Anthropogenic Threats to Alligator Snapping Turtles (Chelydridae: *Macrochelys*)

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Abstract - With the conservation status of *Macrochelys* (alligator snapping turtles) being examined at the national level, our objective was to compile categorical data on threats from anthropogenic interactions. We included information from (1) author-collected anecdotes on human–turtle interactions and (2) radiographs to assess the prevalence of ingested fishing hooks. We placed 173 interactions involving 192 incidents into 9 IUCN threat categories and found bycatch involving fish hooks to be 4 times more numerous than the second-most numerous threat, turtle persecution. Fishing bycatch resulted in a high proportion of turtle mortalities (39%), and bycatch incidents in several cases preceded the highest-mortality threat (53%), persecution of individuals involving shooting or blunt trauma. We recommend fishing bycatch-mitigation measures and educational efforts to help conserve *Macrochelys*.

Introduction

Species-conservation efforts require identifying species at risk of extinction, protection for populations to limit additional losses, and recovery of populations to self-sustaining levels (Wilcove 2010). The identification of sources of mortality are vital to the development of conservation plans and species-status assessments (Maxwell et al. 2016, Ripple et al. 2019). Anthropogenic sources of mortality can severely reduce population growth rates, causing population declines (IUCN 2012b). Marine megafauna, including sea turtles, have received abundant attention regarding these types of threats (Lewison et al. 2014, National Research Council 1990, Wallace et al. 2010), but many of the same threats affect freshwater megafaunal vertebrates (He et al. 2017, 2019), including several reptiles. Moreover, despite

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serious conservation challenges, reptiles (Gibbons et al. 2000, Mittermeier et al. 1992) have attracted less attention and support than birds, mammals, or non-reptile marine megafauna (Clark and May 2002). Globally, over half of all turtle species are threatened with extinction (Cox et al. 2022, Rhodin et al. 2018) due to 2 primary threats: (1) exploitation for the meat and pet trade, and (2) habitat loss and degradation (Stanford et al. 2020).

Macrochelys (alligator snapping turtles) are subject to a variety of anthropogenic threats, including a history of consumptive use by commercial fishers and turtle trappers primarily in southern states (Pritchard 1989, Sloan and Lovich 1995, White 1986). Commercially harvested turtles have been captured using a variety of techniques including trotlines and baited hoop nets (Dobie 1971, Elsey 2006). Louisiana was the last state to close the commercial harvest of *Macrochelys* in 2004 (Boundy and Kennedy 2006), marking the end of legal commercial exploitation of wild *Macrochelys*. The genus *Macrochelys* is now considered to consist of 2 species, *Macrochelys temminckii* (Troost in Harlan) (Alligator Snapping Turtle) and *M. suwanniensis* Thomas, Granatosky, Bourque, Krysko, Moler, Gamble, Suarez, Leone, Enge, and Roman (Suwannee Alligator Snapping Turtle). Of these 2 species, it remains legal to harvest *M. temminckii* recreationally in Louisiana and Mississippi. In Louisiana, a licensed recreational fisher may harvest 1 Alligator Snapping Turtle of any size per person per vehicle per day regardless of whether the animal was intentionally caught or not (LDWF 2021). In Mississippi, a person can possess and harvest only 1 Alligator Snapping Turtle per license-year, and the turtle must have a carapace length ≥24 inches (MDWFP 2019). In Louisiana, there are no data collected on the extent of the recreational harvest (USFWS 2021), but with the Mississippi minimum size requirement, only large males would be vulnerable to legal take.

In addition to the legal, recreational harvest of *M. temminckii,* abandoned fishing gear and bycatch have been identified as potential threats to *Macrochelys* (USFWS 2020, 2021). Bycatch is defined as animals caught and discarded by commercial or recreational fishers that are unwanted or illegal to keep (NOAA 2019). Fishing bycatch of turtles has been studied more extensively in marine ecosystems (Wallace et al. 2010) than freshwater ecosystems (Raby et al. 2011). Mortality due to bycatch can have significant negative impacts on populations, especially in species that are slow to mature like *Macrochelys* spp. (Congdon et al. 1993, 1994; Sloan and Lovich 1995; Steen and Robinson 2017). The loss of adult females is especially harmful to populations of long-lived and slow-growing species like *Macrochelys* spp. (Reed et al. 2002).

Bjorndal (2020) highlighted the possibility that significant biotic interactions and the scope of anthropogenic threats might be elucidated through the collection and evaluation of anecdotal information. With respect to anthropogenic threats, knowledge of their chronology and geographic distribution can inform management decisions, but these data sources are limited due to their qualitative nature (Bjorndal 2020). Using qualitative data sources to inform quantitative models is difficult, and such difficulty is evident in the caveats concerning precision and accuracy of estimates based on expert elicitation when modeling population effects of threats to *Macrochelys* (USFWS 2020, 2021). However, in the absence of quantitative data sources, qualitative data, such as anecdotal information, can provide considerable value in conservation assessments. With the aforementioned in mind, our objective was to compile a collection of observations of threats to *Macrochelys* to gain insights on how anthropogenic threats (IUCN 2012a) negatively impact populations (IUCN 2012b). In addition, we collected observations from our review of the literature and examined radiographs of *Macrochelys* spp. for the presence of ingested hooks (Steen et al. 2014).

Methods

We compiled information on anthropogenic threats based on our 170 y of accumulated experience with *Macrochelys* (mean = 12.1 y, min–max = 2–28) spanning 1994–2022. We included descriptions of human–turtle interactions from 3 sources. Our main source of interactions was the authors' collective unpublished incidents recorded during fieldwork across Gulf coastal drainages from Texas to Florida and in Illinois. We also included some communications from colleagues, personal contacts, or social media. In the case of social-media posts, an author directly contacted the person via private messages to ascertain useful details of the incident. Secondly, we examined radiographs to detect ingested hooks. Lastly, we included anecdotal observations of human–turtle interactions from project reports, theses, and primary literature.

Human–turtle interactions database

We asked each author, or research group, to enter observations into a database in a specified format; otherwise, we took narrative accounts and extracted the information into columns (see Supplementary Table S-1 and its corresponding metadata and literature cited in Supplemental File 1, available online at https://www.eaglehill.us/SENAonline/suppl-files/s22-sp12-S2754cc-Shook-s1, and for BioOne subscribers, at https://www.doi.org/10.1656/S2754cc.s1). As defined by Salafsky et al. (2008), a biodiversity threat is a cause of stress on a population, the most obvious of which is mortality because it decreases population size. We sought to gather information that would be most appropriate for assessing threats based on the IUCN classification schemes (IUCN 2012a, b) used in the Red List assessment process (IUCN 2016).

During compilation of incidents, we initially allocated each to an informal threat category, intentional or unintentional. We considered intentional threats to be those where someone deliberately attempted to harm an animal, successfully killing it or not (e.g., shooting or hitting it; Ripple et al. 2019). We defined unintentional threats as those that harmed, or had the potential to harm an animal by accident, without human intent or deliberate action (e.g., fishing bycatch or turtle crossing a road). Additionally, we categorized each human–turtle interaction as a specific threat type using the IUCN Threats Scheme (IUCN 2012a, Salafsky et al. 2008). In some cases, we parsed a single interaction into 2 (or 3) component threat incidents so that human–turtle interactions could be tallied separately by threat category. For example, a turtle could be caught unintentionally on a hook while fishing and then intentionally shot to death, a sequence of 2 distinct threats. All threats in the scheme (Salafsky et al. 2008) are "direct" threats to our "targets", the species of *Macrochelys*. The specific "stress" applied to the target is the impact on population size (i.e., loss of individuals), so we scored each threatening incident as to the individual's status after the interaction—alive or dead. All threats we recorded concern stress 2.1: species mortality or 2.3.7: reduced reproductive success (IUCN 2012b). Stress 2.3.7 would apply only to a clutch of eggs (nest), so all other life stages are covered under stress 2.1.

We recorded the date of each incident to enable assessment of the temporal aspect of past, on-going, and future threats, as well as the geographic location with respect to the spatial extent of threats (Salafsky et al. 2008). We also recorded demographic information about the turtle specimen(s) involved in an incident, potentially informative regarding the severity of a threat (IUCN 2012b, Salafsky et al. 2008). For each incident, we recorded variables such as number of individuals, life stage (egg/hatchling/juvenile/adult), sex if adult (male/female), and size (carapace length [mm] and mass [kg]). Such information can be useful; for instance, losing an adult female from a population is more impactful than losing a hatchling (Reed et al. 2002).

