international food markets identified as a primary cause in many areas (Dobie 1971, Pritchard 1989, Reed et al. 2002, Sloan and Lovich 1995). On 9 November 2021, the Alligator Snapping Turtle was proposed as threatened under the Endangered Species Act (USFWS 2021). The Alligator Snapping Turtle is an iconic species in the southeastern United States not only because of its impressive size,

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longevity, distinct morphology, and unique ability to attract prey, but also because of its cultural significance as a food source.

Gadow (1909:340) first described the lingual lure of Alligator Snapping Turtles stating, "In order to attract fishes they protrude a pair of worm-like pale pink filaments from the tip of the tongue". *Macrochelys* are the only reptiles known to have a predatory lure that is activated completely inside their mouths (Drummond and Gordon 1979). This unique lingual appendage is attached to the tongue in the lower jaw and is described as having an anterior horn, body, and posterior horn (Spindel et al. 1987). The lingual lure is innervated by the lingual nerve, which divides into 3 smaller branches, 2 in the anterior horn and 1 in the posterior horn (Spindel et al. 1987). These nerves, along with the presence of structures morphologically similar to taste buds, may permit a rapid response to the presence of prey based on chemical and mechanical cues (Spindel 1980, Spindel et al. 1987).

The color of the lingual lure depends upon both the pigmentation of the lure tissue and the presence of blood near the surface in the lingual appendage mucosa. The blood supply for the lingual appendage arrives via 1 or more small arterial branches off the lingual arterial arch, which is a terminal anastomosis of the lingual arteries that branch off the external carotid arteries (Spindel et al. 1987). In hatchling turtles, the lure is unpigmented and appears bright red (Winokur 1988). Juvenile and adult turtles have variable amounts of pigmentation, giving the lure a pink or gray color (Drummond and Gordon 1979, Spindel et al. 1987, Winokur 1988). Allen and Neill (1950) state that the lure is whitish or pale gray when not actively luring but turns pink when set in motion, presumably from suffusion with blood.

The coloration, enlargement, and wriggling movement of the lure are thought to resemble a worm, leech, or insect larva to unsuspecting prey (Drummond and Gordon 1979, Spindel et al. 1980). Carr (1952) believed that this sit-and-wait approach was used by Alligator Snapping Turtles during the day as they lay concealed and motionless on the substrate but was not used at night when they actively foraged. Allen and Neill (1950) reported capturing *Macrochelys* in Florida as they fed at night on baited lines on the substrate, but they also reported a juvenile luring at night in Mississippi. An adult male was observed luring in a clear-water river in Arkansas, presumably during the day (Hiler et al. 2006). Ewert et al. (2006) reported observations of adult Alligator Snapping Turtles in Florida actively foraging at night along the stream bottom, periodically lowering their snouts to the substrate to presumably detect chemical cues. Daytime activity, including presumed foraging activity beyond sit-and-wait luring, has been documented (Ewert et al. 2006).

Drummond and Gordon (1979) performed several experiments on neonatal Alligator Snapping Turtles with no prior feeding experience and determined that contact by the fish on the lingual lure was necessary to initiate an attack (snap) in nearly all cases. Likewise, Heusser (1968, 1971) stated that although the initial predatory behavior of luring is instigated at the sight of a nearby fish, the snapping response of a young Alligator Snapping Turtle commenced after the fish tugged on the lingual lure. According to Spindel et al. (1987), these behavioral observations relating turtle snap to a fish contacting the lure indicates that touch receptors must

be present. They went on to suggest the nerve fibers they observed terminating in the lure mucosa might be the receptors.

Spindel et al. (1987), in discussing the results of Drummond and Gordon (1979), expressed doubt that the highly innervated and vascularized lingual appendage could remain functional under persistent attacks by prospective fish prey unless the snapping response was fast enough to avoid damage. They stated that young Alligator Snapping Turtles may avoid injury to the lingual lure by quickly learning to attack prior to actual contact by prey. Spindel et al. (1987) also asserted that the flexibility of the lingual lure made it less likely to be grabbed by prospective prey, which would also reduce the chance of being injured. Spindel et al. (1987) agreed with Drummond and Gordon (1979) that experience and learning by young Alligator Snapping Turtles may help them avoid injury to the lure by snapping prior to prey making physical contact. There was some indication in their behavioral experiments that contact with adjacent areas of the turtle's body could elicit the initial snap response (Drummond and Gordon 1979). The variety and complexity of skin tubercles on the head and neck of Alligator Snapping Turtles, and perhaps the lingual papillae, may play a role as sensory receptors in the snapping response (Winokur 1982). Another possibility are the gular barbels, which exhibit an unusual pattern of ontogenetic variation in that they attain maximum size in hatchlings and juveniles (Winokur 1982), which is opposite the developmental pattern found in most other turtles.

