Same but different: Intersexual and age-related habitat use of the threatened West African *Trionyx triunguis* clade – a four-country comparative study

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Abstract

Keywords

Introduction

It is widely known that interspecific resource partitioning affects community structuring (e.g., Laliberté et al., 2014; Kent & Sherry, 2020; Nicholson & Clements, 2021). However, intraspecies differences in resource use are seldom studied (Cloyed & Eason, 2017; Giménez et al., 2017; Rehling et al., 2021). These differences, whether ontogenetic or sexual, are especially critical to consider when attempting to conserve all life-stages within a population, a crucial component of any successful conservation initiative (Petrovan and Schmidt, 2019; Knoerr et al. 2022).

Few taxa require this holistic conservation approach as much as chelonians, which begin their life-cylcle as a vulnerable egg, followed by a perilous hatchling and juvenile period characterized by slow growth and incrementally better survival until maturity. Most importantly, these stages occupy both terrestrial and aquatic environments and a wide spectrum of habitats within those systems (Steen et al. 2012). Though turtle life-history is often characterized by eventual high adult survivorship (e.g. Currylow et al., 2011; Cayuela et al., 2019; Garcés-Restrepo et al., 2019; Escoriza et al., 2020), an anthropogenically changed world, where turtles are experiencing habitat loss and degradation, overcollection and consumption, disease, and pollution, is leading to widespread chelonian population collapses (Rhodin et al., 2018; Stanford et al., 2020). In fact, over half of all turtle species are considered Threatened with extinction (CR+EN+VU; Rhodin et al. 2018).

Amongst this threatened group, the softshell turtles in the family Trionychidae represent one of the most threatened clades, with nearly 80% of evaluated species recognized as either CR, EN, or VU by the IUCN (Rhodin et al. 2018). In Africa, a previous assessment of the threat levels for all continental turtle species revealed that all softshell species were to be considered vulnerable to widespread declines, particularly due to their overall large body sizes which make them a valuable and sought after food resource for local communities (Luiselli 2009). One such species, *Trionyx triunguis*, a large species ranging from Senegal to Turkey (TFTSG 2021), is considered VU by the IUCN Redlist (IUCN, 2023). Though this species benefits from a widespread distribution, it is both highly persecuted and little studied throughout its range, with most of the previous work restricted to Mediterranean populations (Akçinar and Taskavak, 2017). The scant data available from west Africa suggests rapidly dwindling populations, with catch-per-unit-effort (CPUE) down by 98% over the past two generations (van Dijk et al. 2017). Additionally, preliminary studies suggest a genetically distinct west African clade, with differences in mDNA and nDNA supporting separate management units between Mediterranean and African populations and genetic differences between central (Gabon, Republic of the Congo) and west African populations (Cote d'Ivoire; Güçlü et al. 2011). If confirmed after increased sampling in west African range countries , these populations will require immense conservation effort to recover this threatened lineage.

Species-habitat relationships are an important topic in the literature given their importance in both ecology and evolutionary biology as well as their influence on the success of conservation actions. Concerning freshwater turtles, studies on species-habitat relationships have focused on nesting habitats (Steen et al., 2012; Micheli-Campbell et al., 2013), basking sites (Vignoli et al., 2015; Pittfield & Burger, 2017), overwintering sites (Markle & Chow-Fraser, 2017; Freeman, 2022), and microhabitat features such as waterbody depth, river width, velocity, vegetation structure, substrate type, etc. (Akani et al., 2018; Luiselli et al., 2020). These studies have begun to decode the variables dictating species habitat use, revealing differences between generalist and specialist species (Riedle et al. 2009) as well as detailing habitat characteristics that are important for certain species (Graves and Anderson 1987; Barko and Briggler 2006). Though the competitive or adaptive reasoning for the partitioning may not always be evident, knowledge of its existence is what ensures that managers can have a focused approach to managing population persistence.