We organized fishing-related incidents into active and passive as defined by fisheries biologists (Hayes et al. 2013, Hubert et al. 2013). Fishing gear employing hooks included active angling with rod and reel, typically used in recreational fishing. We retained local terms (e.g., bush hook, jug line) within incident descriptions while organizing them into more inclusive categories for passive fishing-gear types (i.e., "fixed line with a single hook" or a "multi-hook device"; Hubert et al. 2013). We categorized passive fishing-gear types that are baited and left unattended as either individual hooks on fixed lines (e.g., limb line, jug line, bush hook, etc.) or a multi-hook device with a long horizontal line and many shorter vertical lines with a hook (i.e., trotline). We also used a general "hook" category that included both passive and active gear types using hooks, as well as threat instances lacking sufficient information to allow identification with greater resolution than the mere presence of a hook ("fishing gear-unknown"). Passive gear types without hooks included both entrapment (e.g., hoop net) and entanglement (e.g., gill net) devices (Hubert et al. 2013). Most recreational passive fishing-gear types, such as trotlines and hoop nets, target catfish.

Radiographic data

We examined radiographic prints and images obtained over 14 y (2008–2021; Carr et al. 2010, Enge et al. 2014, Holcomb and Carr 2011; see also Supplementary Table 1 in Supplemental File 1). In Louisiana, we trapped and opportunistically hand-captured *M. temminckii* during projects in Ouachita Parish (Johnson et al. 2023 [this issue]). We obtained radiographs of females to assess reproductive status at a local veterinary hospital or the University of Louisiana Monroe, and of 1 juvenile museum specimen to examine the skeleton. In Florida, we trapped *M. suwanniensis* along the Suwannee River as part of a population-status survey and recorded radiographic images with an Eklin Mark III digital radiograph/MinXRay generator combination (Sound Technologies, Carlsbad, CA) at the nearest boat ramp to document ingested hooks (Enge et al. 2014).

We examined radiographs for ingested hooks and other fishing gear (e.g., Steen et al. 2014). We also recorded the extent of the subject animal in view, as well as the presence and type of foreign object. If the entire animal was not visible, we could have missed a foreign object embedded in the body. Limbs, tail, head, or neck were often excluded from radiographs, but because we were primarily interested in hooks that had been ingested, our focus was the digestive tract beginning with the buccopharynx and ending with the cloaca. Radiographs allowed us to examine the body cavity, which contains the majority of the esophagus, plus the stomach and intestines. An ingested hook stuck in the buccopharynx is usually visible when the turtle opens its mouth, and the cloacal region is typically included in radiographs under the posterior carapace. Only a hook embedded in the buccopharynx or anterior-most esophagus in the neck could be missed in an X-ray; thus, our hook-ingestion rates could be considered conservative. We included hooks discovered using radiographs in our compilation (see Supplementary Table 1 in Supplemental File 1).

Data compilation and analysis

We compiled data from all authors in an Excel™ (Microsoft, Redmond, WA) spreadsheet (see Supplementary Table 1 in Supplemental File 1), which we also used to sort and tabulate numbers in various categories (e.g., threats and hook location). We calculated mortality (%) for each threat as the fraction of dead individuals divided by the number of live or dead individuals subjected to that threat, which represents only a rough index of the severity of the threat to *Macrochelys*. To graph the frequency of observations for each threat, we used 5 categories: hook, persecution, infrastructure, net-device bycatch, and other. The hook category includes all passive and active hook-based threats (4 of the 5.4.3 threats; IUCN 2012a). Persecution contains all intentional human-derived threats (threat 5.4.5). We combined incidents involving transportation corridors (threat 4.1) with residential and commercial structures (threats 1.1 and 1.2) for the infrastructure group. All non-hook-based bycatch events (threats 5.4.3 and 5.4.4), which largely consisted of hoop-net and gill-net captures, were included in a net-device bycatch category. All other threat types were included in the other category. We summarized all incidents by the status of the individual or nest and the threat category with R version 4.1.3 (R Core Team 2022) within RStudio version 2022.07.2 (RStudio Team 2022) using the dplyr package (Wickham et al. 2022). We did the same to summarize hook-only incidents by status and hook source. We plotted these summaries using the 'ggplot2' package (Wickham 2016).

Results

We assembled a list of 173 human–turtle interactions divided into 192 threat incidents; 119 from the authors and 73 from the literature (Tables 1–3, see also Supplementary Table 1 in Supplemental File 1). Threat incidents within the IUCN classification scheme are summarized in Table 1, demographic information on

Table 1. Classification of human–turtle interactions for *Macrochelys* according to the IUCN-CMP Unified Classification of Direct Threats, v. 3.2 (IUCN 2012a). The lowest level is our designation for threats within the 2nd or 3rd-level IUCN classification; see text for additional details. Species (*M. suwanniensis* [Ms], *M. temminckii* [Mt]); and the source of the information on the incident (either literature [LT] or this study [TS]). The underlying, incident-level details are in Supplementary Table 1 in Supplemental File 1.

Threat type	Species	Source
Intentional		
5.4.5 Biological resource use: fishing and harvesting aquatic resources: persecution/control		
Gunshot	Ms, Mt	LT, TS
Poaching	Mt	LT, TS
Blunt trauma	Mt	LT, TS
Penetrating trauma	Mt	LT
Unintentional		
1.1 Residential and commercial development: housing & urban areas		
Suburb: swimming pool	Mt	TS
1.2 Residential and commercial development: commercial and industrial areas		
Power plant: water intake	Mt	TS
2.1.4 Agriculture and aquaculture: annual and perennial nontimber crops: scale unknown/unrecorded		
Agricultural field: corn	Mt	LT
4.1 Transportation and service corridors: roads and railroads		
Road: paved	Mt	LT, TS
Road: unpaved	Mt	LT, TS
Road: unspecified	Ms, Mt	LT, TS
Railroad: freight	Mt	TS
5.4.3 Biological resource use: fishing and harvesting aquatic resources: unintentional effects: subsistence/small scale (recreational bycatch)		
Hooks: unspecified	Ms, Mt	LT, TS
Active: rod & reel	Ms, Mt	LT, TS
Passive: fixed-lines	Ms, Mt	LT, TS
Passive: trotlines	Mt	LT, TS
Passive: hoop net	Mt	LT, TS
Passive: gill net/net	Mt	LT, TS
5.4.4 Biological resource use: fishing and harvesting aquatic resources: unintentional effects: large [commercial] scale (bycatch)		
Passive: comm. gill net/net	Mt	LT, TS
6.1 Human intrusions and disturbance: recreational activities		
Boat strike	Ms, Mt	TS
6.3 Human intrusions and disturbance: work and other activities		
Industrial equipment	Ms, Mt	LT

threatened turtles is presented in Table 2, and the temporal and geographic extent of threats are summarized in Table 3. We illustrate selected incidents in Figures 1–4. Our compilation includes both species of *Macrochelys* and 1 or more incidents from 12 of 14 states within the range, lacking only Indiana and Tennessee, from 1858 through 2022. All threats identified would potentially stress a population by mortality of individuals (stress 2.1) except for ovipositing females in particular locations whose clutches of eggs would also be threatened, reducing reproductive output (stress 2.3.7). We recorded 4 intentional threats nested within biological resource use threat 5.4.5 at IUCN's third level and another 16 unintentional threats within 8 second- and third-level IUCN threats. Full source information and details by incident to the extent known are provided in Supplementary Table 1 (see Supplemental File 1). Additional details for many incidents (e.g., turtle size and specific localities) are available upon request for conservation purposes.

Intentional anthropogenic threats

We recorded 33 interactions as intentional threats to both *Macrochelys* species from 6 states (Tables 2, 3; Figs. 1, 2; see also Supplementary Table 1 in Supplemental File 1). The 4 specific types of persecution (threat 5.4.5) were gunshots (73%), blunt trauma, penetrating trauma, and poaching. Gunshots were recorded from 6 states (Table 3, Fig. 1; see also Supplementary Table 1 in Supplemental File 1), with

Table 2. Simplified classification using our threat categories in the same order as Table 1 with demographic information about the turtles threatened. Species (*Macrochelys suwanniensis* [Ms] , *M. temminckii* [Mt]); life stage threatened (egg [E], hatchling [H], juvenile [J], adult [Ad], unknown or unrecorded [U]); sex if adult (female [F], male [M], unknown or unrecorded [U]); and the number of incidents and number of individual turtles threatened. Complete details by incident are in Supplementary Table 1 in Supplemental File 1.