A lack of published reports of missing or damaged lingual lures suggests Alligator Snapping Turtles successfully protect them while feeding; however, there has been no formal assessment of lure condition in Alligator Snapping Turtles. Our primary objective was to describe and report the incidence of missing or damaged lures from various Alligator Snapping Turtle populations to better understand how often this occurs and to determine whether any trends exist with respect to geographic location, turtle size, or other factors. Secondarily, we summarized lingual lure colors observed by researchers and introduced standardized terminology and categories for future long-term assessment of lingual lure coloration, damage, and structure.

Methods

B.M. Glorioso solicited data related to observations of lingual lure damage and color from Alligator Snapping Turtle researchers across the species' range. Data were summarized and collated into a list with: (1) name of individual(s) reporting data, (2) state, (3) parish or county name, (4) year observed, (5) observation type (captive, wild, headstart), (6) age class (hatchling, juvenile, adult), (7) sex (male, female, unknown), (8) total number of individuals reported, (9) lingual lure color, and (10) any instances of missing (no anterior or posterior horn) or damaged (at least 1 horn is partially or completely absent) lures.

Because of inconsistencies in lure color specification across research programs, we standardized lingual lure condition and color before summarizing lingual lure

color and the incidence of missing or damaged lures (Table 1). Additionally, we followed Spindel et al. (1987) for all terms describing lure anatomy. Some researchers documented 2 broad color categories (i.e., gray and pink). Others documented multiple color categories with descriptors (i.e., light or dark). All lure color data were standardized to the following categories: red, pink, pinkish-gray, gray, white/clear, or mottled. We summarized any observations of colors with descriptors into their base-color category with the descriptors removed. Data from Mississippi documented bi-coloration in lure structure based on anterior and posterior horn colors. We prioritized anterior horn color for standardization with other programs. Definitions and example photos for each color category are documented in Table 1 and Figure 1, respectively.

Illinois turtles were all translocated headstarts from 2 sources: Tishomingo National Fish Hatchery in Tishomingo, OK (TNFH) and the Peoria Zoo in Peoria, IL (PZ). The TNFH breeds and rears Alligator Snapping Turtles for reintroduction throughout the Mississippi River drainage. The PZ quarantines and raises Alligator Snapping Turtles from various sources, such as confiscations and unwanted zoo animals, for release in Illinois. Individuals from TNFH were exclusively juveniles, but PZ turtles varied in development from juvenile to sexually mature. A subset of translocated individuals was fitted with radio transmitters (Holohil; Carp, ON, Canada). In spring and fall of each year (2014–2019), individuals with radio transmitters were tracked to their location and hand captured for visual examination. All other states captured wild Alligator Snapping Turtles primarily with hoop nets baited with fresh or frozen fish.

Results

We summarized data from 7 research groups: 3 in East Texas, 2 in Louisiana, 1 in Mississippi, and 1 in Illinois (Table 2). From Texas, we have data from

Table 1. Suggested standardized lingual lure color categories with descriptions, including a category for missing/damaged lures.

Color category	Description
Red	Predominantly red coloration (similar to oxygenated blood), little/no mottling with other colors
Pink	Predominantly pink coloration (pastel or muted in tone compared to red), little/no mottling with other colors
Pinkish-gray	Even distribution of pink and gray colorations; may be mottled with just 2 tones, includes purple
Gray	Predominantly gray (light, dark, etc.), limited mottling or gray = most pronounced color
White or clear	No predominant coloration, lure obviously clear or even distribution of white tones
Mottled	Even distribution of multiple colors (red, pink, gray, white, purple, etc.)
Missing/damaged	Lack of obvious lure structure; visible damage to lure location in mucosa

