CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group

Edited by

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**_Trionyx triunguis_ (Forskål 1775) –
African Softshell Turtle, Nile Softshell Turtle**

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Trionyx triunguis (Forskål 1775) – African Softshell Turtle, Nile Softshell Turtle

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Summary. – The African Softshell Turtle, *Trionyx triunguis* (family Trionychidae), is a large (up to >100 cm straight-line carapace length), fresh- and salt-water tolerant species predominantly found in moderately deep streams, rivers, estuarine systems, and lakes. It is the most widely distributed turtle in Africa, ranging from the mouth of the Nile River system south to Lakes Turkana (Rudolf) and Albert in eastern Africa, and from the Cunene River in northern Namibia to Senegal in western Africa. Additionally, it is found in the western Mediterranean region from the Turkish coastal zone to Israel. African populations are thought to have experienced significant declines in recent decades and Mediterranean populations have been considered Critically Endangered by the IUCN. While there is little published about the habitat preferences and ecology of the species, it appears to prefer medium to large sized rivers and permanent waterbodies with muddy, organic substrates, abundant emergent vegetation, and forested banks. Most accounts of nesting come from Mediterranean populations, where nesting takes place between May and July–August, with hatchling emergence from July to September after an incubation of 54–75 days. Clutch sizes seem to be highly variable between studies, seasons, and countries, with clutch size averages ranging from 23.0–44.7 eggs; up to 66 eggs have been recorded. The near spherical eggs are roughly 30–35 mm in diameter and weigh ~20 g. Most nests are between 20–40 cm deep and laid within 15 m of the water's edge. As seen in all other trionychids, *T. triunguis* does not exhibit temperature-dependent sex determination. Optimal nest temperatures are between 24–33ºC, with around 30ºC producing maximum hatching success. Nest predation seems to be high where nesting has been recorded, with monitor lizards, domestic dogs, weasels, foxes, and jackals reported as the predominant predators. Hatchlings typically measure 40–51 mm SCL and weigh 10–15 g. Double and triple clutching have been noted in the species (though the frequency of multiple clutches remains unknown). Other than high nest predation rates, threats include entanglement in fishing gear, subsistence hunting, targeted hunting for the bushmeat trade, wanton killing, pollution, sand mining, and destruction of nesting beaches and sandbanks. The species is estimated to be Vulnerable and decreasing throughout its range and increased conservation efforts are warranted.

Distribution. – Angola, Benin, Burkina Faso, Cameroon, Central African Republic, Chad, Congo (DRC), Congo (ROC), Egypt (*extirpated*), Equatorial Guinea, Eritrea, Ethiopia, Gabon, Gambia, Ghana, Greece (*vagrant*), Guinea, Guinea-Bissau, Israel, Ivory Coast (Côte d'Ivoire), Kenya, Lebanon, Liberia, Mali, Mauritania (*extirpated*?), Namibia, Niger, Nigeria, Senegal, Sierra Leone, Somalia, South Sudan, Sudan, Syria, Togo, Türkiye (Turkey), Uganda.

Synonymy. – *Testudo triunguis* Forskål 1775, *Amyda triunguis, Trionyx triunguis, Pelodiscus triunguis, Aspidonectes triunguis, Tyrse triunguis, Amyda triunguis triunguis, Testudo striata* Suckow 1798, *Trionyx egyptiacus* Geoffroy Saint-Hilaire 1809a, *Trionyx aegyptiacus* Geoffroy Saint-Hilaire 1809b, *Trionyx (Aspidonectes) aegyptiacus, Testudo nilotica* Shaw and Nodder 1810, *Trionyx niloticus, Tyrse nilotica, Aspidonectes niloticus, Trionyx labiatus* Bell 1835, *Trionyx (Pelodiscus) labiatus, Trionyx mortoni* Hallowell 1844, *Aspidonectes aspilus* Cope 1859, *Gymnopus aspilus, Fordia africana* Gray 1869, *Trionyx triunguis rudolfianus* Deraniyagala 1948.

Subspecies. – None currently recognized.

Status. – IUCN 2025 Red List Status: Vulnerable (VU A4bcd, assessed 2017), Mediterranean Subpopulation: Critically Endangered (CR, assessed 1996); CITES: Appendix II (2017).

Taxonomy. — The African (or Nile) Softshell Turtle was first described as *Testudo triunguis* by Forskål (1775), with the original specimens being from the Nile River itself. When establishing the generic name *Trionyx* for most of the world's softshell turtles at that time, Geoffroy Saint-Hilaire (1809a) renamed the species *Trionyx egyptiacus* and then *T. aegyptiacus* (Geoffroy Saint-Hilaire 1809b). A further synonym, *Testudo nilotica*, was published by Shaw and Nodder (1810). Populations of the species from the lower and upper Nile River were considered to be different species by Gray (1844, 1864, 1869, 1873), calling the former *Tyrse nilotica*, and the latter, from near Khartoum, Sudan, *Fordia africana*. This subdivision was based upon alleged differences in the alveolar surfaces of the jaw and the presence or absence of a slight symphysial ridge. However, Boulenger (1889) concluded that variation in the alveolar surfaces alone did not justify the separate taxa proposed by Gray and placed both in synonymy with *Trionyx triunguis*.

Deraniyagala (1948) reported the species from Ferguson's Gulf in Lake Turkana (northern Kenya) and named the population there *Trionyx triunguis rudolfianus*. The characteristics of the carapace and plastron on which he based this subspecies were not considered distinctive by Wermuth and Mertens (1961), and subsequent authors have not recognized it as a separate taxon. Loveridge and Williams (1957) identified *Trionyx steindachneri* (now *Palea steindachneri*) and *T. sinensis* (now *Pelodiscus sinensis*) as the closest relatives of *T. triunguis*, based on the typically unreduced 8th pleurals and absent carapacial ocelli. Subsequently, Meylan (1987) suggested that *T. triunguis* is the sister species of a set of five other living species that form two groups: *Rafetus swinhoei* and *R. euphraticus* on the one hand, and the three North American *Apalone*

Figure 1. Adult *Trionyx triunguis* from Dalaman, Türkiye. Photo by Oğuz Türkozan.

Figure 2. A juvenile (top) and adult male (bottom) *Trionyx triunguis* kept at the Abidjan Zoo, Côte d'Ivoire (Ivory Coast). Photos by Pearson McGovern.

species on the other. Until Meylan (1987), all trionychine softshells other than *Chitra* and *Pelochelys* were lumped into the genus *Trionyx*. At present, *Trionyx* is considered a monotypic genus.

More recent molecular phylogenies place *Trionyx* as sister to the giant Asian softshell genera *Chitra* and *Pelochelys*, with an estimated divergence between the two groups occurring during the mid- to late Eocene (Engstrom et al. 2004; Le et al. 2014; Thomson et al. 2021). Engstrom et al. (2004) placed these three genera into the PhyloCode crown clade Gigantaestuarochelys, within the subfamily Trionychinae. This clade is sister to a group

Figure 4. A juvenile *Trionyx triunguis* from Niokolo-Koba National Park, Senegal. Photos by Pearson McGovern.

Figure 3. An adult *Trionyx triunguis* from South Sudan. Photo by Luca Luiselli.

containing all descendants of the last common ancestor of *Amyda cartilaginea* and *Apalone ferox* (Engstrom et al. 2004).

Genetic studies of *Trionyx triunguis* using samples from Africa and the Mediterranean have had variable findings. Gidis et al. (2011) and Shanas et al. (2012) found little evidence of genetic divergence among Mediterranean and African populations, although each study only included one specimen from Africa (from Cameroon and Liberia, respectively) in their analyses. Güçlü et al. (2011) used a more extensive dataset of 102 individuals from five countries (Türkiye, Israel, Gabon, Republic of Congo, Ivory Coast) and 13 localities and found a total of nine African and four Mediterranean haplotypes. The authors deemed the mtDNA and nuDNA differences between African and Mediterranean populations to be significant. Güçlü et al. (2011) also found significant support for two separate Management Units (MUs), one in the eastern Mediterranean and the other in western Türkiye. However, African samples presented the highest genetic diversity (Güçlü et al. 2009, 2011). Gaspar et al. (2025) combined

Figure 5. A juvenile *Trionyx triunguis* from near Murchison Falls, Uganda. Photo by Mathias Behangana.

mitochondrial DNA tandem repeat-region profiling with genome-wide SNP data and found moderate levels of genetic differentiation among Israeli populations and evidence of long-term geographic and genetic separation between samples from Israel and Türkiye.

Vernacular Names. — Known local common names (language in parentheses) for *T. triunguis* include: Kifo or Fato (Malinke; changes based on the dialect), Ña (Bambarra), Makhourde or Taw (Pular; changes based on the dialect); Khouo and Pallala (Wolof), Ambok (Bedik), Yey Kurana (Jalunke), Ase (Oueme), Na-meenga or Meenga (Mole Dagbani), Sivri burun, Sinibağasi, or Yahudi Kaplumbağasi (Turkish), Nyiir (Bari). Additionally, Loveridge and Williams (1957) provided a list of local common names from throughout the species' range: Abibi (Alua and Gang from West Nile), Abu geda (Arabic on White Nile), Bekoom (Liberia), Ger (Alva and Gang for any aquatic turtle), Gondo (Catumbela), Kunda (Banziri), Navingo (Bagungu of Bunyoro), Neko (Sango), Terseh, Tirse, Tyrse, Cirse, or Thirse (Arabic; from Anderson, Forskål, Geoffroy Saint-Hilaire, and Burton, respectively), Um diraga ("riverine Arabs"; from Flower).