To properly understand ecological distribution patterns and to inform and improve conservation actions for *T. triunguis* in west Africa, we studied their habitat use and intraspecific niche partitioning in four different countries (Liberia, Cote d'Ivoire, Ghana, and Nigeria). No previously published data exist for this species in Liberia and Cote d'Ivoire (except for a mention of *T. triunguis* presence in Taï National Park; Iri et al. 2024), whereas limited data have been published for Nigerian and Ghanaian populations (Akani et al., 2018). In each country, we focused on four independent microhabitat variables (river width, substrate type, bank vegetation, emergent aquatic vegetation) to evaluate their affect on the presence of *T. triunguis* at both the inter-sexual and age-based level. Due to the currently scant data for this species in west Africa and the importance of accurate sex-ratios and demographies in estimating population size and level of conservation need (Otten and Refsnider 2024), we aimed to describe both inter-sexual and inter-age habitat differences that may reveal potential biases or inaccuracies if populations of this species are monitored or modeled without accounting for these differences (Bulté et al. 2008). More specifically, with this study we aim to answer the following key questions:

(1) Do *T. triunguis* preferentially partition available habitat by sex or age? This is particularly interesting given the dramatic ontogenetic change in body size of this species, with hatchlings growing from a few centimeters to over one m in carapace length (Taskavak 2009). Reptiles have been shown to exhibit significant ontogenetic changes in habitat use based on body size (Blouin-Demers et al., 2007; Hyder et al., 2021) and sex (Stevenson et al., 2007; Agha et al., 2018).

(2) Do inter-country populations of *T. triunguis* differ in their habitat preferences? This question allows managers to deliberate whether custom management strategies are needed between populations.

(3) Are inter-sexual and age-class related habitat preferences consistent between different west African populations? This question aims to understand whether *T. triunguis* is homogenous in its habitat use throughout West Africa or whether there is behavioural structuring within this threatened clade.

Materials and methods

Study areas

The field study included data collected in four West African countries (Liberia, Cote d'Ivoire, Ghana and Nigeria). The average distances between sites in Nigeria, Ghana, and Cote d'Ivoire were 192.6, 407.5, and 52.0 km, respectively, and there was only one survey site in Liberia. Average intercountry site distances were; 1,056.4 km between Nigerian and Ghanaian sites, 740 km between Ghanaian sites and the one site in Liberia, 637.8 km between Ghanaian and Ivorian sites, 1,669.0 km between Nigerian sites and the sole Liberian site, 1,560.8 km between Nigerian and Ivorian sites, and 113.5 km between the Ivorian sites and the Liberian site. The survey design was standardized in Liberia and Cote d'Ivoire and opportunistic in Ghana and Nigeria (see below for the methodological details), leading us to separate many of the analyses between these groups of countries. Standardized surveys were carried out at a few coastal localities in the Sassandra region of southwestern Cote d'Ivoire and in the Harper region of Maryland County, Liberia (Figure 1). The study areas are characterized by a subequatorial climate with two rainy seasons, averaging >1800 mm of annual rainfall. The human population, particularly dense along both country's coastlines, is predominantly dedicated to agriculture, fishing, and mining. These extractive activities, which cause deforestation, sand removal, and habitat alteration in the form of dams, fields, and settlements, has lead to an overall degraded landscape surrounding the rivers along the coast. The area can now be characterized as a mosaic of plantations, remnant gallery forest patches, marshlands and fallow fields that become seasonally flooded. Coastal evergreen and swamp forests have been reduced by 94% in the last 45 years, with mangroves and coastal savannah becoming more widespread amidst the agricultural landscape (Mallon et al. 2015).