132 wild captures from the San Jacinto drainage in Harris County and 53 wild captures from the Sabine and Neches drainages in southeastern Texas and the Trinity drainage in Tarrant County. In addition, we have data from a wild clutch of 29 hatchling turtles from Cherokee County, TX. From Louisiana, we have data from 45 wild captures from the Atchafalaya, Calcasieu, and Vermilion–Teche drainages in southwestern Louisiana, including 8 that were head-started in captivity (Glorioso and Waddle 2021a, b; Glorioso et al. 2020). We also have data from

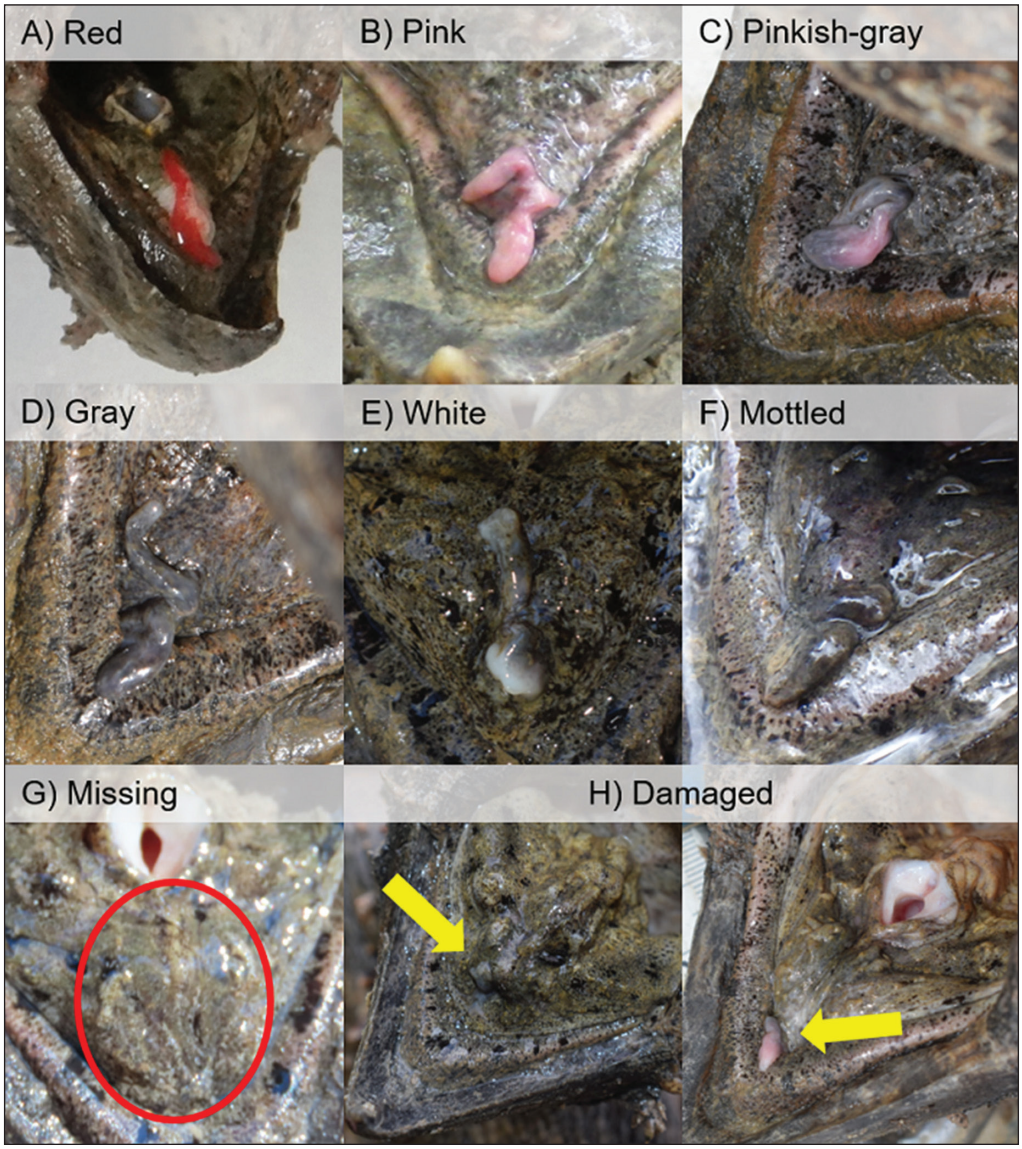

Figure 1. Standardized Alligator Snapping Turtle lingual lure colors and conditions based on anterior horn coloration (A–F). Red circle denotes location of missing lure (G); yellow arrows denote damaged lures (H: missing anterior horn and portion of posterior horn in left; posterior horn missing in right). Photographs © B. Glorioso, M. Gordon, and L. Pearson.