Description. — *Trionyx triunguis* is a large, dark-colored, often-speckled softshell turtle. In mature specimens, sexual dimorphism is evident only in the morphology of the tail; in males the precloacal part of the tail is significantly longer and wider, and the tail extends well beyond the posterior margin of the carapace (Atatür 1978; Gidis and Kaska 2004). Females may exhibit slightly greater body depths, though this is difficult to detect without measurements (Akçinar 2012).

Straight-line carapace length (SCL) in adults can exceed 100 cm (Anderson 1898; Taskavak and Akçinar 2009) and the species has been reported to weigh as much as 90 kg (Duméril 1861; Boulenger 1889; Ditmars 1933; Ernst and Barbour 1989; Burghardt et al. 1996). Herz and Rudolphi (2006) referred to Löhlein (2001) in mentioning the purported existence of a 120 cm female *T. triunguis* from the Munich Zoo; however, this measurement has been confirmed to have been the total length of the individual, including the carapace, tail, and outstretched neck and head (Eric Diener, in litt. to Taskavak; specimen voucher nr. ZIMS - MIG12-28572607).

Taskavak and Akçinar (2009) reported a 108.4 cm SCL male that was caught by a bottom trawler at a depth of 55 m in Iskenderum Bay, Türkiye, likely the largest specimen ever recorded. Another exceptionally large individual with the following reported measurements was found washed up on a coastal beach in Angola near the mouth of the Congo River: 106 cm curved carapace length (CCL), 55 cm curved bony disc length, and 54 cm curved bony disc width (Klein 2009).

Akçinar (2012), based on 267 individuals (mean CCL = 55.5 cm) caught from Kükürtlü Lake and its surroundings in Dalaman, Türkiye, reported a maximum CCL of 80 cm for a male and 69.5 cm for a female. The maximum male (*n* = 148) and female (*n* = 69) weights from this same population were 35.3 kg and 22.1 kg, respectively (mean adult weight was 13.5 and 15.9 kg for females and males, respectively; Akçinar 2012). Gramentz (1990, 1993, 2005) reported a mean CL, CW, and PL of 59.2 cm (range, 12.1–75.5 cm), 46.0 cm (range, 10.5–56.3 cm), and 40.4 cm (range, 8.9–51.1 cm), respectively, for 19 specimens from Dalyan and Dalaman, Türkiye. Atatür (1978) measured 27 specimens from the same localities and reported an average CL, CW, and PL of 50.5 cm (range, 27.8–65.0 cm), 39.7 cm (22.7–49.8 cm), and 35.0 cm (19.6–44.0 cm), respectively. In a sample of 57 individuals from 32 localities throughout West Africa, Akani et al. (2018) reported a mean SCL of 28.6 cm (range, 10.5–43.0 cm). The average CL, CW, PL, and mass of 10 individuals collected in Gabon by Gramentz (2005) were 47.8 cm (range, 19.2–83.0 cm), 34.6 cm (range, 7.0–59.6 cm), 33.4 cm (range, 13.8–58.1 cm), and 9.4 kg (range, 0.5–33.2 kg; *n* = 9), respectively.

A wild-caught individual at the Abidjan Zoo (Ivory Coast) measured 69 cm SCL, 55 cm maximum carapace width (MCW), and had a 39 cm bony disk in 2022 (McGovern et al., unpubl. data). A smaller individual in the same enclosure weighed 4.93 kg and had the following SCL, MCW, bony disk, and straight plastron length (PL) measurements (cm): 40.7, 30.5, 26.0, 27.6. Three butchered specimens from Senegal had bony disk lengths of 34.4, 29.0, and 26.5 cm with corresponding bony disk widths of 33.3, 26.0, and 24.5 cm (McGovern et al., unpubl. data). Four carcasses found in the Göksu Delta, Türkiye, measured 72, 60, 55, and 32 cm SCL, the latter three had

Figure 6. Eggs and hatchling *Trionyx triunguis* produced at a captive breeding facility in Winter Haven, Florida, USA. Parents were exported from Cameroon from an unknown collection locality. Photos by Joel Garcia.

the following PL measurements: 49, 40, and 23 cm (van der Winden et al. 1994). The largest of 16 individuals taken from Lake Albert by Worthington (1929) weighed 37 kg. Burghardt et al. (1996) reported that a captive male *T. triunguis* with a CL of 15 cm in 1940 had reached a CL of 79.8 cm and weighed 30 kg at the time of its death in 1993 (53+ years old) at the National Zoo, Washington, DC. A male estimated to be at least 33 years old was cared for at the Toronto Zoo (Krause et al. 1999).

Adults have a dark olive-brown to black base color on the carapace, dorsal aspects of the head, neck, and extremities, and the tail; the coloration is lighter in juveniles and subadults. Though sometimes absent on the largest, oldest individuals, immatures and small adults are adorned with yellow, orange, or creamy-white small specks and spots (2–10 mm diameter). Usually, the spots on the limbs are larger and more sparse than those on the carapace, head, and neck. The size of the specks decreases gradually with age and growth, eventually becoming indistinct.

Adults have a pale white plastron, while the ventral surfaces of the head, neck, and the distal parts of the extremities are darkly pigmented. The plastral bones are easily seen beneath the thin skin. Occasionally, an individual with a darkly pigmented venter is encountered, in which case the throat exhibits alternating dark and light transverse bands, the ventral surfaces of the extremities are dark, and a roughly reticulated dark pigmentation is evident on the ventral surface of the carapace margins, plastron, and tail; intermediate individuals also occur.

Dorsal coloration of hatchlings is dark to light brown, overlain by roundish yellow spots of various sizes, which differ from those of the adults by having thin brown-black peripheral rings. Similar spots are present on the lateral parts of the head and neck. Usually, the carapace is circled marginally by a narrow light-yellow band, except in the nuchal region. Juveniles have a fleshy-white venter, while the head and throat are greenish brown, covered with progressively larger light yellow or off-white spots from the tip of the snout to the base of the neck, where the spots become indistinguishable. The plastron and ventral carapace margin frequently have an irregular reticulate pattern, which is rarely retained in adults. Hatchlings have many longitudinal rows of posteriorly directed, blunt-tipped tubercles, approximately one mm in height, over the entire carapace, being particularly dense in the nuchal region. These gradually disappear as the juveniles enter their second or third year of growth. Total SCL, PL, and mass of hatchlings are between 40–54 mm, 29–38 mm, and 8–17 g, respectively (Atatür 1978; Gramentz 1993; Gramentz 2005; Dağgöl and Yilmaz 2023). A projecting proboscis, with the distance from the tip to the orbit being longer than the orbital diameter, is seen in both young and adults (Loveridge and Williams 1957).

Osteology. — The bony carapace of *T. triunguis* lacks a prenuchal bone and marginal ossifications and usually includes seven (rarely 6 or 8) neurals in a continuous series (see Gramentz 2005:22). Alternatively, following the hypothesis that the first discrete neural element is actually the first neural fused to the second (Webb 1962; Gaffney 1979; Meylan 1987), the typical neural count becomes eight. However, Alizarin Red-S preparations of two *T. triunguis* juveniles from Türkiye showed no "preneural" element or subsequent fusing to the first neural (Atatür 1978). There are usually eight (rarely 7) pairs of pleurals, and a prominent nuchal bone, the lateral parts of which overlay the second pair of ribs. In juveniles, a transverse medial fontanelle behind the nuchal gradually closes to form two small, rounded scapular fontanelles; with sexual maturity these too completely disappear (see Gramentz 2005:51). The whole bony carapace surface is heavily pitted and this morphology can be used to easily distinguish *T. triunguis* skeletons from those of sympatric cyclanorbine softshell species. Sutures between the bones of the carapace in adults become characteristically extremely irregular, either wavy or jagged, to the extent that the neural bones, generally identifiable as hexagons throughout most of the series in most softshells, become essentially shapeless.

The plastron exhibits anteromedial, posteromedial, and xiphiplastral fontanelles in juveniles and subadults; the xiphiplastral fontanelle progressively closes with the onset of maturity. Distinct dermal ossifications (plastral callosities), also with pitting, are located on the hyo-hypoplastra and xiphiplastra. These are not in contact medially and develop and enlarge with age. A juvenile (21.7 cm CL) examined by Loveridge and Williams (1957) did not yet present callosities. In old age, a small, fifth callosity sometimes appears on the anterior edge of the entoplastron (fused epiplastra of Williams and McDowell 1952). In adults, the angle formed by the two posterior projections of the entoplastron varies between 81–85°, while in a 4-month-old juvenile it was measured as 96.5° (Atatür 1978).

The skull is depressed and elongate with three posterior projections. The temporal region is highly emarginate posteriorly and the mandible usually lacks a symphysial ridge (only rarely is it slightly ridged). The most salient characteristic of the *T. triunguis* skull is the separation of the pterygoids from the exoccipitals by the basioccipital (Meylan 1987; see also Atatür 1978:fig.11); only rarely do these elements have a common suture.