Threat type	Species	Life stage	Sex	Incidents (*n*)	Individuals (*n*)
Gunshot	Ms, Mt	U, Ad	F, M, U	24	26
Poaching	Mt	U, Ad	F, M	4	61
Blunt trauma	Mt	U, J, Ad	M	4	4
Penetrating trauma	Mt	Ad	U	1	1
Suburb: swimming pool	Mt	Ad	F	1	1
Power plant: water intake	Mt	Ad	M	1	1
Agricultural field: corn	Mt	E, Ad	F	1	1
Road: paved	Mt	U, H, J, Ad	F, M, U	8	9
Road: unpaved	Mt	E, J, Ad	F, U	6	6
Road: unspecified	Ms, Mt	U, E, J, Ad	F, M, U	10	10
Railroad: freight	Mt	Ad	F	3	3
Hooks: unspecified	Ms, Mt	U, J, Ad	F, M, U	46	47
Active: rod and reel	Ms, Mt	U, J, Ad	F, M, U	16	17
Passive: fixed-lines	Ms, Mt	U, J, Ad	F, M, U	23	34
Passive: trotlines	Mt	U, J, Ad	F, M, U	29	45
Passive: hoop net	Mt	U, J, Ad	F, M, U	7	14
Passive: gill net/net	Mt	Ad	M, U	2	2
Passive: comm. gill net/net	Mt	Ad	M	2	2
Boat strike	Ms, Mt	Ad	F, M, U	3	3
Industrial equipment	Ms, Mt	Ad	M	2	2

6 wounds from shotgun pellets and 7 from bullets (Fig. 1A, B, D). There were 11 gunshots to the head and 5 to the carapace. Additionally, we interpreted 11 (46%) gunshot interactions as involving old, healed wounds that were not the proximate cause of death or where the turtle was alive and appeared healthy. In 3 gunshot incidents involving 5 turtles, the lethal gunshot(s) was a sequel to an unintentional fishing bycatch incident (threat 5.4.3). This sort of bycatch followed by persecution (threat 5.4.5) was also the case in 2 of 4 blunt-trauma incidents.

Among the other 3 persecution types (threat 5.4.5.), we documented 4 blunt-trauma interactions (Table 2, see also Supplementary Table 1 in Supplemental File 1). Two involved unsuccessful attempts to kill turtles by beating them on the head using available instruments such as a boat paddle (Fig. 2E) or hatchet. The other 2 instances involved death by a broken neck, which we imagine was a form of blunt trauma. We found only 1 incident of penetrating trauma, when a fishing gig was used to impale a turtle in Oklahoma ca. 1945—a technique we have not encountered in current use. Although we collected limited information on poaching (n = 4), we note that poaching involved a large number of turtles per incident (mean = 15).

Unintentional anthropogenic threats

We recorded 159 unintentional incidents in 8 IUCN threat categories from 12 states (Tables 1–3; Figs. 1–3, 5; see also Supplementary Table 1 in Supplemental

Table 3. Simplified classification using our threat categories in the same order as Table 1 with temporal and spatial information on the threats. Species (*Macrochelys suwanniensis* [Ms], *M. temminckii* [Mt]); dates represent the year span (earliest to latest year) recorded in our compilation; and states refers to the geographic extent of the threat by state (postal abbreviations). The underlying, incident-level details are in Supplementary Table 1 in Supplemental File 1.

Threat type	Species	Dates	States
Gunshot	Ms, Mt	1858–2020	AR, FL, LA, MS, OK, TX
Poaching	Mt	1995–2016	FL, LA
Blunt trauma	Mt	2007–2019	LA, MS, OK
Penetrating trauma	Mt	1945	OK
Suburb: swimming pool	Mt	2020	LA
Power plant: water intake	Mt	2007	LA
Agricultural field: corn	Mt	1973	FL
Road: paved	Mt	<1991–2021	AL, FL, LA, MS, TX
Road: unpaved	Mt	2012–2019	FL, LA
Road: unspecified	Ms, Mt	<1982–2021	AR, FL, MS, OK
Railroad: freight	Mt	2009–2013	LA
Hooks: unspecified	Ms, Mt	1858–2021	AL, AR, FL, GA, LA, MS, TX
Active: rod & reel	Ms, Mt	1982–2021	AL, FL, GA, LA, MS, OK, TX
Passive: fixed-lines	Ms, Mt	1991–2020	AL, FL, GA, KS, KY, LA, MO, MS
Passive: trotlines	Mt	1957–2021	AL, AR, GA, LA, MS, OK, TX
Passive: hoop net	Mt	1992–2019	AL, AR, IL, LA
Passive: gill net/net	Mt	1985–1995	AL, LA
Passive: comm. gill net/net	Mt	1947–2007	LA, OK
Boat strike	Ms, Mt	2011–2022	FL, MS
Industrial equipment	Ms, Mt	2009–2021	GA, OK

File 1). Fishing bycatch accounted for 124 (78%) of 159 incidents, which corresponds with the second-level threat 5.4—unintentional effects of fishing and harvesting aquatic resources: biological resource use. At the third level, we found 2 threat categories: threat 5.4.3—unintentional effects for small-scale fishing (i.e., recreational); and 5.4.4—unintentional effects for large-scale fishing, which we considered to be commercial. Based on the number of incidents, we identified the 2 predominant threats as threat 5.4.3 (biological resource use: fishing: small-scale [recreational bycatch]) and threat 4.1 (transportation corridors: roads and railroads) with 122 (77%) and 27 (17%) incidents, respectively (Table 2, Fig. 5A). We recorded only 10 incidents (6%) among the other 6 unintentional threat categories, which were represented by only 1–3 incidents each (Table 2).

Within the total fishing bycatch, we found 2 incidents of threat 5.4.4 involving commercial fishing. The 2 incidents involved 1 adult male turtle each (both survived) and nets, 1 of which was specifically identified as a gill net. With respect to the recreational fishing threat 5.4.3, we found examples of 2 kinds of passive

Figure 1. (A) Adult female *Macrochelys temminckii* trapped in Black Bayou Lake (6 May 2006) with an old, healed bullet hole in the snout, Ouachita Parish, LA. Photograph © J.L. Carr. (B) Two skeletal adult *M. temminckii* photographed in situ with bullet holes in the skulls, Anderson County, TX (15 September 2018). Photograph © C.J. Franklin. (C) Adult female *M. suwanniensis* with 2 parallel, healed gashes inferred to be boat propeller wounds in the anterior carapace, caught alive during turtle surveys, Suwannee River, Suwannee County, FL (14 October 2011). Photograph © K.M. Enge. (D) Adult female *M. temminckii* trapped in Black Bayou Lake with old, healed wounds from 1 or more shotgun blasts—evidenced by a hole in the posterior carapace and scattered, embedded lead pellets in the carapace; Ouachita Parish, LA (28 October 2019). Photograph © J.L. Carr.