46 wild captures from northeastern Louisiana, with all but 1 from the Ouachita drainage. We have data from 809 wild captures from 43 counties in Mississippi representing the major river drainages of the Mississippi, Pascagoula, and Pearl among others (Table 2). From Illinois, we have data from 953 lingual lure assessments of 490 captive-reared and released Alligator Snapping Turtles, including once at pre-release and any subsequent captures. In total, we have lingual lure data from 2067 assessments from 4 states.

Missing or damaged lures

No instances of missing or damaged lures were found in Illinois. One of 3 juveniles from a site in the Calcasieu drainage in southwestern Louisiana was completely missing its lure. Of 3 juveniles from the Ouachita drainage in northeastern Louisiana, 1 had a damaged lure and 1 had a missing lure. In Texas, 1 juvenile from the Trinity drainage was completely missing its lure. In Mississippi, 22 of 809

Table 2. Incidence of damaged or missing lures of non-hatchling Alligator Snapping Turtles from sites in Louisiana, Mississippi, Texas, and Illinois by drainage basin. Total individuals in age class and sex are given, with the number in parentheses indicating how many of that total number had a damaged or missing lure.

		Age class/sex			
			Adult		
State	Drainage basin	Juvenile	male	female	unknown
Louisiana					
	Atchafalaya	15	5	4	2
	Calcasieu	15 (1)	2	0	0
	Ouachita	16 (2)	8	14	7
	Red	0	1	0	0
	Vermilion-Teche	1	0	1	0
Mississippi					
	Bayou Pierre (Mississippi)	11	9	11	0
	Big Black (Mississippi)	62 (3)	12	4	0
	Jourdan	3	1	3	0
	Mississippi	3	12	3 (1)	0
	Pascagoula	152 (7)	37 (2)	54	0
	Pearl	76 (3)	19 (2)	16	0
	Tombigbee (Mobile)	11	3	5	0
	Yazoo (Mississippi)	125 (2)	88 (2)	89	0
Texas					
	Neches	8	10	5	3
	Sabine	2	1	1	0
	San Jacinto	20	48	63	1
	Trinity	4 (1)	8	7	4
Illinois					
	Mississippi	472	6	12	0
	Total	996	270	292	17
	Damaged/missing	19	6	1	0

(2.7%) wild captures had missing or damaged lures, consisting of 9 lacking a visible lure and 13 with damaged lures (Table 2). Of the 9 lacking a visible lure, 5 were juveniles and 4 were adult males. Of the 13 with damaged lures, 10 were juveniles, 2 were adult males, and 1 was an adult female (Table 2).

Lure color

From the onset of the project, it was clear that research teams reported lingual lure coloration differently. In southwestern Louisiana, the lure was given a binary designation, either pink or gray. Both Texas research teams primarily used these categories, but a third category called pinkish-gray was also frequently used. Additionally in Texas, 1 juvenile was noted with a red lure, 1 adult and 2 juveniles were noted to have clear lures, and 2 adults were noted to have mottled lures. Northeastern Louisiana used pink, gray, red, or clear/white as their categories. Mississippi had 12 categories to describe lingual lure color. Illinois had 29 categories, with descriptors like light, pale, dark, deep, and bright before the colors, with seeming overlap between some of the unique descriptors.

The varied approaches in describing lure coloration make it difficult to make comparisons. At a southwestern Louisiana site, 22 of 26 (84.6%) Alligator Snapping Turtles had pink lures, whereas at a site in Harris County, TX, 109 of 124 (87.9%) had gray lures. Across Mississippi, 431 of 809 (53.3%) Alligator Snapping Turtles had pink lures, whereas 298 of 809 (36.8%) had gray lures (Table 3). When examining lure coloration of recaptures in Mississippi over 3 months apart, 14 of 22 (63.6%) retained the same lure color. All 29 neonate turtles had red lures from the Cherokee County, TX, site. Of 953 lure color examinations in Illinois, 516 were pink, 209 were white, 175 were red, 47 were gray, 3 were mottled, and 3 were pinkish-gray. Of 286 Illinois turtles with at least 2 captures, 145 displayed 1 lure color, 118 displayed 2 lure colors, 22 displayed 3 lure colors, and 1 displayed 4 lure colors (Table 4).