A shared trait of all trionychines is the presence of 1–10+ round bony elements that compose the epibranchial II of the hyoid apparatus. This trait is even more fixed in the Gigantaestuarochelys clade (*Chitra* + *Pelochelys* + *Trionyx*; Engstrom et al. 2004) that always possess two bony elements, which are partially fused in *Trionyx*. Species in this clade also possess an edge formed by the posterior portion of the cornu branchiale II, however, in the clade containing *Chitra* + *Pelochelys*, those species

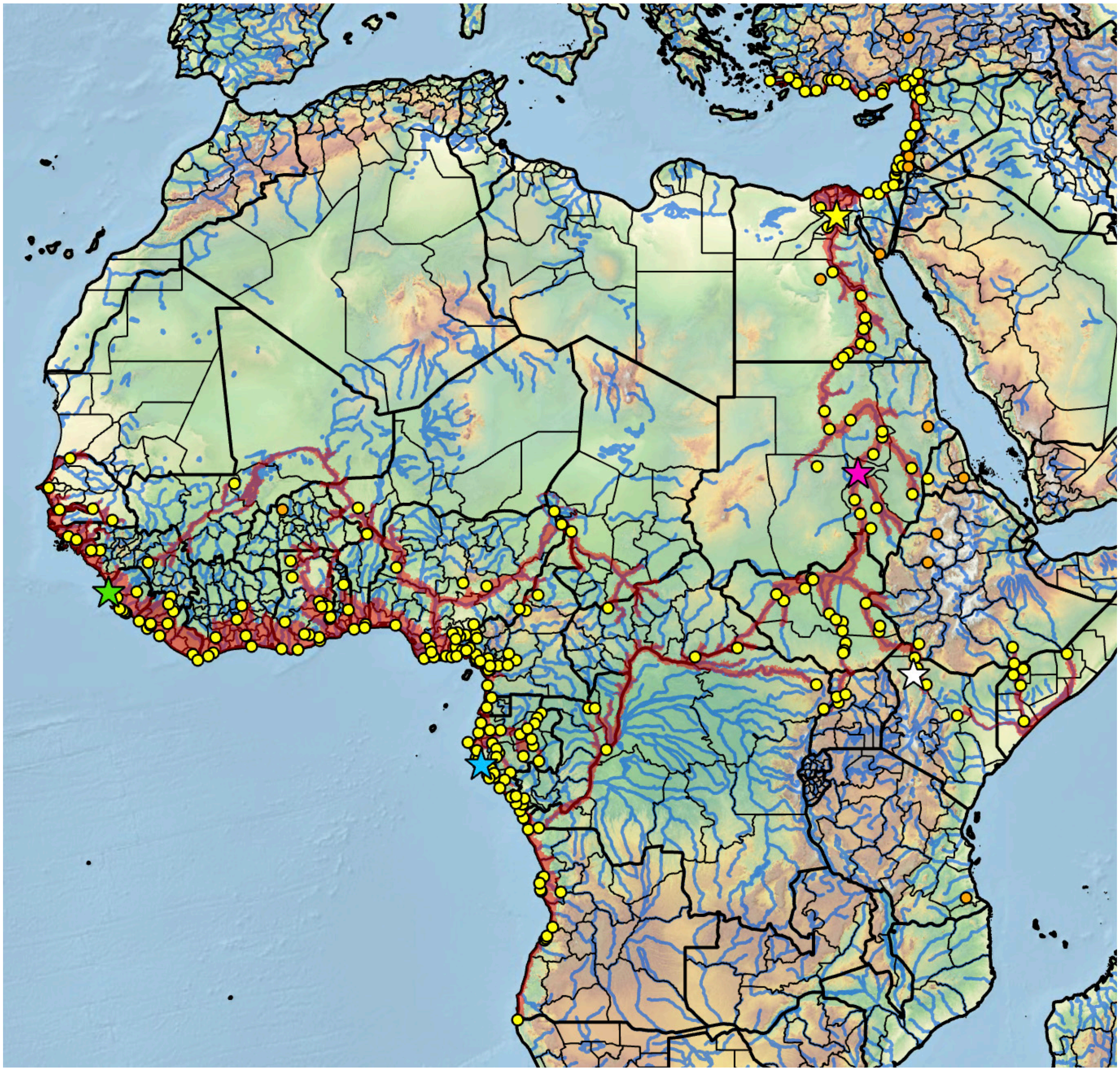

Figure 7. Distribution of *Trionyx triunguis* in Africa and the Mediterranean region. Yellow dots = museum and occurrence records of native population based on literature records (Iverson 1986, 1992; TTWG 2021, 2025); orange dots = probable trade or translocated specimens; stars = type localities (yellow = *Trionyx triunguis* and *Trionyx egyptiacus*, green = *Trionyx labiatus*, blue = *Aspidonectes aspilus*, pink = *Fordia africana*, white = *Trionyx triunguis rudolfianus*). Colored shading = estimated historical indigenous range. Distribution is based on fine-scaled GIS-defined level 12 HUCs (hydrologic unit compartments) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs, based on TTWG (2021, 2025) and adjusted based on data from the authors. Map by Chelonian Research Foundation.

possess a cartilaginous structure that contacts this edge anteriorly and that can be used to differentiate them from *Trionyx*, which do not possess this cartilaginous structure (Jorgewich-Cohen et al. 2024).

Distribution. — The African Softshell Turtle has an extensive range from the eastern Mediterranean to sub-Saharan Africa. In the Mediterranean, it is known from the Turkish coastal zone; including the Dalaman River watershed, Esen Creek, the Antalya-Belek-Manavgat region near Aksu-Acısu, Evrenseki Creek, Köprüçay, Sarısu, Acısu (Kundu), the Göksu River, Tarsus Stream, Anamur, the Berdan River, the Ceyhan (Seyhan) River delta, the Tuzla and Karataş drainage channels, the Asi (Orontes) River, as well as between Güngörmez Shoal and the Tersane-Domuz Islands (Haas 1951; Eiselt 1976; Atatür 1978; Sella 1981; Berk et. al. 1988; Baran and Kasparek 1989; Kasparek and Kinzelbach 1991; Medasset 1999; Kasparek 2001a; ÖÇKB 2010; Yilmaz et al. 2020; Taskavak, unpubl. data). In Hatay province, Türkiye, the species was reportedly also found in Lake Amik, which

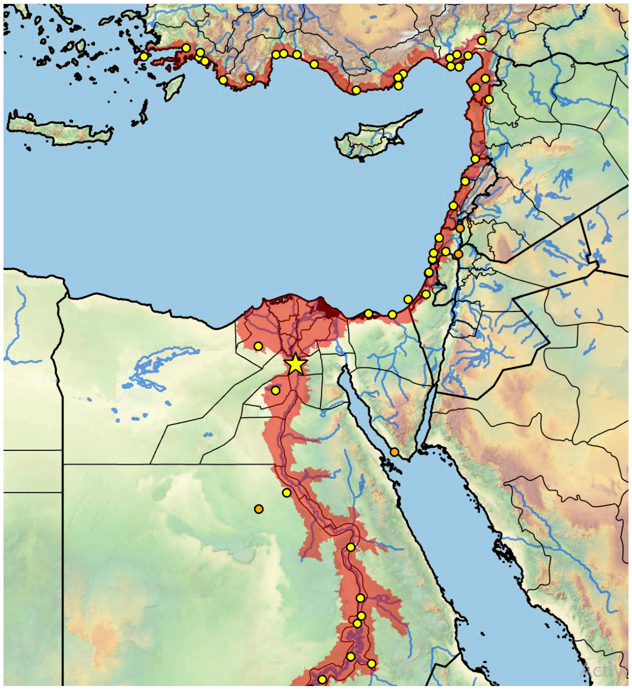

Figure 8. Close-up of distribution of *Trionyx triunguis* in Egypt and the eastern Mediterranean region. Legend as in Fig. 7. Map by Chelonian Research Foundation.

completely dried up at the end of the 1960s (Haas 1951; Sindaco et al. 2000). The westernmost limit in Anatolia is Gökova Bay, based on bones found by Taşkavak and Akçınar (2007).

There are also records from Greece, including Kalymnos, Leros, Rhodes, and Kos (likely vagrant individuals). Fossil material from Greece has been reported by Dimaki (2002), Dimitropoulos and Ioannidis (2002), Corsini-Foka and Masseti (2008), and Avrithis and Georgalis (2024). The Kos specimen represents the westernmost record in the Mediterranean region.

Records exist from Syria (Aidek et al. 2024), Lebanon (recently confirmed, including reports of juveniles by locals, after no sightings since the 1930s; Kasparek 2001a,b; Carlino et al. 2019), and the major streams and rivers draining along the mainland Levantine coast (Boettger 1879; Lortet 1887; Strauch 1890; Siebenrock 1913; Gruvel 1931; Haas 1951; Serruya 1978; Sella 1981; Ilani 1983; Ilani and Shalmon 1984; Yom-Tov and Mendelssohn 1988; Kasparek and Kinzelbach 1991; Taskavak et al. 1999; Oruc 2001; Horwitz 2011; Shanas et al. 2012; Carlino et al. 2019).

In Israel, the most current data suggest the species can still be found in the following rivers/streams: Alexander, Ada-Taninim-Dalia complex, Naaman, Yarkon, Kishon, Sorek, and Hadera (Tikochinski, unpubl. data); an introduced population exists in the Hula Lake area in the Jordan River basin (Bouskila, *in* Dolev and Perevolontsky 2005; Gaspar et al. 2025).

Though present historically, the species seems to have been extirpated from Egypt (Fischer 1968; Baha El Din and Salma 1992; Nada 2002; Horwitz 2011). In Africa the historical range extends throughout the Nile River system, including the lakes in the Wadi el Natrun Valley (Egypt), the White and Blue Nile (Ethiopia, Sudan, and South Sudan), and Lake Turkana (Rudolf) in Kenya and Lake Albert in Uganda. The eastern African range includes Eritrea (Largen 1997; Sindaco and Jeremcenko 2008), Rwanda (Hinkel and Fischer 1988), the Juba and Scebeli rivers in Somalia and the coastal strip of Tanzania (Gray 1856; Anderson 1898; Deraniyagala 1948; Lanza and Sassi 1966; Iverson 1986).