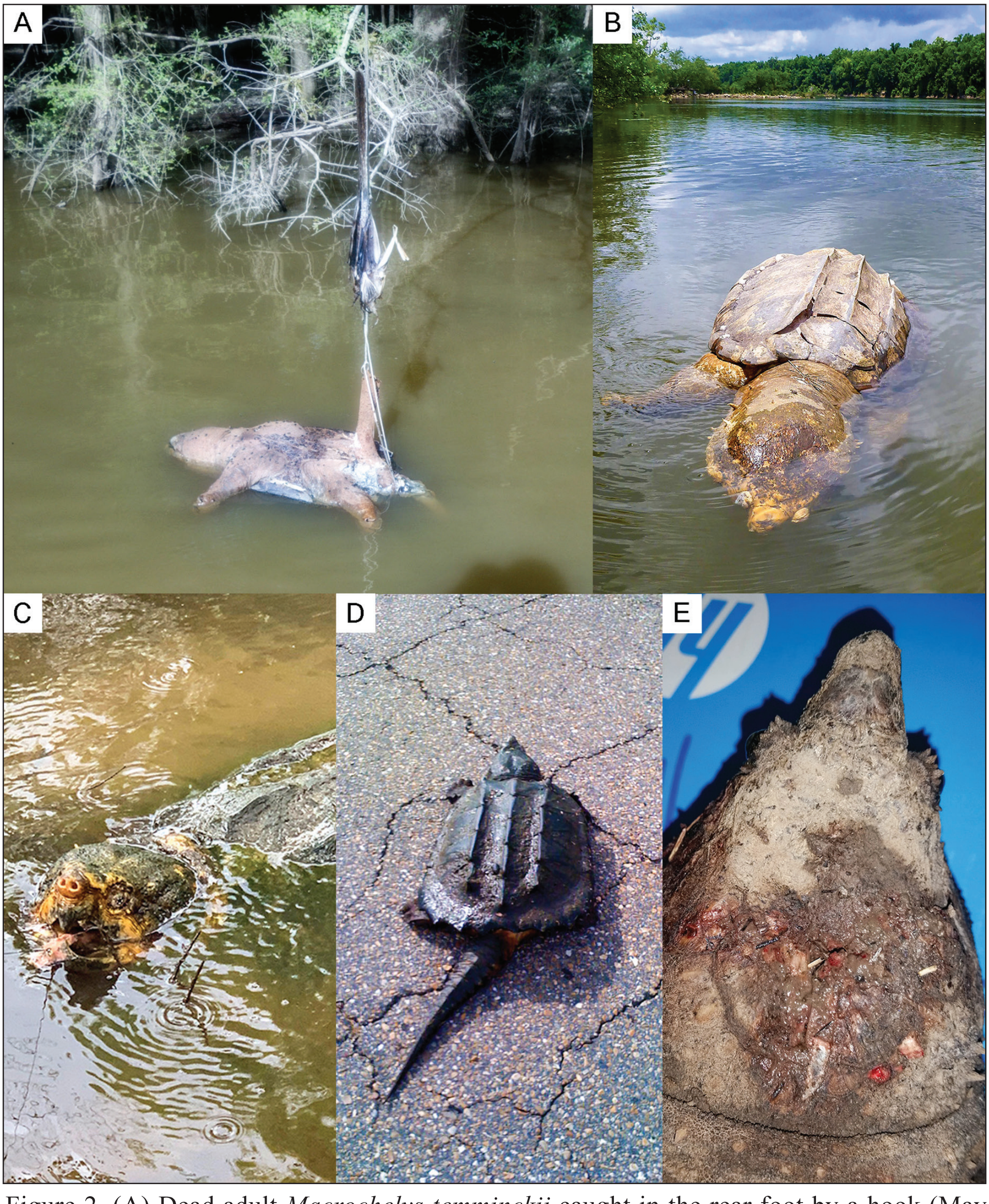

Figure 2. (A) Dead adult *Macrochelys temminckii* caught in the rear foot by a hook (May 2014) and with line wrapped around the tail in the Tombigbee River, AL. Photograph © Aaron Kern. (B) Dead adult male *M. temminckii* hooked (bush hook, 4 June 2015) in the nape of the neck in the Apalachicola River, Liberty County, FL. Photograph © J.D. Mays. (C) Live adult male *M. suwanniensis* hooked in the buccopharynx (mouth) by rod and reel (1 June 2019) in the Alapaha River, Tift County, GA. Photograph © Mike Withers. (D) Live adult *M. temminckii* photographed on asphalt pavement of Richland Place Road, Ouachita Parish, LA. Photograph © C. Foster. (E) Live juvenile *M. temminckii* captured in a hoop net in the West Fork of the Calcasieu River and then bludgeoned on top of the head (2 March 2016), Calcasieu Parish, LA. Photograph © C.D. Battaglia.

fishing nets. We identified 2 incidents involving 1 turtle each (1 mortality) in gill nets (or an unspecified net) and 7 incidents involving hoop nets (also called hoop traps). With respect to hoop-net incidents, 13 of 14 (93%) trapped turtles died.

With regard to recreational fishing bycatch (threat 5.4.3), most threats came from fishing gear with hooks: 113 (71%) of the unintentional incidents (Table 2; Figs. 2A–C, 3A, 3C, 4, 5B). Many incidents from 7 states lacked details and we classified them as "unknown fishing gear with hooks" (41%), which included both live and dead turtles. Among known fishing-technique incidents, the 2 passive fishing techniques accounted for 46% of all hook incidents. Twenty-three incidents of

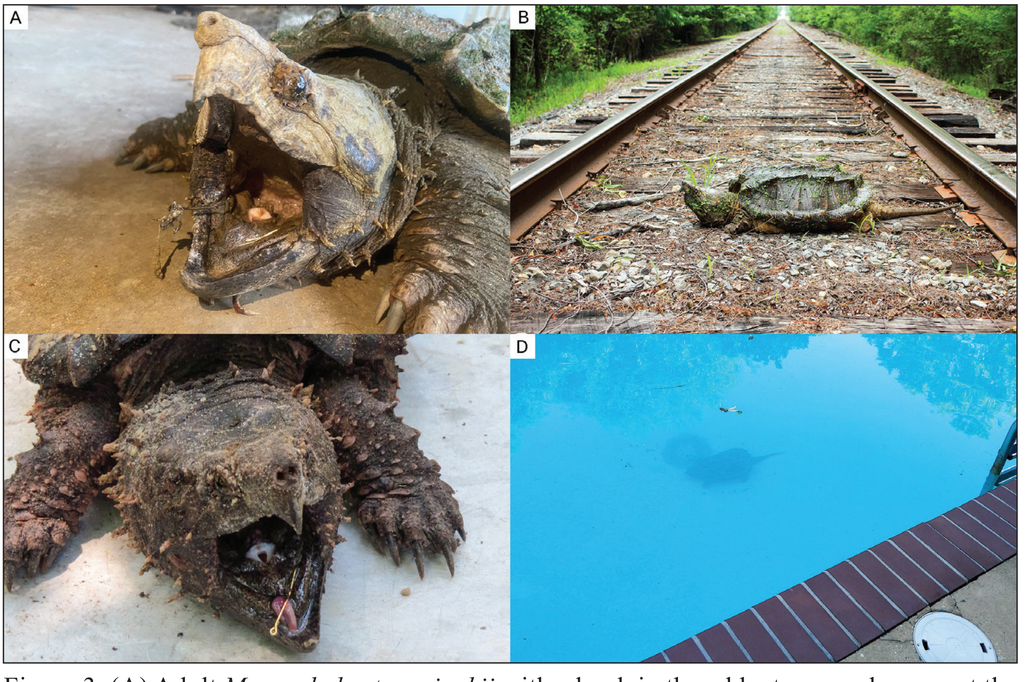

Figure 3. (A) Adult *Macrochelys temminckii* with a hook in the adductor muscle mass at the angle of the jaws, left side, captured during a survey in the Trinity River, Tarrant County, TX (8 March 2021). Photograph © C.J. Franklin. (B) Adult female *M. temminckii* photographed as she crossed a railroad track during the nesting season (23 May 2013), Black Bayou Lake National Wildlife Refuge, Ouachita Parish, LA. Photograph © C.D. Battaglia. (C) Juvenile *M. suwanniensis* with a hook in the floor of the anterior buccopharynx, caught alive during turtle surveys, Withlacoochee River, Lowndes County, GA. Photograph © D.J. Stevenson. (D) Adult female *M. temminckii* that fell into a swimming pool (30 April 2020) along Lake Bartholomew, Morehouse Parish, LA. Photograph © J.L. Carr.

Figure 4. Radiographs depicting hooks in *Macrochelys temminckii* (A, D) and *M. suwanniensis* (B, C) specimens. (A) Juvenile with 1 hook in the buccopharynx from Bayou DeSiard, Ouachita Parish, LA. (B) Adult female with 3 hooks from the Suwannee River, Suwannee County, FL. (C) Adult female with 1 hook in the buccopharynx from the Suwannee River, Dixie County, FL. (D) Adult female with 1 hook in the esophagus from Bayou DeSiard, Ouachita Parish, LA.