Discussion

The incidence of missing or damaged lingual lures was very low and not widespread, as only 4 of the 7 research teams noted any missing or damaged lures, which

Table 3. Lingual lure color (based on anterior horn coloration) of Alligator Snapping Turtles captured in Mississippi. For turtles in each color category, straight carapace length (SCL, mm) and mass (kg) are presented as mean (minimum–maximum).

Color category	*n*	SCL	Mass
Red	10	27.29 (12.6–44.8)	7.05 (0.45–20.14)
Pink	431	34.09 (8.6–65.4)	13.35 (0.175–66.64)
Pinkish gray	46	33.98 (7.6–60.2)	12.89 (0.125–51.68)
Gray	298	30.10 (12.6–59.7)	9.15 (0.375–51.5)
White	10	28.96 (14.2–45.8)	8.33 (0.675–23.73)
Mottled	3	30.97 (23.7–43.6)	9.24 (3.1–20.73)
No lure, damaged (no color taken), other	11	30.20 (11.9–61.8)	10.95 (0.325–53.41)

were found in low numbers in less than half of sampled river drainages. Based on the work by Drummond and Gordon (1979), it may seem plausible that naïve juveniles allow predators to grab the lingual lure before the snapping response, which might have caused the damaged or missing lures observed in this study. We did not find a difference between juvenile and adult incidence rates, but we do not know when the adult lures were damaged. It is possible the damage occurred as a juvenile, and either individuals learn to use other senses to capture prey when luring to limit risk to their lures, or adults rely less than juveniles upon luring for prey.

Prey may be more likely to grab the lingual lure before the snapping response in turbid waters, where turtles may not see their prey approach, assuming Alligator Snapping Turtles lure in these habitats. However, in Buffalo Bayou in Houston, TX, and Clear Creek in Illinois, where the water is very turbid, missing or damaged lures were not observed. Nonetheless, predators grabbing the lingual lure may be a primary cause of damaged lures. For those completely missing a lingual lure, perhaps a prospective prey item removed the whole lure, or alternatively, the missing lure may be a congenital defect or the result of repeated damage to the lure. Whatever the cause of a missing lure, it is unknown whether this condition causes behavioral changes or reduces an individual's foraging success. For instance, do individuals without lingual lures still exhibit luring behavior or do they switch exclusively to active foraging? If these animals still attempt luring behavior, is foraging success reduced resulting in reduced growth rates? The answers to these questions remain unknown, as does the ultimate impact on fitness and survival in individuals without lingual lures.

Lingual lure color is certainly not static. There may be an ontogenetic change in lure color from pink to gray, as suggested by Drummond and Gordon (1979) and Spindel et al. (1987), but this does not hold true everywhere. In Illinois, 49.3% of recaptured turtles displayed at least 2 lure colors, with 1 individual displaying 4 of the 6 lure colors identified herein (Table 1). Additionally, in other regions, recaptured turtles sometimes had a different lure color than during their previous assessment. In fact, we have observed rapid changes in lure color while processing captured turtles, which could be a stress response from being handled out of the water. For instance, handling of *Glyptemys insculpta* (LeConte) (Wood Turtle) has been documented to cause tachycardia (Cabanac and Bernieri 2000), a condition that reduces blood flow.

Table 4. The number of unique lure colors of Alligator Snapping Turtles recaptured in Illinois by the number of unique captures. The proportion of unique lure colors per individual within each capture history is shown in parentheses.