In west and central Africa, the species occurs from the Cunene River at the Angola-Namibia border up through the major river systems of the Democratic Republic of Congo, Republic of Congo, Gabon, Cameroon, Chad, Niger, Nigeria, Benin, Togo, Ghana, Burkina Faso, Mali, Ivory Coast, Liberia, Sierra Leone, Guinea, The Gambia, and Senegal. The northern limit in west Africa was historically the Senegal River between Senegal and Mauritania (Gray 1856; Siebenrock 1913; Gadow 1923, Flower 1933; Lanza and Sassi 1966; Penrith 1971; Iverson 1986; Branch 1988; Griffen and Channing 1991; Luiselli et al. 2000; Maran and Pauwels 2005; Taskavak and Akçinar 2009; Segniagbeto et al. 2014; Akani et al. 2018; Demaya et al. 2019; Luiselli et al. 2020; Gbewaa et al. 2021; Lobon-Rovira et al. 2022; McGovern 2022; Segniagbeto et al. 2022). However, the species is likely now extirpated from the Senegal River, which is the only place it had been recorded in Mauritania (in 1870; Loveridge and Williams 1957).

Marine habits of this species are well established for the Mediterranean basin (Gruvel 1931; Corsini-Foka and Masseti 2008; Taskavak and Akçinar 2009; Akçinar 2012). Individuals have even been documented nesting on marine beaches, including Belek, Burnaz, Dalaman, Dalyan, Göksu, Manavgat, and Tuzla Beaches in Türkiye (Gidiş and Kaska 2004; Türkozan et al. 2006; Candan 2018; Yilmaz, pers. obs.; Taskavak, pers. obs.).

Outside of the Mediterranean, *T. triunguis* has also been found in saltwater habitats in Angola, Gabon, Liberia, Namibia, Nigeria, The Gambia, Togo, and Senegal (Loveridge and Williams 1957; Villiers 1958; Atatür 1978; Carr and Carr 1985; Griffin 2003; Segniagbeto et al. 2014; Akani et al. 2018; T. Diagne, pers. comm.; Luiselli et al., unpubl. data). In coastal West Africa, the species nests along the banks of freshwater wetlands and rivers and is not known to nest on marine beaches.

Prehistorical Distribution. — Fossils of the "*Trionyx triunguis* lineage" have been identified from Europe and Africa by numerous authors (see reviews in DeBroin 2000; Georgalis and Joyce 2017), beginning with Reinach (1900). However, confident assignment to the genus *Trionyx* (sensu stricto; Meylan 1987) is problematic as it requires nearly complete plastral material (Georgalis and Joyce 2017). Although Karl (1999) suggested placing all fossil trionychids from the Tertiary of Europe into *T. triunguis*, Georgalis and Joyce (2017) argued that only those specimens with a complete plastron can be placed confidently in the *T. triunguis* lineage. They suggested that this lineage displays evidence of anagenesis and might be considered a series of chronospecies that eventually led to *T. triunguis*. They did not assign any fossil material from Europe to *Trionyx triunguis*.

De Broin (2000) argued that *Trionyx* sensu stricto is part of a Palearctic fauna that reached Africa only in the Neogene, noting that the *T. triunguis* lineage is present in Europe from the Paleocene but does not appear in North Africa until the Miocene. African fossil and sub-fossil occurrences referred to *T. triunguis* in De Broin (2000) fall within the modern range of the species. These include records from Chad, Egypt, Kenya, Libya, Mali, Niger, Senegal, and Sudan. A skull found near present day Lake Turkana in the Koobi Fora Formation was dated to be between 1–2.5 mya (Wood 1979). Cakirlar et al. (2021), in their review of turtle remains from the ancient eastern Mediterranean (3000 BCE–1200 CE), recovered fossils from three sites (Burak, Kinet, Fadous) along the Levantine coast and mentioned that *T. triunguis* shells may have played a role in Egyptian funerary rituals and that Egyptian slate palletes "mimic the *Trionyx* form."

Habitat and Ecology. — *Trionyx triunguis* prefers large, permanent waterbodies. Ideal habitats include moderate to slow-flowing rivers, streams and still lakes, reservoirs, or forest pools, preferably with sandy to muddy-sandy bottoms, emergent aquatic and woody vegetation, sandy nesting areas, and forested banks (Akani et al. 2018; Gbewaa et al. 2021; Tikochinski, unpubl. data). Young individuals prefer smaller rivers with reedy (e.g., *Phragmites*) or bushy banks, and a high abundance of aquatic vegetation. For example, along the White Nile River, juveniles prefer papyrus-dominated wetlands (Luiselli et al., unpubl. data). In a four-country comparison study, Eniang et al. (2024) found that 70–91% of all juveniles sighted/captured in Liberia and Côte d'Ivoire (Ivory Coast) were from rivers <10 m wide. The authors also found that adults showed clear preference for highly vegetated banks, while juveniles occurred in habitats with high amounts of emergent aquatic vegetation, yet variable types of bank vegetation, allowing them to avoid predation in open waters. Though there were slight inter-country differences in the use of either predominantly bushy vegetation or gallery forest along the banks, all populations in the four countries (Ivory Coast, Liberia, Nigeria, Ghana) preferred muddy substrates, large rivers (with smaller rivers for juveniles in the countries where age-class was recorded), abundant aquatic vegetation, and at least partially vegetated banks (Eniang et al. 2024).

Akani et al. (2018) compared microhabitat use between *Cyclanorbis senegalensis* and *T. triunguis* from 32 localities in West Africa and found that though they were sympatric in a variety of macrohabitats, they differed in their use of all four microhabitat variables recorded in the study. *Trionyx triunguis* used larger, more densely vegetated waterbodies and muddier substrates compared to *C. senegalensis*. Gbewaa et al. (2021) also confirmed the preference of *T. triunguis* for muddy, organic substrates and woody, emergent vegetation in Ghana, which is also where Eniang et al. (2024) found that 57.5% of all encountered individuals were using areas with muddy substrates and 47.1% were seen in areas with what the authors considered abundant aquatic vegetation. All 15 individuals captured or seen by Gbewaa et al. (2021) were found in permanent waterbodies, with 10 being found in forest pools or forested swamps (the other five came from permanent river sites). There is no evidence that this species uses temporary waterbodies that dry seasonally; however, because juveniles have been shown to readily consume anuran eggs, they may make use of these waterbodies during peak annual resource availability.

In Benin, Luiselli et al. (2020) were only able to catch five *T. triunguis* (out of 630 total turtle captures); however, all were found in areas with moderate to high water current speed. Though *T. triunguis* can be found in permanent lakes, ponds, and forested swamps, these habitats (lakes and ponds) are predicted to be less favorable than large rivers based on extirpations in these habitats after an oil spill, presumably a result of reduced fish stocks post-spill (Luiselli et al. 2006), or direct effects of poisoning (Dundee and Rossman 1989).

While *T. triunguis* is active year-round (Atatür 1978), most captures and sightings seem to occur in the wet season in the parts of their range that experience wet and dry seasons (although see Segniagbeto et al. 2022). Though increased water levels would suggest a decreased likelihood of capture for a water-obligate species like *T. triunguis*, the increase in sightings is reflective of their increased movements during the wet season (Gbewaa et al. 2021; Eniang et al. 2024). However, Carlino et al. (2019) noted that locals reported most sightings during low water levels in June–July in Lebanon. Individuals from the breeding populations of Türkiye are primarily diurnal and active year-round (Gidis and Kaska 2004), although some specimens are caught on fishing lines at night.

When undisturbed, adults sometimes bask singly or in groups on banks close to the water. Gramentz (1994) studied the species' thermoregulatory patterns in Kükürt Lake, Dalaman, Türkiye, and found an average basking time of 9.6 min based on 22 observations of the behavior. Girgis (1961) found that *T. triunguis* could remain submerged for up to six hours, aided by pumping water over the pharyngeal area to absorb oxygen from the water. The author suggested this pumping may also serve an olfactory purpose.

Gidis and Kaska (2004) reported a minimum water temperature of 23.3°C between February–September at