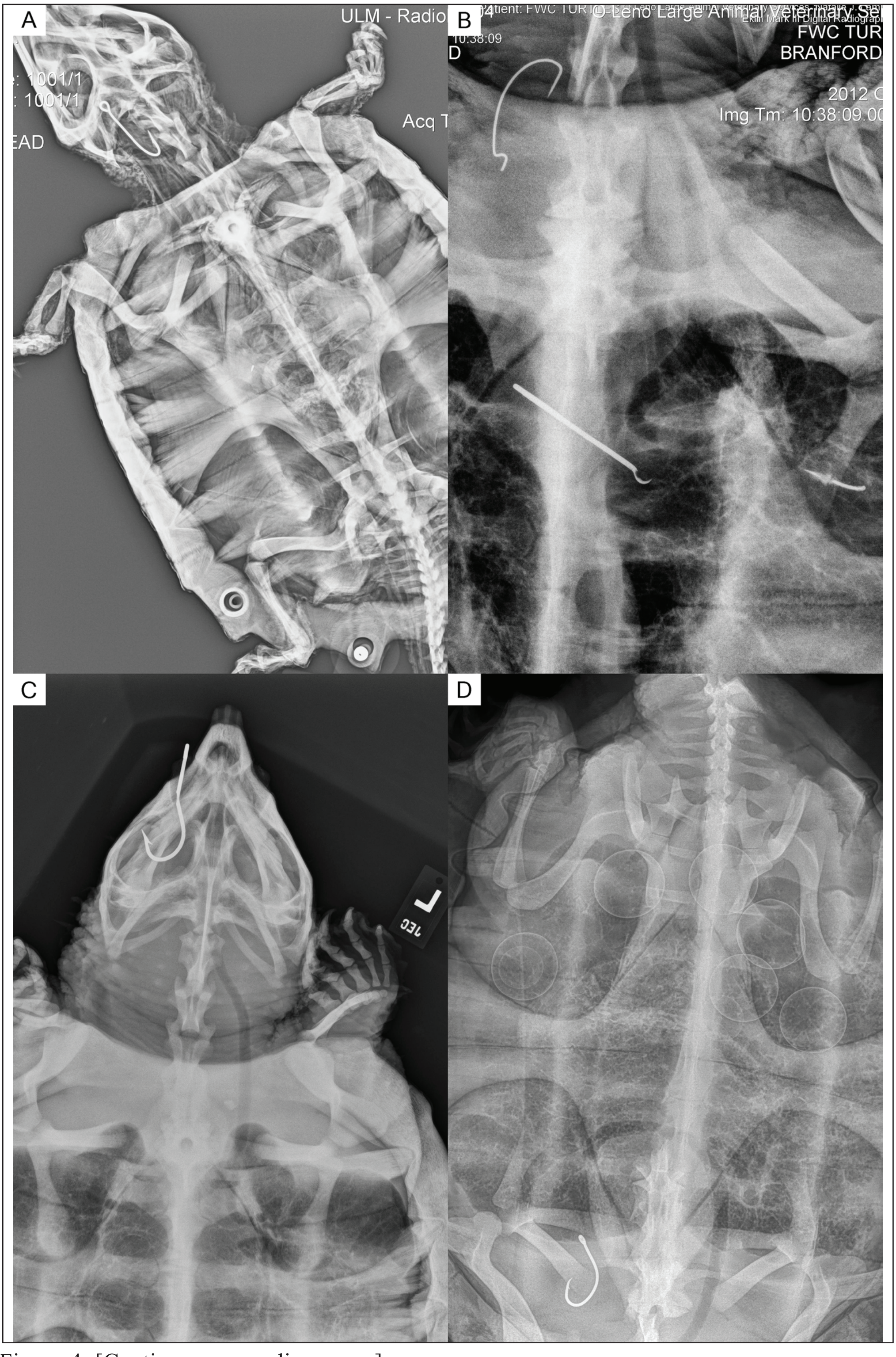

Figure 4. [Caption on preceding page.]

fixed lines with a single hook (e.g., stump hooks, jug lines, or bush hooks) involved 34 turtles, and 29 trotline (multi-hook devices) incidents involved 45 turtles. The active fishing incidents with rod and reel accounted for only 14% of our recorded hook incidents. Among our 4 fishing-hook threat types (Tables 1, 2; Fig. 5B), the highest mortality rate (58%) was found in the trotline group, followed by fixed lines, unknown, and rod and reel (Fig. 5B). Relatively few deaths were associated with the active rod and reel incidents that are human attended, as opposed to the 2 passive, unattended fishing techniques (Fig. 5B). The unknown hook category is undoubtedly some mixture of the other 3 techniques.

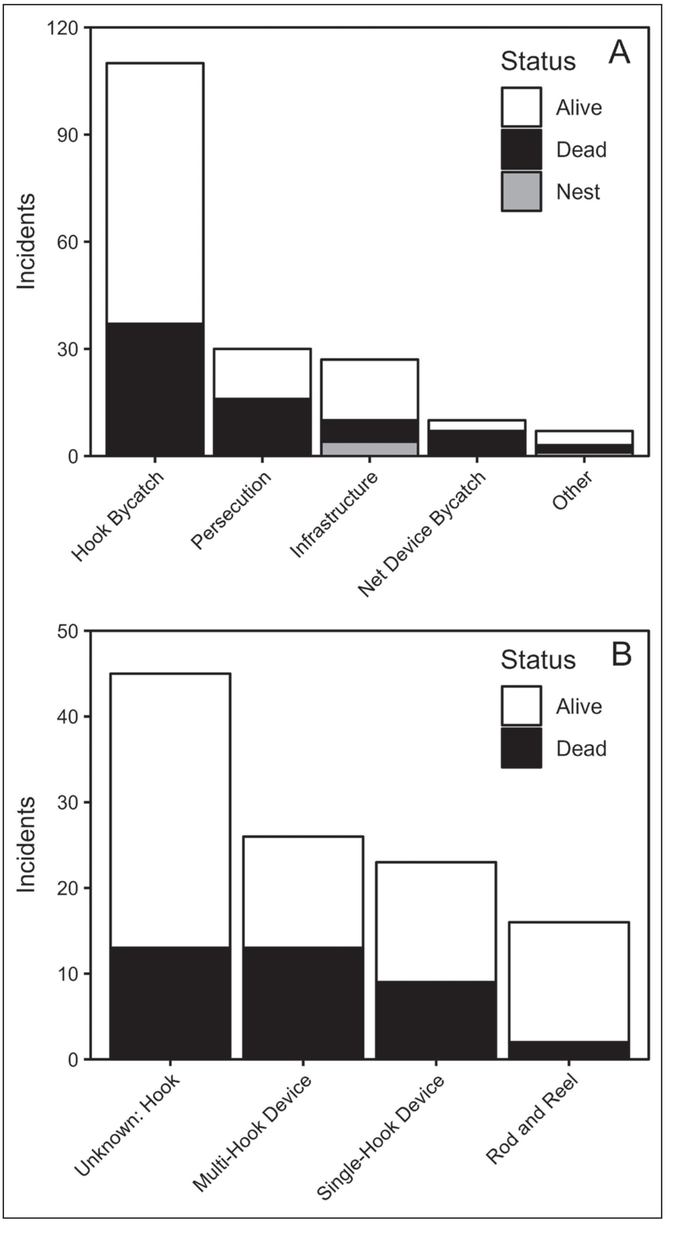

Figure 5. Incidents for threat categories compiled for *Macrochelys* in Supplementary Table 1 in Supplemental File 1. Some categories have been lumped to reduce the number of groupings. The Status indicates whether the turtle(s) survived the human–turtle interaction (alive), or did not survive (dead), or was a nest oviposited in a dangerous location (nest). Incidents with unknown outcomes have been removed to improve interpretability. Categories in A are: hook bycatch = all fishing gear using a hook; persecution = all intentional threats; infrastructure = roads, railroads, swimming pool, and water intake; net-device bycatch = all the entanglement and entrapment fishing gear types; other = remaining threats. Categories in B are a breakout of the hook bycatch in panel A into the 4 constituent parts: unknown hook devices (specific device type unknown); multi-hook device, i.e., trotlines; single-hook device, i.e. a fixed, single line with a single hook; rod and reel.

Of 113 hook incidents we recorded, relatively few mentioned the type of hook or location hooked. Hook types included both J-hooks and a circle hook (Fig. 4). We found 44 (39%) of 113 hook incidents specified the location of the hook in the body (Table 4). Seventy percent of hooks were ingested, and the rest were in external body parts (Table 4; Fig. 2A, B). We recorded instances of mortality associated with both internal and external hook locations, including turtles snagged in body parts such as a limb or the neck (Fig. 2A, B; see also Supplementary Table 1 in Supplemental File 1). Internal locations included the buccopharynx (27%; Fig. 2C), where one would expect to find recently ingested hooks, and which would be the easiest to see in the open mouth (Fig. 3A, C). More caudal locations along the digestive tract, including the esophagus, stomach, and gastrointestinal (GI) tract (unspecified) (Table 4), were only detected with radiographs (Fig. 4), dissections, or under special circumstances (e.g., Trauth and Kelly 2017).

Most transportation-corridor incidents (threat 4.1) involved roads (n = 24; Fig. 2D), which we tallied as paved, unpaved, or unspecified road type (Tables 1, 2). We recorded railroad incidents (n = 3; Fig. 3B) at a well-studied location where we documented nesting females crossing the tracks. We documented mortality on roads in both species of *Macrochelys* but not on railroads (see Supplementary Table 1 in Supplemental File 1). When identified, most transportation-corridor incidents involved adult females during the expected nesting season, but we found examples of hatchling, juvenile, and male turtles crossing roads (Table 2, see also Supplementary Table 1 in Supplemental File 1). We recorded a relatively low degree of mortality on roads (Fig. 5A). In addition, we found instances of females nesting in an unpaved road or on the road margin or associated corridors (e.g., bridge abutments). In such cases with nesting females, there is a proximate threat to the life of

Table 4. Summary of hook incidents (part of threat 5.4.3), the number of individual *Macrochelys* involved, and the anatomical location of known hook traumas. Some percentages do not sum to 100 due to rounding error. The underlying, incident-level details are in Supplementary Table 1 in Supplemental File 1.