# of unique lure colors	Unique captures				
	2	3	4	5	6
1	112 (69.6%)	26 (40.0%)	6 (19.4%)	1 (11.1%)	0 (0%)
2	49 (30.4%)	47 (56.0%)	18 (58.1%)	4 (44.4%)	0 (0%)
3	-	11 (13.1%)	7 (22.6%)	3 (33.3%)	1 (100%)
4	-	-	0 (0%)	1 (11.1%)	0 (0%)

In southwestern Louisiana, 13 of 14 adult Alligator Snapping Turtles had pink lures. Conversely, about 88% of all individuals in the Harris County, TX, population had gray lures, with similar percentages in adults and juveniles. The lure color of Alligator Snapping Turtles is not only red or pink when in the water, as nesting females on land in northeastern Louisiana have been noted to possess pink lingual lures. Additionally, the Mississippi research group documented differences in color between the anterior and posterior horns of the lure. If the blood flow were sufficient to both horns, one would expect both to respond the same and appear the same color. Perhaps some degree of damage to the blood supply or other circulatory rationale can explain bi-colored lures, but the topic warrants further investigation.

There may be differences observed in the lingual lure color of Alligator Snapping Turtles captured in baited traps versus those that are hand captured by snorkeling, radiotelemetry, or other means. Perhaps those captured and sitting in baited traps do not have the propensity to lure as often or at all compared to free individuals. Presumably, active luring will change the color of the lure to some degree. It is also plausible that an Alligator Snapping Turtle may still lure even while in a trap. Some believe luring is much more commonly employed by juvenile turtles (Ewert et al. 2006). This possible decrease in luring with age may be associated with the decline in relative size of the gular barbels present in Alligator Snapping Turtles (Winokur 1982). Pritchard (1989) reported the high contrasting color of the lure compared to the tongue and mouth, as well as the vermiform shape, decline as turtles age. Ewert et al. (2006) stated that the lure may lose distinctness or even become proportionately shorter with age. That said, we have observed luring by several adult Alligator Snapping Turtles as they reached for sinking bread that they were conditioned to feed upon from a restaurant deck in Texas. However, the presence of many fish also feeding on the bread could explain the luring. Regardless, large individuals certainly lure, as a turtle over 55 kg was observed exhibiting this behavior.

Another consideration with respect to the lingual lure involves the often-turbid water that many Alligator Snapping Turtles inhabit. One may assume that luring is not as effective in very turbid waters with poor visibility, and turtles in these habitats either do it infrequently or never. Does habitat affect the color of the lure? If so, and we assume that seldom or never used lures would be gray, this could be a major driver of lure coloration seen among populations and worth exploring in more detail. In East Texas, 36 Alligator Snapping Turtles from wild populations were captured in waters with clarity varying from 144 cm to 878 cm. Though 6 color categories were described for these individuals, no significant relationship was detected between lure color and water clarity.

Less than half of Alligator Snapping Turtle researchers who responded to the initial data call had data on the lingual lure. Moving forward, we suggest researchers record data about the condition and coloration of the lingual lure, which requires limited effort when handling individuals because they gape in defense. Only with additional information on missing or damaged lures, as well as the color of the lingual lure, will it be possible to address ecological and evolutionary questions concerning the unique lingual appendage in the Alligator Snapping Turtle.

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Literature Cited

Allen, E.R., and W.T. Neill. 1950. The Alligator Snapping Turtle, *Macrochelys temminckii*, in Florida. Ross Allen's Reptile Institute Special Publication 4:1–15.

Cabanac, M., and C. Bernieri. 2000. Behavioural rise in body temperature and tachycardia by handling of a turtle (*Clemmys insculpta*). Behavioural Processes 49:61–68.

Carr, A. 1952. Handbook of Turtles: The Turtles of the United States, Canada, and Baja California. Cornell University Press, Ithaca, NY. 542 pp.

Dobie, J.L. 1971. Reproduction and growth in the Alligator Snapping Turtle, *Macroclemys temmincki* (Troost). Copeia 1971:645–658.

Drummond, H., and E.R. Gordon. 1979. Luring in the neonate Alligator Snapping Turtle (*Macroclemys temminckii*): Description and experimental analysis. Zeitschrift für Tierpsychologie 50:136–152.

Ewert, M.A., D.R. Jackson, and P.E. Moler. 2006. *Macrochelys temminckii* – Alligator Snapping Turtle. Pp. 58–71, *In* P.A. Meylan (Ed.). Biology and Conservation of Florida Turtles. Chelonian Research Monographs, Lunenburg, MA. 376 pp.