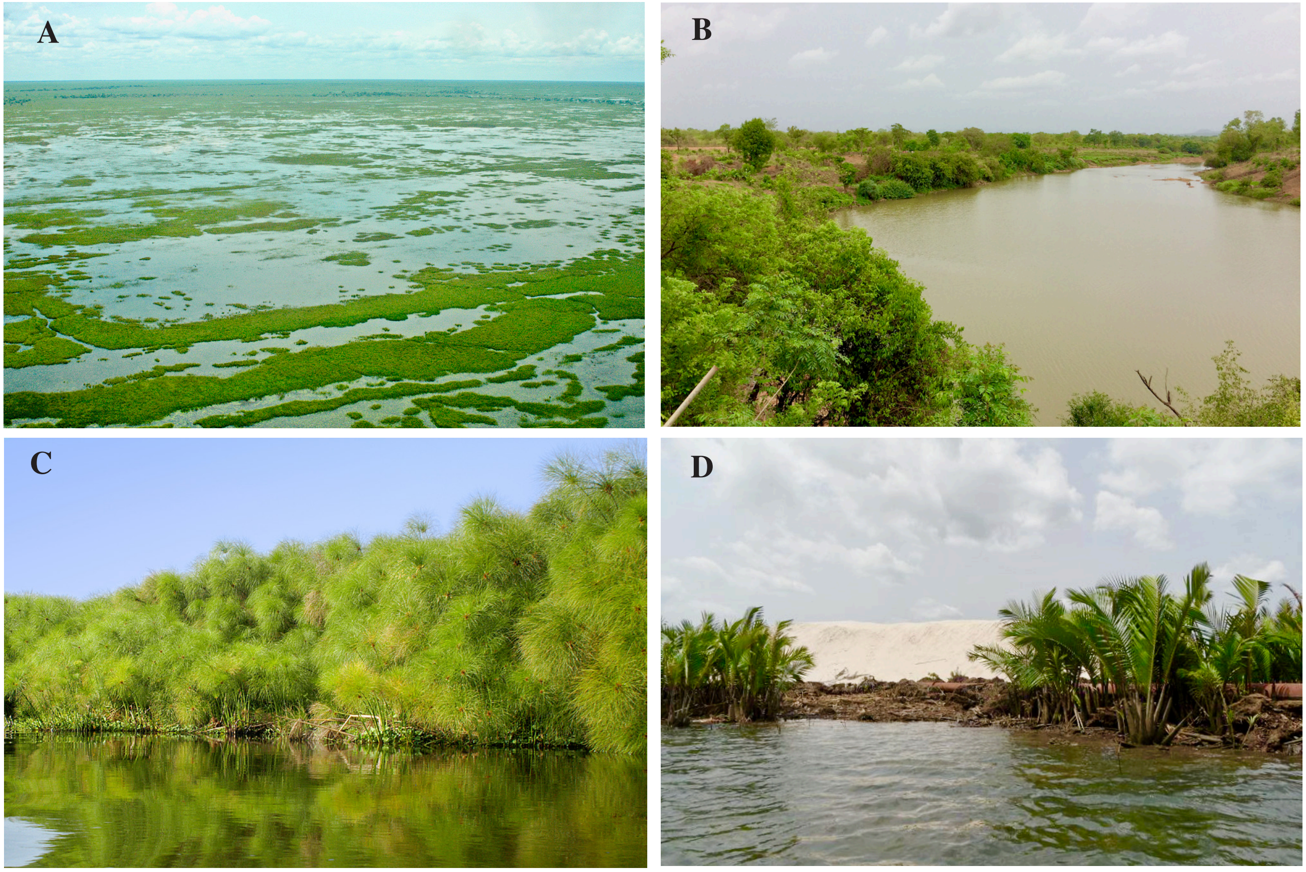

Figure 9. Habitats of *Trionyx triunguis*: **A**) Sudd wetlands, South Sudan: habitat of sympatric *T. triunguis, Cyclanorbis elegans*, and *C. senegalensis*; **B**) Mono River near Adonko, Togo: Guinea savannah habitat supporting *T. triunguis* and *C. senegalensis*, together with *Pelusios castaneus*; **C**) White Nile River near Onigo, northern Uganda: habitat of sympatric *T. triunguis* and *C. elegans*; and **D**) New Calabar River near Port Harcourt, Nigeria: habitat of *T. triunguis*, heavily impacted by oil industry activities and local pollution from oil spills, where it occurs in sympatry with *P. castaneus* and *P. niger*. *Pelomedusa* spp. occur sympatrically in surrounding ephemeral waters in all these habitats. Photos by Luca Luiselli.

Lake Sulphurous in Muğla, Türkiye. In Lakes Kükürt and Kargın, Dalaman, Türkiye, home to one of the largest Mediterraean populations, the maximum depth is between 3.5–4 m (Atatür 1978). In this area, warm, sulphurous waters from several springs keep the yearly aquatic temperature range between 15–28°C, while the pH fluctuates between 6.4–7.25 (Atatür 1978; Akçinar 2012). The banks bordering the lakes and their canal system, which connects the lakes to the Mediterranean Sea and is thus slightly more basic (pH >7.75), are rich in *Arundo donax* and *Juncus acutus*, along with *Myrtus* sp., *Cistus* sp. and *Tamatrix* sp. Similar to the preferred habitats in Africa, the bottom of the lakes have abundant organic detritus with some sand and rocks. Gramentz (2005) reported *T. triunguis* to inhabit waterbodies with pHs ranging from 5.5–8.5.

Other turtle species with which *T. triunguis* has been found sympatrically include *Cyclanorbis senegalensis, C. elegans, Pelusios castaneus, P. niger, P. adansonii, Pelomedusa* spp., *Cycloderma aubryi, Emys orbicularis,* and *Mauremys rivulata* (Luiselli et al. 2004; Herz and Rudolphi 2006; Luiselli et al. 2020; Gbewaa et al. 2021; Luiselli et al., unpubl. data; Taskavak, pers. comm.). In the Mediterranean marine environment, *Trionyx* is also found alongside *Caretta caretta* and *Chelonia mydas*, both in open water and on nesting beaches. Prehistorically, *T. triunguis* may have also been sympatric with *Cycloderma frenatum* in Lake Turkana (Wood 1979; Meylan et al. 1990), but that species no longer occurs that far north.

Diet. — *Trionyx triunguis* is primarily carnivorous, with largely ichthyophagous and molluscivorous habits, and also readily feeds on carrion (Anderson 1898; Worthington 1929; Akani et al. 2001). Cansdale (1955) described the species as entirely carnivorous, primarily feeding on fish, while Villiers (1958) suggested that while fish are the main food source, it also feeds on aquatic insects, mollusks, amphibians, and even birds. Worthington (1929) also observed aquatic insects in the stomach of one dissected individual, finding 10 dragonfly nymphs. Meesen (1952) reported that the population in Lake Albert (now Lake Mobutu Sese Seko) consumed fish, worms, mollusks, and crocodile hatchlings. Krause et al. (1999) reported the following stomach contents: live and dead insects, crustaceans, mollusks, frogs, fish, palm nuts, and dates. Similarly, Tikochinski (unpubl. data) has recorded

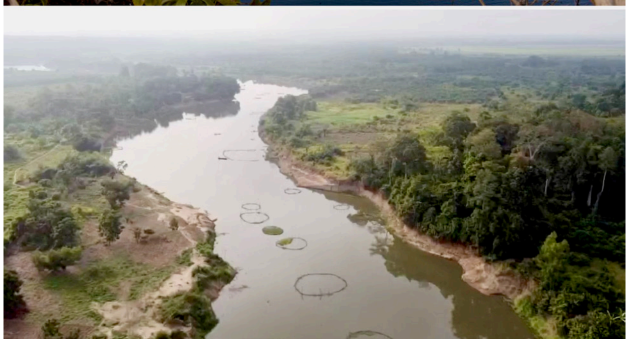

Figure 10. Habitats of *Trionyx triunguis*: The Gambia River, Senegal (top) and the Oueme River, Benin (bottom), both of which are habitat for *Trionyx triunguis*. Circular fish traps can be seen in the bottom photo. Photos by Pearson McGovern.

Figure 11. Two large (>60 cm CL) *Trionyx triunguis* in habitat in Evrenseki Creek, Manavgat, Türkiye. Photo by Ertan Taskavak.

a diet of fish, amphibians, birds, invertebrates, and carrion for individuals from Israel. Maran (2006) reported the following dietary items for *T. triunguis* in Gabon: fish (*Sphyraena piscatorum, Polynemus quadrifilis, Caranx hippos, Chrysichthys maurus, C. nigrodigitatus, Elops lacerta, Lutjanus endecacanthus, L. dentatus, Ethmalosa fimbriata, Pomadasy jubelini, Liza falcipinnis*), fruit, aquatic invertebrates (particularly by juveniles), carrion (birds and mammals), and crabs (including terrestrially). A specimen dissected by Atatür (1978) contained the following stomach contents: *Natrix natrix*, *Gambusia affinis*, *Palaemonetes antennarius*, *Gammarus* sp., *Sphaeroma* sp., *Zostera* sp., and anthozooans. Akçinar et al. (2017) successfully trapped the species in Türkiye using hoop traps baited with chicken and offal.

Akani et al. (2001) analyzed stomach contents from 28 individuals from southern Nigeria and reported a primarily carnivorous diet composed of fish (60.7% of individuals), tadpoles (53.6%), adult anurans (17.9%), Bivalvia (17.9%), Gastropoda (17.9%), Crustacea (10.7%), Insecta (10.7%), *Pelusios* sp. (3.6%), and carrion (32.1%). The authors also observed 20 individuals consuming the carcasses of a goat and a bush pig along the Sombreiro River. More than 14% of individuals also consumed either aquatic plants or fruits/seeds. The same authors also analyzed fecal samples from another 41 individuals and found fruits and seeds (in 14.6% of individuals), aquatic plants (7.3%), Gastropoda (12.2%), Crustacea (26.8%), Insecta (26.8%), fish (80.5%), birds (2.4%), and rodents (4.9%). Luiselli et al. (2004) obtained 14 fecal or gut content samples from southeastern Nigeria and reported Gastropoda, Crustacea, adult anurans (>35% of samples), and tadpoles and fish (both of which were found in >70% of the samples).

McGovern et al. (2025) analyzed fecal samples from 87 individuals from the White Nile in South Sudan and Uganda and found the following contents: aquatic plants, algae (only in adults and unknown if this was consumed indirectly), various invertebrates (Arachnida, Coleoptera, Hymenoptera, Ephemeroptera, Annelida, Gastropoda, Bivalvia, Crustacea), fish, anurans (only in adults), anuran eggs (only in juveniles), tadpoles (only in juveniles), lizards (only in adults), birds (only in adults), and rodents (only in adults).

In Ivory Coast and Liberia during both the dry (October–April) and wet season (May–September; equal sample collection in both seasons), McGovern et al. (2025) documented the same consumed groups, except for arachnids, in a sample of 129 individuals. Nearly the same ontogenetic partitioning of dietary items was found in these two populations as the one from the White Nile, with juveniles consuming smaller, less mobile prey and adults consuming larger prey items as well as some vegetative matter. Other authors have also mentioned herbivorous habits (Rüppell 1835; Büttikofer 1890; Branch 1988; Ernst and Barbour 1989). Loveridge and Williams (1957) reported several individuals congregating under fruiting trees.