Location	No. incidents (%)	No. individuals (%)
Total hooked	113	142
Unknown/known	69 (61) / 44 (39)	98 (69) / 44 (31)
Known: internal		
Buccopharynx	12 (27)	12 (27)
Esophagus	10 (23)	10 (23)
GI tract	8 (18)	8 (18)
Stomach	1 (2)	1 (2)
Total internal	31 (70)	31 (70)
Known: external		
Limb – foot	2 (4.5)	2 (4.5)
Forelimb	5 (11)	5 (11)
Hind limb	2 (4.5)	2 (4.5)
Neck	4 (9)	4 (9)
Total external	13 (30)	13 (30)

the female (stress 2.1) and to the nest, which would represent a reduction in reproductive success (stress 2.3.7). Any such nest would expose all the eggs in a clutch to the danger of being run over and compacted or crushed over a period of months. Additionally, we recorded an incident not on the road itself, just on the right-of-way, of a bush hog (mower) killing a *M. temminckii* (see Supplementary Table 1 in Supplemental File 1).

Among the 6 other IUCN threat types identified, we found a few other unintentional instances of turtles encountering anthropogenic structures (Table 2; see also Supplementary Table 1 in Supplemental File 1), including a swimming pool (threat 1.1; Fig. 3D) and a power-plant water intake (threat 1.2); both turtles survived. We found 1 literature record of nesting by a female in a cornfield in Florida (see Supplementary Table 1 in Supplemental File 1) and 2 incidents involving construction-type equipment (threat 6.3; 50% mortality). We recorded instances of boat strikes (threat 6.1; n = 3, 33% mortality) in Mississippi and Florida (see Supplementary Table 1 in Supplemental File 1), including an adult female *M. suwanniensis* that exhibited 2 parallel scars from a boat propeller on the anterior carapace (Fig. 1C).

Radiographic data

We examined X-rays of 40 individual turtles of both species and found an overall ingested hook prevalence of 15% (Table 5, Fig. 4). The Louisiana sample of 14 *M. temminckii* had a 14.3% prevalence of ingested hooks. One juvenile turtle had a J-hook in the buccopharynx (Fig. 4A), and an adult female had a circle hook embedded in the esophagus (Fig. 4D). The Florida sample of 26 *M. suwanniensis* consisted of juveniles and adults of both sexes with an ingested hook prevalence of 15.4%. One adult female had ingested 3 hooks (Fig. 4B), and another female had a single hook (Fig. 4C). One other Florida female was the only one recaptured, and she had a single hook in approximately the same internal location in X-rays taken 14 months apart. In addition, 1 juvenile had a 4/0 stainless steel hook deeply

Table 5. Number of *Macrochelys* with radiographs examined by life stage to search for the presence of fishing hooks from 2 locations: northern Louisiana (*M. temminckii*) and Florida (*M. suwanniensis*).

Species/life stage	No. Individuals per stage	No. Individuals with complete body	No. Hooked individuals (%)
M. suwanniensis			
Juvenile	2	2	1 (50)
Adult male	15	13	0 (0)
Adult female	9	6	3 (33.3)
Total	26	21	4 (15.4)
M. temminckii			
Juvenile	1	1	1 (100)
Adult female	13	1	1 (7.7)
Total	14	2	2 (14.3)
Macrochelys spp.			
All stages	40	23	6 (15.0)

embedded in the jaw that was surgically removed at the University of Florida veterinary hospital.

Discussion

We based our assessment of threats to *Macrochelys* on the authors' collective observations of human–turtle interactions in the field and familiarity with the literature. We identified 20 threat types among 9 IUCN categories at level 2 or 3 (Table 1; IUCN 2012a). In simplified form, we found recreational bycatch was the most common threat, with turtle persecution and turtle interactions with human infrastructure much less commonly sources of threat. Older listings identified habitat change and commercial exploitation for human consumption as significant threats to *M. temminckii* populations (Pritchard 1989, TFTSG 1996). Post-closure of commercial harvest in all states, the USFWS recently assessed both *Macrochelys* species for listing under the Endangered Species Act (USFWS 2020, 2021). The assessment identified 3 primary threats to *M. suwanniensis*: fishing bycatch and hook ingestion, habitat change, and nest predation (USFWS 2020). It was their assessment that *M. suwanniensis* was minimally affected by past commercial exploitation compared to *M. temminckii*. The assessment for *M. temminckii* identified 4 threats: legal (recreational) and illegal harvest, commercial and recreational fishing bycatch, habitat change, and nest predation (USFWS 2021). The USFWS threat assessments were based on a methodology of expert elicitation of current conditions.

Intentional anthropogenic threats

We found 4 threats related to intentional attempts to harm or remove *Macrochelys* specimens from wild populations (i.e., specific examples of threat 5.4.5: biological resource use involving persecution or control of harvested aquatic resources; IUCN 2012a). In terms of observed mortality rate, this group of threats was the deadliest (>50%), although the number of incidents was only ~20% as many as those involving unintentional hook threats (Fig. 5A). The greatest number of incidents involved gunshots in 6 states from 1858 to 2020 (Table 3). Our observations included numerous instances of turtles living with healed wounds (Fig. 1A, D). For example, we captured a female with a bullet hole in the snout nesting multiple times, apparently suffering no negative effects from the head wound (Fig. 1A). Otherwise, gunshot incidents accounted for the high mortality rate for threat category 5.4.5 and were particularly lethal when the head was targeted. While we uncovered examples of intentional harm to *Macrochelys* in multiple states, we did not attempt to determine the legality of such activities—in the case of poaching, we presume state and federal wildlife agencies would maintain records on documented cases. Additionally, we did not include the obvious threat of legal recreational harvest of *M. temminckii* in Louisiana and Mississippi in our compilation of threats (threat 5.4.1: small-scale intentional harvest of aquatic resources).

Studies that mentioned shooting of other turtle species usually referred to shooting basking turtles for target practice (Ennen et al. 2016, Lindeman 2013, Moll and Moll 2004, Selman and Jones 2011). Since basking is infrequently reported in

Macrochelys (Carr et al. 2011, Mays and Hill 2015) but common among various emydids (Selman and Qualls 2011), *Macrochelys* are not likely at risk from this behavior. We think *Macrochelys* shooting incidents involve close proximity between a person and the turtle on land or in shallow water. Often, such incidents of wanton violence are associated with fishing bycatch, as exemplified by the 1858 incident recounted by Pritchard (1989) in which an Alligator Snapping Turtle was caught while fishing and then shot dead. In other cases, we found turtles killed without using a gun following capture on a fishing line (e.g., broken neck, blunt trauma with boat paddle; see Supplementary Table 1 in Supplemental File 1). Deliberate persecution of *Macrochelys* appears to primarily occur opportunistically, when turtles and humans are unexpectedly in close proximity.

Instances of fishing bycatch followed by violence to the turtle are often due to a perception that turtles are threatening "something they care about" (Peterson et al. 2010:78). Specifically, the concern is the loss of fishing gear and the putative threat the turtle poses to the game fish the fishermen desire (Moll and Moll 2004). Several authors have specifically mentioned the perception that *Macrochelys* harm populations of game fish (Moore et al. 2013, Pritchard 1989). Additionally, *Macrochelys* are awe-inspiring creatures that evoke fear in many people at close proximity. When pulled from the water, *Macrochelys* are impressively large animals with an attention-grabbing, open-mouth threat. This display demonstrates obvious potential for inflicting human bodily harm; thus, the perceived danger (e.g., Agassiz 1857, Kim et al. 2020, Pritchard 1989). Although documented instances of human harm inflicted by a turtle bite are relatively rare (Johnson and Nielsen 2016, Lohr 2018, Pritchard 1989), there are many tall tales recounted of such interactions (Pritchard 1989). Dickman (2010) described miscalculations people make with respect to human–wildlife interactions as a common pattern—a mismatch between human risk perception and actual risk posed by the species. Further, a large, potentially dangerous animal, such as a *Macrochelys* specimen, could provoke a strong and disproportionate response like shooting or beating a turtle to death.

Unintentional anthropogenic threats

Miscellaneous threats. We documented a few instances of *Macrochelys* being trapped in water-related structures (threats 1.1 and 1.2, stress 2.1: species mortality; IUCN 2012b), as well as nesting in a cornfield in Florida (Ewert 1976) and in the turnrow of a cotton field in Louisiana (threat 2.1.4; J.L. Carr, unpubl. data). Although the entrapment in a swimming pool and water-intake structure did not lead to death, accidental entrapment effectively removes them from the population, the same as stress 2.1: species mortality (IUCN 2012b). Nesting in agricultural fields exposes both the female and her clutch to crushing by farm equipment. Two other lesser threats with some mortality involved recreational boats and industrial equipment (threats 6.1 and 6.3). There is a growing literature indicating many turtle species experience strikes from recreational boats (Bennett and Litzgus 2014, Heinrich et al. 2012, Smith et al. 2018).