Gadow, H. 1909. Amphibia and Reptiles. The Cambridge Natural History, Volume 8. MacMillan and Co., London, UK. 668 pp.

Glorioso, B.M., and J.H. Waddle. 2021a. Data from a 2019 occupancy survey of Alligator Snapping Turtles, *Macrochelys temminckii*, in south-central Louisiana: US Geological Survey data release. Available online at https://doi.org/10.5066/P90JT34K. Accessed 3 January 2022.

Glorioso, B.M., and J.H. Waddle. 2021b. Data from a turtle trapping effort targeting Alligator Snapping Turtles (*Macrochelys temminckii*) in the Atchafalaya Basin beginning in 2019: US Geological Survey data release. Available online at http://doi.org/10.5066/P9N40V06. Accessed 3 January 2022.

Glorioso, B.M., C.D. Battaglia, J. Streeter, and J.H. Waddle. 2020. Data from a turtle trapping effort at a release site of head-started Alligator Snapping Turtles, *Macrochelys temminckii*, in southwest Louisiana in 2018 (ver. 2.0, September 2021): US Geological Survey data release. Available online at https://doi.org/10.5066/P9G9BR1D. Accessed 3 January 2022.

Heusser, H. 1968. Das Koderverhalten der Alligatorschnappschildkrote *Macroclemys temmincki.* Der Zoologische Garten 36:147–152.

Heusser, H. 1971. Eine schildkrote geht angeln. Aquarien Magazin 276–277.

Hiler, W.R., B.A. Wheeler, and S.E. Trauth. 2006. *Macrochelys temminckii* (Alligator Snapping Turtle). Feeding behavior. Herpetological Review 37:217.

Johnston, G.R., J.S. Geiger, T.M. Thomas, K.M. Enge, E. Suarez, and B. Davis. 2023. Maximum body size of the Suwannee Alligator Snapping Turtle (*Macrochelys suwanniensis*). Southeastern Naturalist 22(Special Issue. 12):418–428.

Pritchard, P.C.H. 1989. The Alligator Snapping Turtle: Biology and Conservation. Milwaukee Public Museum, Milwaukee, WI. 104 pp.

Reed, R.N., J. Congdon, and J.W. Gibbons. 2002. The Alligator Snapping Turtle [*Macrochelys* (*Macroclemys*) *temminckii*]: A review of ecology, life history, and conservation, with demographic analyses of the sustainability of take from wild populations. Division of Scientific Authority, United States Fish and Wildlife Service. Savannah River Ecology Laboratory, Aiken, SC. 17 pp. Available online at https://srelherp.uga.edu/projects/BobReedAlligatorSnapper-02.pdf. Accessed 27 September 2021.

Rosenbaum, D., D.C. Rudolph, D. Saenz, L.A. Fitzgerald, R.E. Nelson, C. Collins, T.J. Hibbitts, R.W. Maxey, P. Crump, and C.M. Schalk. 2023. Distribution and demography of the Alligator Snapping Turtle (*Macrochelys temminckii*) in Texas: A 20-year perspective. Southeastern Naturalist 22(Special Issue. 12):197–220.

Sloan, K., and J.E. Lovich. 1995. Exploitation of the Alligator Snapping Turtle, *Macroclemys temminckii*, in Louisiana: A case study. Chelonian Conservation Biology 1:221–222.

Spindel, E.L. 1980. The functional mechanism and histologic composition of the lingual appendage in the Alligator Snapping Turtle, *Macroclemys temminckii* (Troost) (Testudines: Chelydridae). M.Sc. Thesis. Auburn University, Auburn, AL. 55 pp.

Spindel, E.L., J.L. Dobie, and D.F. Buxton. 1987. Functional mechanisms and histologic composition of the lingual appendage in the Alligator Snapping Turtle, *Macroclemys temmincki* (Troost) (Testudines: Chelydridae). Journal of Morphology 194:287–301.

United States Fish and Wildlife Service (USFWS). 2021. Endangered and threatened wildlife and plants: Threatened species status with section 4(d) rule for Alligator Snapping Turtle. Federal Register 86:62434–62463.

Winokur, R.M. 1982. Integumentary appendages of chelonians. Journal of Morphology 172:59–74.

Winokur, R.M. 1988. The buccopharyngeal mucosa of the turtles (Testudines). Journal of Morphology 196:33–52.