Additionally, on the Alexander River in Israel, *T. triunguis* adults are often fed by tourists and >10 individuals can be seen at a time (see https://www.youtube.com/watch?v = b7_3SRO-GzU). *Trionyx triunguis* held at the Therme Maris Health and Spa Resort (Dalaman, Türkiye) are fed chicken by visitors and will often approach when food is being offered (Taskavak, pers. obs.). This practice can also be observed at Kükürtlü Lake in the same region (Taskavak, pers. obs.). Perhaps nowhere is *T. triunguis* more visible to tourists than in Evrenseki Creek, Manavgat, Türkiye, where >70 adult individuals can be fed (most

Table 1. Available nesting data for *Trionyx triunguis* in Türkiye and Israel in the eastern Mediterranean, as well as in Gabon.

Study Comments	Number of Nests	Nest Date Range	Clutch Size Mean; Range	Incubation Duration	Hatch Rate	Distance from Water
Ucar and Ergene 2022	4	June–July	47; 37–57	57 days ($n = 1$)	70.9%	23.77 m
Nests ($n = 6$) a mean distance of 2.44 m from vegetation; hatch rate based on non-depredated nests only ($n = 4$)						
Yilmaz et al. 2020	182	June–July	40.8; NA	NA	34.6%	NA
Hatch rate for 137 transferred nests; hatch rate 0.0% for 72 unprotected nests. Clutch means ranged from 36–44 annually						
Dağgol and Yilmaz 2023	10	June–July	36.6; NA	NA	7.7%	NA
Low hatch rate possibly due to egg manipulation during nest transfer to Akyatan Beach; mean egg size 33.6 mm, mass 21.5 g.						
Leshem et al. 1991	16	NA	40; NA	64.5 days	88.3%	NA
Incubation duration and hatch rate under optimal temperature of 30 °C; mean egg mass 17.8 g.						
Leshem and Dmi'el 1986	3	NA	36; NA	77 days	64–99%	20 m
Distance was only measured for one nest; nests were supplemented with varying amounts of water.						
Gidiş and Kaska 2004	22	May–July	31.2; max 59	56 days	69.0%	7.78 m
20% of eggs lost to predation.						
Candan 2018	12	20 May–25 June	34; 15–52	NA	63.0%	10.5 m
Nests were protected from predators.						
Türkozan et al. 2006	29	1 June–20 Sept.	23; 8–37	56 days	59.2%	6.9 ± 3.5 m
Two nests were protected from predators, all other nests were completely depredated (91% rate).						
Baran et al. 1994	13	June–August	25.3; NA	NA	94.8%	NA
Hatch rate 0.0% for 13 unprotected nests of unknown clutch size.						
Kaska et al. 2017	27	NA	52.1; NA	NA	47.4%	NA
Two nests were protected from predators; 25 unprotected nests all depredated by foxes.						
Katilmiş and Urhan 2007	58	July–Sept.	22.5; NA	NA	64–87%	NA
Only nests not depredated by mammals were considered; at least 30/58 nests were infested by ≥1 invertebrate parasite; hatch rate 64% for infested nests, 87% for non-infested nests.						
Tikochinski, unpubl. data	458	NA	21.7; 7–66	NA	65.2%	NA
All nests from Alexander River, Israel, from 2000–2024; another 55 nests were lost to predators.						
Maran 2006	NA	December–March	38; 26–50	NA	NA	3.5–5 m
All nests from Gabon.						

tourists seem to drop bread and eggs, with the bridge being littered with eggshells each day) and observed from the Schildkrötenbrücke Turtle Bridge. Büttikofer (1890) found nothing but palm nuts in the stomachs of two individuals from Liberia, which he, likely incorrectly, speculated they procured on shore. Interestingly, however, Maran and Pauwels (2005) described *T. triunguis* actively pursuing a crab terrestrially. Pope (1956) seems to be the first to have observed and recorded the species feeding, noting that they swallow their food whole, using their forefeet to manipulate the food.

Reproduction. — Like all trionychids for which the sex determining mechanism is known (Rovatsos et al. 2017), *T. triunguis* almost surely has true genotypic sex determination, not temperature-dependent. No data on age at sexual maturity of males or females are available; however, a male of 31.2 cm SCL had a fully developed penis (Atatür 1978). Maran (2006) speculated that mating is likely violent based on significant scarring on the necks of females. In most studied populations in Türkiye, adult males outnumber adult females (Atatür 1978); however, Akani et al. (2018), based on a sample of 53 sexed individuals from eight countries in West and Central Africa found a sex ratio of 1M:2.12 F (though few individuals were captured at each locality and this ratio may represent a sampling bias).

In Africa, *T. triunguis* uses sand banks and islands in rivers for nesting (Kasparek and Kinzelbach 1991; Luiselli et al., unpubl. data; Meylan, pers. obs.), often specifically using banks along tributaries that drain into larger rivers (i.e., White Nile, South Sudan; Demaya, pers. obs.). In the Mediterranean, sandbanks or dunes restricted to river mouths or adjacent to small lakes and canals or streams are usually utilized.

Nesting seems to occur predominantly at night. Gidis and Kaska (2004) reported nesting between May and July and hatching between July and September in Türkiye. All nests ($n = 12$) reported by Candan (2018) were laid between 20 May and 25 June, and Atatür (1978, 1991) reported hatchling emergence from the beginning of August to the first half of September, depending on weather conditions. Ilani (1983) reported new nests in Israel as late as 18 August.

Leshem et al. (1991) reported optimal nest temperatures between 27–33°C in the lab, with maximum hatching success (88.3%) at 30°C and no embryos surviving incubation at 24°C. Incubation duration ranged from 55–82 days for eggs incubated between 27–33°C, with those incubated at 30°C hatching in 64.5 days on average (Leshem et al. 1991). Natural nests had a mean internal nest temperature of 30°C and varied by 1–3°C daily and by ~1°C based on position in the nest, with deeper eggs experiencing cooler temperatures (Leshem 1989). Hatching rates were highest for eggs losing ≤15% of their initial mass to water loss, with no hatching success with mass loss above 30% (Leshem and Dmi'el 1986). Three nests on Dalaman beach had average nest temperatures of 29.2–33.3°C (Gidis and Kaska 2004). Candan (2018) recorded mean nest temperatures between 30.7–32.7°C. Nests with larger clutches had higher mean temperatures, seemingly a result of metabolic heating (Candan 2018). Gaspar et al. (2025) recorded genetic evidence of double and triple clutching in Israel, as well as sperm storage and multiple paternity based on genetic testing of hatchlings.

Anderson (1898) reported *T. triunguis* to nest in Egypt in April with 50–60 eggs being buried in sandbanks. In Sub-Saharan Africa, the nesting season is dependent on the regional dry season, which in Gabon occurs between December and March (Gramentz 2000; Maran and Pauwels 2005; Maran 2006). Worthington (1929) reported 27 shelled eggs and "possibly 100 more" follicles developing in the ovaries in a female from Butiaba, Uganda. Baker (1867) claimed to have removed "upwards of a hundred eggs" from a female he had hunted. A clutch from Koobi Fora Spit on Lake Turkana, Kenya, hatched on 1 September (Meylan, pers. obs.).

Atatür (1978) speculated that females probably produce several clutches during a season, though the inter-annual nesting frequency and the frequency of multiple clutches is unknown. Atatür (1978) reported three clutches from Türkiye of 8, 14, and 34 hard-shelled spherical to subspherical eggs with diameters of approximately 35 mm. The three nests were built on gently sloping sandy shores 5–20 m from, and 1.0–1.5 m above the water line. Nest cavities were 20–25 cm deep with a rough maximum diameter of 20 cm. Türkozan et al. (2006) found *T. triunguis* to prefer nesting on the slopes of vegetated dunes. Twelve nests from three beaches in southwestern Türkiye were found at an average of 10.5 m from the shoreline (Candan 2018). Gramentz (1993) reported nests up to 20 m from the water's edge, while Maran and Pauwels (2005) found most nests to be between 3.5–5.0 m from shore. Twenty-two nests from Dalaman, Türkiye averaged 7.8 m from the shoreline, 16.75 cm in nest diameter, and 34.47 cm in nest depth (Gidis and Kaska 2004).

Nest depth has been found to be positively correlated with clutch size (Dağgöl and Yilmaz 2023) and probably also with CL. Eggs are deposited in several layers, with thin layers of sand in between (Atatür 1978). Ucar and Ergene (2022) documented four non-depredated nests on Anamur Beach, Türkiye, with a mean clutch size of 47.3 eggs (range, 37–57) and a 70.9% hatch rate (Table 1). Between 2009–2018, Yilmaz et al. (2020) recorded a total of 209 nests (range, 5–55 nests per year) along the Seyhan River, Türkiye, 94% of which were found along a 50 m long sand dune. Over the 10-year period, the authors excavated 182 nests and transferred 137 nests to Akyatan Beach to minimize nest predation; they recorded a mean clutch size of 40.8 eggs amongst all excavated nests (annual mean clutch size range = 36.1–44.7). The 137 relocated nests resulted in a 34.6% hatch rate. Türkozan and Yilmaz (2010) recorded 28 nests with a mean clutch size of 35 eggs during the 2009 nesting season along the Seyhan River. The authors relocated and measured 366 eggs (10 nests); the eggs had a mean diameter of 33.6 mm (range, 30.7–35.3 mm) and mean weight of 21.5 g (range, 16.7–25.1 g). These means for egg diameter and egg weight correspond with reported values for other *T. triunguis* populations (reported mean egg diameter range, 30–36.5 mm; reported mean egg weight range, 17.8–24.8 g; Atatür 1978; Leshem et al. 1991; Gramentz 2005; Maran and Pauwels 2005; Maran 2006). From the 366 relocated eggs, 28 hatchlings emerged (7.7%; Türkozan and Yilmaz 2010). The reduced hatch rates of these excavated and relocated nests are likely a result of egg manipulation during nest relocation.