Transportation corridors. We found incidents of *Macrochelys* interactions with roads (Fig. 2D) and railroad tracks (Fig. 3B), leading to the possibility of vehicular collisions resulting in death (Tables 2, 3, Fig. 5A, see also Supplementary Table 1 in Supplemental File 1). Unlike small-bodied species of turtles that become trapped between rails (Hartzell 2015, Kornilev et al. 2006), *Macrochelys* and *Chelydra serpentina* (L.) (Common Snapping Turtle) can climb or step over rails (J.L. Carr, pers. observ.) but may not always be quick enough to make it across (Hartzell 2015). Nearly all such cases in which the sex was known involved females during nesting months (Carr et al. 2023 [this issue]; see Supplementary Table 1 in Supplemental File 1). Steen and Gibbs (2004) found that road interactions for chelydrids in North America almost exclusively involved Common Snapping Turtles, which travel an average distance of 39 m from water to nest compared to 16 m for *M. temminckii* (Steen et al. 2012). For Common Snapping Turtles, females are typically the only sex found on roads and subjected to mortality, which can lead to a male-biased sex ratio in a population (Steen and Gibbs 2004, Steen et al. 2006). However, both sexes of Common Snapping Turtles were hit equally by vehicles in Ontario (Carstairs et al. 2019).

Bycatch in net gear. We found that recreational fishing bycatch (threat 5.4.3: unintentional effects of small scale fishing; IUCN 2012a) was the major unintentional threat to *Macrochelys* populations. Commercial fishing bycatch (threat 5.4.4: unintentional effects of large-scale fishing; IUCN 2012a) has been extensively studied in sea turtles, with entrapment or entanglement gear and hook ingestion (with or without attached lengths of line) considered to be primary fatal threats (Di Bello et al. 2013, Lewison et al. 2014, National Research Council 1990, Parga 2012, Schuyler et al. 2014). Similar rates of freshwater turtle mortality result from various other types of commercial and recreational fishing gear (Barko et al. 2004; Browne et al. 2020; Larocque et al. 2012a, 2012c; Nemoz et al. 2004; Steen et al. 2014). Surprisingly, as part of Florida's Fisheries-Independent Monitoring program in 2005–2019, biologists incidentally captured *M. temminckii* in and around Apalachicola Bay using 6.1-m otter trawls (*n* = 15), 21.3-m seine nets (*n* = 2), and 183-m seine nets (*n* = 1) (Meagan Schrandt, Fish and Wildlife Research Institute, St. Petersburg, FL, pers. comm.).

Barko et al. (2004) compared 4 entrapment and 1 entanglement-net types of passive net gear used by freshwater commercial fishers and fisheries biologists. They found substantial bycatch of riverine turtles in the Upper Mississippi River and many instances of drowning, with a mortality rate of 8–36% for various species. The highest mortality resulted from 2 types of fyke nets, followed by hoop nets and gill nets. In their study, the Common Snapping Turtle experienced a 29% mortality rate. Michaletz and Sullivan (2002) reported "high" turtle mortality in some impoundments in southeastern Missouri using various hoop nets to sample for *Ictalurus punctatus* (Rafinesque) (Channel Catfish), but they did not report the species of turtle bycatch. Cartabiano et al. (2015) reported 100% bycatch mortality of *Trachemys scripta elegans* (Wied-Neuwied) (Red-eared Slider) in hoop nets in an Oklahoma lake. Presumably, recreational fish traps for catfish, including slat-traps or netting stretched over hoops (or wire mesh), could result in high turtle capture rates and mortality when set completely submerged for extended periods. However, catfish traps we have seen are often relatively small in diameter (~50 cm) and would not allow entry of most adult *Macrochelys*. In addition, these recreational catfish trap types are illegal in several states within the range of *Macrochelys*.

Gill nets are a type of entanglement device used primarily in commercial fisheries and fisheries research (Hubert et al. 2013). Barko et al. (2004) and Rider et al. (2023 [this issue]) reported low rates of turtle bycatch using gill nets. Barko et al. (2004) did not work within the geographic range of *M. temminckii* but did capture Common Snapping Turtles using the 5 gear types compared; gill nets had the lowest turtle bycatch rate. Rider et al. (2023 [this issue]) reported capturing *M. temminckii* in Alabama at a rate of ~0.079 per gill net-night (24-h period). We recorded 1 instance of a Louisiana commercial fisherman capturing a 40-kg *M. temminckii* in a gill net (see Supplementary Table 1 in Supplemental File 1). Recreational gill nets are illegal in most states.

Bycatch with hooking devices. We used radiographs from 2 separate geographic areas to estimate the rate at which *Macrochelys* incidentally ingest hooks. Two caveats regarding this form of hook-data acquisition are: (1) identifying a hook in a turtle radiographically does not allow inferences regarding the specific type of gear employed (active or passive), and (2) because of the large size of many turtles relative to the X-ray equipment used, the entire body was often not visible in the radiographs, making it possible that we missed hooks despite most of the length of the digestive tract being included in images. The prevalence of hooks in our samples of 2 *Macrochelys* species in 2 states was 15%, which was comparable to the 3.6–33% reported for Common Snapping Turtles in Tennessee and Virginia (Steen et al. 2014), 18% for a population of *Emys orbicularis* (L.) (European Pond Turtle) in France (Nemoz et al. 2004), and 12.5% for the impact of recreational fishing on *Lepidochelys kempii* (Garman) (Kemp's Ridley Sea Turtle; Heaton et al. 2016). Our *Macrochelys* dataset cannot provide an estimate of the mortality rate in relation to ingested hooks—all we can conclude is that some individuals survive hook ingestion, such as the *M. suwanniensis* that still had an ingested hook 14 months later (see Supplementary Table 1 in Supplemental File 1).

Heaton et al. (2016) suggested that, compared with active recreational fishing, passive fishing techniques with prolonged soak times, such as commercial longline fishing (Casale et al. 2008), would result in a greater proportion of hook locations in the caudal digestive tract such as they reported for Kemp's Ridley Sea Turtles along the Mississippi coast, and the more caudal locations are considered more dangerous. However, Heaton et al. (2016) recorded the successful passage of hooks within 1–19 d in 73% of turtles held for observation. In the 1 *M. suwanniensis* that we examined radiographically twice, 14 months apart, there appeared to be no movement of the hook. Heaton et al. (2016) also reported 22 hooks that did not move over time in Kemp's Ridley Sea Turtles, but most hooks showed signs of deterioration after release back to the wild. Recreational trotlines and fixed lines used by freshwater anglers are comparable to the passive, longline marine fishing technique, whereas active fishing with rod and reel by freshwater anglers is more similar to the recreational fishing described by Heaton et al. (2016).

We found hook location recorded (or determinable) in only 39% of hook incidents (Table 4), 70% of which were in the digestive tract. The most common location was in the buccopharynx (27%), where one would expect recently ingested hooks to be. These incidents included actively fished gear (rod and reel) and passive gear types (i.e., trotlines and fixed lines). We found internal hook locations that corresponded with those reported in other turtle species (Di Bello et al. 2013, Hyland 2002). Internally located hooks are the primary source of hook-based mortality in sea turtles (Finkbeiner et al. 2011, Orós et al. 2004, Parga 2012). Clinical accounts of wildlife veterinary interventions with freshwater turtles frequently mention trauma from fishing hooks or fishing (Brown and Sleeman 2002, Hartup 1996, Rivas et al. 2014, Sack et al. 2017, Schenk and Souza 2014, Stranahan et al. 2016), but none are from within the range of *Macrochelys* and none mention the anatomical site of hook trauma. A single veterinary assessment of free-living *Macrochelys* did not mention anthropogenic trauma or hooks (Chaffin et al. 2008).

A dietary study not included in our compilation reported on commercially harvested *M. temminckii* that had been taken by trotline hooks or turtle traps (i.e., hoop nets), primarily in Louisiana (Elsey 2006). Of 109 turtles in which both the stomach and intestines (only) of the same individual were examined, 11 had hooks in the stomach and 1 had a hook in the intestines. One additional specimen included the esophagus in addition to the stomach and intestines, and there was a hook in the esophagus (R. Elsey, Louisiana Department of Wildlife and Fisheries, Rockefeller Wildlife Refuge, LA, unpubl. data). These figures suggest that only a small portion of the samples were collected using trotlines, or that hooks had fallen out or were primarily in more cranial portions of the unexamined digestive tract. Elsey (2006) specified that turtles may have been held for several days before being sacrificed, providing substantial time for hooks to move along the digestive tract and reach the stomach. Judging by the passage rate of hooks in Kemp's Ridley Sea Turtle (1–19 d), it should not be surprising to learn that hooks may travel the digestive tract once ingested (Elsey 2006) and perhaps pass all the way through with no apparent harm, as occurred in a controlled rehabilitation environment (Heaton et al. 2016). Pritchard (1989:74) reported "many informants said that the [Alligator Snapping] turtles could ... straighten the hooks or swallow them and pass them right through."