The mean CL, carapace width, plastron length, and plastron width of the 28 hatchlings were 43.2 mm (range, 40.4–47 mm), 42.2 mm (range, 38.7–46 mm), 33.6 mm (range, 33.1–37.1 mm), and 33.8 mm (range, 29–36.8 mm), respectively. See Table 1 in Türkozan et al. (2006) for additional carapace, plastron, head, and limb measurements for 16 hatchlings from Dalyan, Türkiye.

Leshem et al. (1991) reported a mean clutch size of 40.0 eggs and a mean hatchling weight of 11.83 g (n = 49) from 16 nests along the Alexander River in Israel. Also in Israel, Tikochinski (unpubl. data) has recorded clutch sizes between 7–66 eggs based on 458 nests from eight nest sites between 2000–2024 (Table 1).

Sixteen hatchlings from Dalyan, Türkiye had an average weight of 11.58 g (Türkozan et al. 2006). Sites in Türkiye produced the following average clutch sizes: 31.2 eggs from 22 nests in Dalaman (Gidiş and Kaska, 2004), 23.0 from 29 nests in Dalyan (Türkozan et al. 2006), 32.0 eggs from seven nests in Belek, 29.0 eggs from three nests in the Göksu Delta, and 23.0 eggs from two nests on Burnaz beach (Candan 2018). The 12 nests reported by Candan (2018) had a 36.1 cm average nest depth and a 63% hatching rate after being protected from predators. Kaska et al. (2017) also used nest cages to protect eggs on Dalyan and Dalaman beaches in Türkiye in 2016 and reported a 47.4% hatch rate for protected nests; 25 unprotected nests were all depredated. Based on annual data between 2002–2016, the authors calculated a mean of 30.1 and 36.4 nests per year on Dalaman and Dalyan, respectively. Katilmiş and Urhan (2007) reported 10 and 48 non-depredated *T. triunguis* nests in 2002 and 2003, respectively, from Kükürtlü Lake, Dalaman. At least 30/48 nests were infested with invertebrates and the authors found that hatchling emergence was 64% for infested nests and 87% for nests where no invertebrates were found (Katilmiş and Urhan 2007). Hatch rates for these nests (63%, 47.4%, 87%) compared favorably to those of the aforementioned manipulated and relocated nests (34.6%, 7.7%); however, see Taskavak et al. (2006) where 59.2% of 49 relocated eggs hatched successfully.

Parasites and Epibionts. — Tenebrionids (Coleoptera), muscids (Diptera), hymenopterans, and Oribatida (formerly Cryptostigmata; Acari) are known egg and hatchling parasites of *T. triunguis* in Türkiye (Katilmiş and Urhan 2007). Tenebrionids infested 19/58 (32.8%) of *T. triunguis* nests over two seasons (2002, 2003), damaging 78/1304 (6.0%) eggs. Significantly fewer nests were infested when laid >1 m from the nearest vegetation. Muscid larvae were found in 30/58 (51.7%) nests over the same two seasons, infesting 33 eggs and killing at least 26 hatchlings. Ants (Hymenoptera) were only found in 6/58 (10.3%) nests and only infested eight total eggs. Orobatida were only recorded in 2003 and infested 7/48 (14.5%) nests and 8 total eggs, but the authors counted up to 214 individual mites in a single egg. The authors assumed that the orobatid mites enter through egg pores invisible to the naked eye (Katilmiş and Urhan 2007).

Khalil (1963) removed several *Cucullanus niloticus* nematodes (Baylis 1939; Campana-Rouget 1957) from the gastrointestinal tracts of *T. triunguis* along the White Nile River near Khartoum, Sudan. The trematode parasites *Astiotrema reniferum, A. odhneri*, and *A. sudanensis* have been found in the intestinal tracts of African specimens (Looss 1898; Bhalerao 1936; Khalil 1959). Aisien et al. (2021) listed *Cotylaspis lenoiri* (Aspidogastrea; Cotylaspidinae) as a parasitic trematode flatworm known from *T. triunguis* and *Cyclanorbis senegalensis*.

Populations. — *Trionyx triunguis* was originally widely distributed in the whole Nile system, its terra typica including the upper reaches of the White and Blue Nile Rivers of Sudan and South Sudan down to the river's delta complex and small lakes of the Natrun Valley to the west of the delta (Gray 1856; Boulenger 1889; Anderson 1898; Siebenrock 1913; Flower 1933; Mar 1968). The species has been consumed by people in Egypt since ancient times (Boessneck 1988). Over time, the species has become scarce in the Nile. Flower (1933) was only able to record four individuals along the Nile River, from Kom Ombo (Aswan Province), Giza, and the Ezbet Semada Saleh in the al-Fayum basin. Rzoska (1976) claimed the species to have been extinct in Egypt since the 1930s; however, Sella (1981) and Kinzelbach (1986) both provided evidence of single individuals from Bardawill Lake and Luxor District, respectively. The most recent sightings of the species in Egypt were by Baha El Din and Salama (1992), who reported seven carapaces (two of which were freshly butchered) from the surroundings of Lake Nasser and an individual caught by a fisherman in the Mediterranean off the coast of El-Arish. The fishermen around Lake Nasser were also familiar with the species' habits and nests and eggs (Baha El Din and Salama 1992). By 2002, Nada (2002) found the species was likely extirpated in Egypt after only 2/154 fishermen and fishmongers from throughout the Nile Delta were able to identify the species. Both positive identifications came from fishermen on Bardawill Lake, but neither of the two fishermen had seen the species in 20+ years. However, Nada (2002) did not do interviews at Lake Nasser, which was previously reported to be "the main stronghold" for the species in Egypt (Baha El Din and Salama 1992). Nada (2002) also concluded that this would be the most likely place to find the species possibly surviving in Egypt.

Nearly a century ago, Flower (1933) deemed the species to be rarer in Egypt than in the Sudan, where the human population was less dense. Demaya et al. (2019) reported the species to be "very common" between the Sudd Wetlands in South Sudan and the Ugandan border, with over 100 individuals being caught per year by single villages along this portion of the While Nile. Juveniles were also frequently observed in this area (Demaya et al. 2019). The authors added that the species is most commonly encountered during the rainy season in flooded areas outside of the main river channel. Along the White Nile River in Uganda the species is widespread but uncommon and mostly associated with papyrus areas. Around Murchison Falls and Lake Albert, *T. triunguis* is reportedly easily seen, especially in the highly vegetated marshes (Luiselli and Behangana, unpubl. data).

Further west, in Ghana, only 15 of the 120 turtles caught or seen (in markets or fishermen catches) were *T. triunguis* (Gbewaa et al. 2021). Surveys at 22 localities throughout west and central Africa between 1995–2017, found *T. triunguis* to be "rare" at 9/22 sites and possibly extinct at one site (Akani et al. 2018). The "rare" classification was based on local fishermen reporting that the species was seldom caught and the authors only catching 1–2 individuals at a site during their own sampling. For comparison, *Cyclanorbis senegalensis* was deemed to be rare at just 1/10 sites surveyed by the same authors.

Similarly, Luiselli et al. (2020) found *T. triunguis* to be the rarest of all turtle species captured during a 90 km mega-transect survey in Benin, with only five individuals captured out of 630 total turtle captures at just two of seven localities surveyed. Segniagbeto et al. (2014) reported that *T. triunguis* is virtually unknown in Togo, with country-wide fishermen surveys suggesting the species is "extremely rare." However, more recent surveys in Togo by the same authors confirmed numerous (n = 21) individuals in the Nagbeto Dam reservoir (Segniagbeto et al. 2022).

In Nigeria, the species is widespread in the Niger River, Akwa-Ibom, and Cross River regions; however, it appears to be rare at most sites (Luiselli, Akani, Eniang et al., unpubl. data). In Côte d'Ivoire (Ivory Coast) it is also widespread but generally rare, with seemingly greater densities in the waterbodies on the eastern side of the country than in those in the western districts (Petrozzi et al., unpubl. data).

Kasparek and Kinzelbach (1991) suggested an estimate of fewer than 500 adults for the whole Mediterranean part of the species' range. However, this estimate has subsequently been considered obsolete since further survey data have been made available. Kasparek (2001a) mentioned 15 subpopulations in Türkiye, and Akçinar (2012) marked 267 *T. triunguis* in under two years (124 field days) just in Dalaman, Türkiye. Akçinar (2012) estimated the Dalaman population at 396 ± 36 individuals with a density estimate of 14/ha. The male:female sex ratio was 2.14:1 and 50/267 individuals were juveniles and could not be sexed (<50 cm CL). In addition, the Asi River and the Nahr al-Kabir al-Shamali, both of which flow through Syria and Lebanon, are probably also inhabited by this species (Kasparek and Kinzelbach 1991), but its reproductive status at these sites is not known. Literature on the presence of the species in Nahr al-Kalb and Nahr al-Litani (Leontes) further south in Lebanon is vague (Boettger 1879; Strauch 1890; Gruvel 1931; Haas 1951).

There are various reports of its presence and also nesting in many of the westward-flowing small rivers of Israel (Haas 1951; Sella 1981; Yom-Tov and Mendelssohn 1988). Unpublished data collected by Tikochinski and colleagues between 2006–2024, suggest two primary populations in Israel, one in the Alexander River, averaging 28 nests per year between 2006–2020, and another in the Ada-Taninim-Dalia stream complex, producing 39 nests per year. Additionally, over the same time period, 11 and 7 nests per year were recorded from the banks of the Naaman (including the Ein Afek Nature Reserve) and Yarkon streams, respectively. Fewer than three nests per year were recorded from Kishon, Sorek, and Hadera streams during that same period and these populations are likely made of up of vagrant individuals possibly entering from the sea.

A likely introduced population in the Hula Nature Reserve, Israel, geographically isolated from all other populations, had approximately 50 adult females in 2007; however, due to translocations of both adults and hatchlings to coastal streams since that time, only ~10 nests per year are recorded from the reserve in recent years. As of 2024, Tikochinski et al. (unpubl. data) estimated an approximate area of occupancy of ~384 km^2 for *T. triunguis* in Israel. Gaspar et al. (2025) calculated a breeding population of ≥82 adult individuals (45 females, 37 males) based on genetic samples from three localities in Israel (Alexander, Taninim, and Hula).

Threats to Survival. — In a recent review of turtle research and conservation priorities for all chelonian species found in West Africa, McGovern and Luiselli (2023) calculated *T. triunguis* to be the sixth most threatened species of the 13 whose ranges overlap the region. When data from only West Africa were used in the analysis, *T. triunguis* became the third most threatened species in the region.

Figure 12. Adult *Trionyx triunguis* being butchered for consumption in Uganda. Photo by Mathias Behangana.

Trionyx triunguis is threatened primarily by activities that negatively affect its habitat, such as increased pollution levels in the water and degradation of nesting and basking sites. These include sand mining (west and east Africa) and riverbank degradation (agricultural activities and irrigation practices), habitat loss to urbanization (particularly in the Niger River delta in southern Nigeria), and potentially boat traffic (both commercial and touristic), especially near breeding areas (Kasparek 1994).

In Israel, threats include loss of riverbank nesting habitat, nest and hatchling predation by invasive predators (canids, catfish), water pollution, and to some extent illegal hunting by foreign workers (Tikochinski, unpubl. data). Güçlü et al. (2009) mentioned fishing, pollution, and dam construction as the greatest threats to the species in the Mediterranean.

Of these, the greatest source of mortality for adults in the Mediterranean appears to be bycatch during mid-water and bottom-trawl fishing. Oruc (2001) reported 437 individuals recovered from just 12 trawling boats in the Mediterranean over one year. Venizelos and Kasparek (2006) reported mid-water trawls as a greater threat than bottom trawling. Fisheries-induced mortality also includes accidental capture in fish traps, long-lines, and other fishing nets. Incidentally captured *T. triunguis* are generally killed as a "nuisance" in Türkiye but kept as food or for medicinal purposes when captured in much of their African range, as well as in Syria and, historically, in Egypt (Kasparek and Kinzelbach 1991).

In South Sudan, where *T. triunguis* is sympatric with another large trionychid, *Cyclanorbis elegans*, it seems to be the less sought-after species, though still opportunistically consumed (Demaya et al. 2019). *Trionyx triunguis* was the species most often provided to the authors by local people in Ghana during a country-wide turtle survey. Of all *T. triunguis* seen during the study, 26.7% were received from fishermen (compared to 12.5% for *Pelomedusa* sp., 17.4% for *Pelusios castaneus*, and 21.4% for *C. senegalensis*; Gbewaa et al. 2021). This shows the propensity for this species to be caught as either bycatch or even specifically targeted by fishermen.

Additional threats to *T. triunguis* include egg and hatchling predation. Nest and hatchling predators include ghost crabs (*Ocypode cursor*), red fox (*Vulpes vulpes*), feral dogs (*Canis familiaris*), golden jackals (*Canis aureus*), weasels (*Mustela nivalis*), and pigs (*Sus domesticus*) (Gidis and Kaska 2004; Türkozan et al. 2006; Kaska et al. 2017; Yilmaz et al. 2020; Ucar and Ergene 2022). *Varanus niloticus* and *V. ornatus* have also been observed depredating nests in Gabon, South Sudan, Uganda, and Nigeria (Gramentz 2005; Luiselli et al., unpubl. data). Of 72 non-transferred natural nests reported by Yilmaz et al. (2020) in Türkiye, all were depredated by red foxes and golden jackals. Eight of 12 nests found near Anamur Beach, Türkiye in 2006–2007 were depredated, primarily by canids (Ucar and Ergene 2022). Kaska et al. (2017) reported that 14/23 (60.8%) and 11/29 (37.9%) nests found in 2016 were depredated by foxes on Dalyan and Dalaman beaches, Türkiye, respectively. All but 49 of 577 eggs counted on Dalyan beach by Türkozan et al. (2006) were depredated by foxes. The 49 remaining eggs were relocated in front of the authors' campsite for protection, resulting in 29 emerged hatchlings (Türkozan et al. 2006).

Water pollution in both the Mediterranean and Africa also poses a threat to the species. Pollution is primarily caused by the extensive use of artificial fertilizers and pesticides that then make their way into waterbodies in the Mediterranean region and by oil spills, mining waste, and plastics in Africa. Luiselli et al. (2006) and Luiselli and Akani (2003) found reduced or extirpated *T. triunguis* populations after oil spills in the Niger River delta (Nigeria), with the authors speculating that the reduction in fish stocks due to the spill led to the decline.

No data are yet available on how mining waste and the leaching of associated toxins are affecting populations through direct mortality, potentially decreased hatching rates, and/or altered growth rates. Only one study on heavy metal contamination in *T. triunguis* eggshells is available (Gidis and Kaska 2004). Moderate to heavy anthropogenic pollution is tolerated by adults; however, juveniles are likely much more sensitive (Werner 1991; Kasparek and Kinzelbach 1991). No data are yet available on the possible effects of cold and sediment-poor reservoir outflows on populations below dams.

Although the extent and direct impact of trade have not been assessed, there is domestic as well as some international trade of this species.

Conservation Measures Taken. — *Trionyx triunguis* is protected as an Annex II species in Europe under the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) and was added to Appendix II of CITES in 2017. The species has been assessed as Vulnerable (VU A4bcd) since 2017 on the IUCN Red List for Threatened Species (van Dijk et al. 2017), but should be re-assessed within the next few years. The Mediterranean subpopulation has been listed separately since 1996 on the IUCN Red List as Critically Endangered (CR C2a) (ERASG 1996), but requires reassessment.

The two breeding populations in Türkiye (Lake Koycegiz-Dalyan complex and Kukurt-Kargin Lake system) have been officially under protection since 1991, in that they inhabit "specially protected areas"; however, these sites are partly or entirely open to some degree of tourist activity. This likely constitutes a stress upon the populations, especially during the breeding and nesting seasons (Atatür 1991).

In Israel, roughly 34% of the species' range lies within approved or already declared nature reserves. Additionally, streams within these reserves, namely the Naaman and the Dalia, are also undergoing ecological restoration, including removal of pollutants and improved water flow regimes. In the past five years, Tikochinski et al. (unpubl. data) have been using genetics to monitor populations throughout Israel, and more consistent nest site monitoring has also been a focus in the country in recent years.

In Africa, the species is generally only protected within protected areas, where fishing often still occurs, resulting in bycatch and death of some individuals. In Kenya, an apparently important nesting site, Koobi Fora Spit, is within Koobi Fora National Park. In Senegal, one of only two known localities for the species is located in Niokolo-Koba National Park.

Conservation Measures Proposed. — Detailed surveys are needed to further clarify the turtle's present distribution limits and its population status, especially on the African continent. Additional data on movement patterns, habitat conditions, pollution levels, impact of urbanization, natural predation, and natural and pollution-induced diseases or demographic changes are needed.

Some habitats, or at minimum, nesting areas and vulnerable wetlands, occupied by naturally reproducing populations should be considered for designation as areas of national protection and all activities, including mining, tourism, urbanization, etc., should be monitored and limited according to local laws. Mediterranean populations would benefit from nesting beach and nest site protection (particularly from canid predators) during the breeding season, to increase hatching success and recruitment. Local communities should be engaged and educated about the threatened status of the species and the ecosystem benefits that it provides.

Captive Husbandry. — It is quite easy to maintain hatchlings and juveniles in captivity. They adapt quickly to aquarium life in moderately large tanks with 5–10 cm of sand substrate without vegetation. Effective filtering is needed, and water temperature should not drop below 15–18°C. For egg incubation, Leshem and Dmi'el (1986) found that keeping water loss in eggs to ≤15% of initial egg mass resulted in successful hatching. Hatchlings flourish on *Tubifex* worms. As they grow, they will readily consume *Tubifex*, *Gammarus*, *Asellus*, macerated frog meat, and raw or slightly boiled liver (Atatür 1978).

The lifespan of *T. triunguis* is unknown in the wild; Flower (1937) mentioned a living individual aged ~22 years. The oldest *T. triunguis* reported by Hughes (1986) in his survey of captive African herpetofauna was an individual that had been in captivity for 42 years at the Tel Aviv Zoo and was estimated to be 57 yrs old by Dr. Yom-Tov in 1980 (pers. comm. in Hughes 1986). Biegler (1966) reported 37 yrs as the record longevity for the species, citing a captive individual at London Zoo. A male *T. triunguis* was kept at the National Zoo in Washington D.C. for >50 years (Burghardt et al. 1996). He was kept in a 2.9 m x 3 m tank with a water depth of 88 cm and a water temperature between 24.4–26.7°C and was fed six large (20 cm) goldfish twice per week and a large dead rat once per week. Self-mutilation behavior was observed occasionally; novel items such as rubber hoops, hoses, and basketballs seemed to decrease the urge; however, their novelty faded if left in the enclosure for extended periods (Burghardt et al. 1996).

Current Research. — The Rufford Foundation has supported surveys of *Trionyx triunguis* in both Senegal (confirming the species in the Gambia River within Niokolo-Koba National Park) and Ghana (re-confirming the species from the Offin River) in 2021–2024. The ecology and distribution of the species is currently being studied in Côte d'Ivoire, Togo, Nigeria, South Sudan, and Uganda by Luiselli, Behangana, Eniang, Segniagbeto, Petrozzi, et al., concurrent with ongoing studies of sympatric turtle species. Taskavak and colleagues plan to investigate the *Trionyx triunguis* population where the Manavgat River enters the Mediterranean Sea.

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