In our accounts, 30% of all hooking locations were external body parts and involved both active and passive fishing gear types (Tables 2, 4; see also Supplementary Table 1 in Supplemental File 1). Other investigators have also documented freshwater turtle species becoming entangled in fishing line and/or hooked in external body parts (e.g., Browne et al. 2020, Nemoz et al. 2004). We found a number of instances in which *Macrochelys* were still tethered by the capture line or entangled in it (e.g., Enge and Murray 2021), including dead turtles with the hook attached to the neck or an appendage, even just in the webbing of a foot (Table 4; Fig. 2A, B; see also Supplementary Table 1 in Supplemental File 1). Normal attempts to feed on a baited hook would be expected to result in hooks in the buccopharynx, or in a forelimb as a turtle is clawing or pinning a food item with the manus (Drummond and Gordon 1979). We presume a significant proportion of external hooking locations result from the turtles becoming snagged on hooks of abandoned fishing gear due to their size and bottom-walking mode of locomotion (Zug 1971). During fieldwork in multiple states, we often saw passive gear that had been abandoned and/or missing identifying tags required by state law (e.g., Alabama, Louisiana, and Florida). One study mentioned a higher prevalence of fishing hooks ingested by *Macrochelys* when more limb lines (fixed lines) were present in the environment (Thomas 2013), while another found an inverse correlation between *M. temminckii* relative abundance and fishing gear abundance (Rosenbaum et al. 2023 [this issue]). Specifically with respect to our data and active fishing, we found that rod and reel angling seemed to result in numerous instances of hooks snagged in appendages or the buccopharynx (Fig. 2C) and turtles released alive (Fig. 5B, see also Supplementary Table 1 in Supplemental File 1).

Bycatch mitigation. To reduce sea turtle mortality, investigators have prioritized reducing bycatch (Gilman et al. 2010, Parga et al. 2015). A variety of modifications in entanglement and entrapment nets, as well as with hook-device fisheries (e.g., using longlines), have proven effective (FAO 2010). Similar modifications have been made to freshwater fyke nets and hoop nets used in inland commercial fisheries and research to reduce turtle bycatch (Bury 2011, Cairns et al. 2017, Fratto et al. 2008, Larocque et al. 2012b), but none of these modifications were developed and tested within the geographic range of *Macrochelys* using recreational-size gear.

Two principal aspects of research into bycatch reduction in marine longline fisheries have been modifications of hooks and bait (Gilman and Huang 2017, Parga et al. 2015, Reinhardt et al. 2018). In some cases, bycatch of some sea turtle species was reduced by 90% (Watson et al. 2005). Similar observations have been made with respect to bait used in freshwater fishing. Two studies examined the use of soap (Zote™) as trotline bait for catfish, which was not attractive to turtles (Barabe and Jackson 2011, Cartabiano et al. 2015)—presumably the same would be true with fixed-line, single hook devices. Interestingly, the Barabe and Jackson (2011) study included a field component in coastal rivers of Mississippi within the range of *M. temminckii*. Though using soap as bait was effective in reducing hook-based bycatch, it did not prevent turtle bycatch when used in hoop nets targeting catfish (Cartabiano et al. 2015). Anecdotal reports by anglers in southeastern Oklahoma indicated that *M. temminckii* was not usually attracted by catfish stink baits (Heck 1998), perhaps another possibility for use with angling gear. Use of biodegradable lines in gear preparation could also help with the problem of abandoned and lost gear (Gilman 2016, Kim et al. 2016).

Modeling population viability. Models of turtle population growth have generally found that losing even a small number of reproductive females can have devastating consequences on a population (Congdon et al. 1993, 1994; East et al. 2013; Folt et al. 2016; Midwood et al. 2015; Reed et al. 2002; Thomas et al. 2022). The recent species-status assessments highlight the dire situation with respect to long-term viability of *Macrochelys* species based on current knowledge of the threats they face (USFWS 2020, 2021). A population-viability analysis comparing the effects of additional adult female mortality due to a small-scale commercial fishery in Ontario, Canada, found that all 4 turtle species would experience population declines over a 500-y period from bycatch (Midwood et al. 2015). The Common Snapping Turtle declined most rapidly and was extirpated within 200 y at all levels of additional mortality modeled. We found the rate of ingested hooks in *Macrochelys* (15%) was similar to those used by Steen and Robinson (2017) to model additional mortality due to hook ingestion in 3 species of freshwater turtles, including *M. temminckii*. They combined freshwater turtle hook-ingestion data with data from sea turtles on ingested-hook mortality to model the effect of hook mortality on population size over time; their modeling exercise indicated *Macrochelys* population decline for 3 decades.

Conclusions

The recent species-status assessments for both *Macrochelys* species (USFWS 2020, 2021) identified fishing bycatch and such related threats as hook ingestion and fishing-line entanglement as significant factors affecting the viability of populations. Despite the nature of our data and difficulties in quantifying our compilation, we identify meaningful patterns in the data that elucidate actual and potential impacts of anthropogenic threats for *Macrochelys*.

We identified 9 different threat categories within the IUCN framework (IUCN 2012a), with 3 threats accounting for 96% of the total: (1) fishing bycatch, mainly involving hooking gear (65%, threats 5.4.3 and 5.4.4); (2) persecution (17%, threat 5.4.5); and (3) transportation corridors (14%, threat 4.1). All 3 threats were geographically widespread and involved both *Macrochelys* species. Intentionally trying to harm a *Macrochelys* resulted in the highest mortality rate (53%), followed by fishing bycatch (39%) and transportation corridors (25%). All 3 threats will likely continue without intervention. Although the other 6 threats occur infrequently and are not necessarily fatal, the potential for additive and compounding effects on individuals and populations is of particular concern.

We have 3 broad recommendations, based on lessons learned from sea turtle conservation efforts, to help conserve *Macrochelys* spp.:

(1) We recommend research on bycatch reduction that can serve as the scientific basis for potential regulatory changes. Measures to reduce commercial and recreational bycatch of *Macrochelys* will take significant innovation, regulatory changes, and possible legislative action at the state level. Sea turtle researchers have tried a wide variety of techniques to mitigate bycatch via reduction in the catch rate or reducing mortality once caught (FAO 2010; Reinhardt et al. 2018; Swimmer et al. 2017, 2020). Changes in hook type, size, and bait had significant effects on bycatch rate and hooking locations (Gilman and Huang 2017, Parga et al. 2015). Other research areas may lead to development of net material and fishing lines that biodegrade more readily (Gilman 2016, Kim et al. 2016), which could help alleviate the problem of abandoned and lost fishing gear. There has also been fisheries research on making ingested hooks that pass more easily through the digestive tract and corrode more rapidly when abandoned in the environment (McGrath et al. 2011). Additional research on such techniques will determine which may transfer to the freshwater environment and *Macrochelys*.

(2) We recommend undertaking organized, collaborative data collection on threats affecting *Macrochelys* to more accurately assess their severity and spur mitigation strategies. Educational and training materials for coordinated and consistent data collection of fishing bycatch like those that exist for sea turtles would help determine bycatch rates and mortality rates of various gear types (Belskis et al. 2009, NMFS-SEFSC 2008). We recommend wildlife agencies coordinate the collection of dead *Macrochelys* to conduct standardized necropsies that could provide information on cause of death (Jacobson 1999, Rae and Touloupaki 2020, Stacy et al. 2017), such as done by sea turtle-stranding networks and the corresponding databases that compile records (e.g., Adimey et al. 2014, Howell et al. 2021, Shaver and Teas 1999).

(3) Education campaigns should take advantage of *Macrochelys* as flagship-umbrella species (Carrizo et al. 2017, Kalinkat et al. 2017), focusing on their size and many unique and intriguing physical attributes (Pritchard 1989), as well as their role in the riverine and lacustrine habitats they occupy (Lovich et al. 2018, Pritchard 1989). Changing attitudes and behavior among sportsmen who would shoot or physically assault turtles will take concerted educational and awareness efforts (Dickman 2010, Jacobson et al. 2015, Mittermeier et al. 1992). Similarly, any changes in fishing regulations designed to mitigate persecution or turtle bycatch, including the possibility of changing the legal gear, will take dedicated educational awareness to reach the angling public.

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