Opportunistic research was carried out in southeastern Nigeria (at several sites in Akwa-Ibom State) and in Ghana (Mole National Park, Digya National park, Amansuri wetlands and Tano river). The landscape in Akwa-Ibom State (Nigeria) is made up of forest plantations and grasslands, with gallery forest or mangroves along the best preserved rivers (i.e. Stubbs Creek), and with many swamps, marshes and ponds spread across the territory. Ghanaian study sites were somewhat variable. Specifically, in Digya National Park survey sites were largely characterized by muddy substrates with emergent dead woody trees and mostly shrubby shorelines. The amansuri wetlands are a blackwater system with wet evergreen forest vegetation and swamp-forest in low-lying areas. The dominant tree in the swamps are *Raphia vinifera*, while drier patches support mainly sedges and grasses. Mole National Park is predominantly savanna woodland with open areas of grassland in areas with shallow soils and iron pans resulting in rocky river basins along sections of the rivers where sampling was conducted. The Tano river is dominated by sandy-loamy soils with woody vegetation along the banks, and food crops in areas where farm lands have encroached up to the river.

Sampling Protocol

The field study in Cote d'Ivoire and Liberia was carried out during both the wet season (May and June 2015, July 2017) and the dry season (November 2018, November 2019 and November-December 2022), for a total of 57 field days (29 dry season days and 28 wet season days) in each country. In both Cote d'Ivoire and Liberia, we selected sampling sites based on preliminary surveys during a 7-day reconnaissance expedition during the 2014 dry season.

In Nigeria, data was recorded opportunistically between 2014 and 2023 (during both the wet and dry season each year), and in Ghana between 2014-2023 (dry season) and 2017-2023 (wet season). In Nigeria the field effort was similar between seasons (but the precise number of field days was not recorded), whereas in Ghana, field effort was heavily skewed towards the dry season (no inter-seasonal data were analyzed for Ghana). Overall, the field effort (visual surveys and trapping only) for each study site in Ghana was: Digya: 48 days, Mole: 36 days, Amansuri: 24 days, and Tano: 24 days.

On each field day, we started surveys at 07:00 h and ended at 18:30 h. We examined turtles that were captured either by fishers (with the precise point of capture being shown to us after interviews) or using funnel traps, and those that were found in local fishing/bushmeat markets (Figure 2). Additionally, we included turtles spotted during boat surveys and transects along the banks using binoculars to examine the river banks. We constructed traps with non-stretch 2.5 cm fine-mesh to avoid turtles ensnaring their legs. Each trap, approximately 180 cm long, had a hoop diameter of 91.44 cm and had fingered throats. The top of the traps remained above water to allow turtles to breathe if captured (no turtles died during this study). We baited all traps with local fish (catfish, tilapia). The same number of traps (n = 30) was deployed at each site on each day. Ten traps were placed in each of the three aquatic vegetation types (see below) at each site, and the corresponding river width, bank vegetation type and substrate type were recorded for each trap-site. On average, we placed traps 50 m apart. We visited each trap twice a day (around 10:00 h and 17:00 h) and removed all turtles for processing. Turtles that were observed but not captured during the surveys were considered as “sex unknown” in our analyses. We did not individually mark each captured turtle, however, when possible we did take photos of each turtle’s carapace in case of recapture. Though it is unlikely, we cannot guarrantee that the same individual may not have been double counted due to this identification method. We released all individuals unharmed at the point of capture, including individuals that we rescued from fishers and market-places (fishers showed us the capture locations when necessary). Though we did not consider them for this study, we observed and captured several other species of turtle (genera *Pelusios, Pelomedusa* and *Cyclanorbis*) during this study as well.

For each turtle, in each of the four countries of study, we recorded four independent variables at the capture/encounter site to investigate the microhabitats used by this species: (a) river width, (b) substrate type, (c) bank vegetation, and (d) emergent aquatic vegetation (Ficetola et al. 2004; Wyneken et al. 2008; Vignoli et al. 2015; Akani et al. 2018; Luiselli et al. 2020) using the following parameters: (a) We divided river width into four categories (< 5 m, 5.1–10 m, 10.1–15 m, > 15 m) by measuring the width at the capture location using Google Earth. (b) We categorzied substrate type within a 10 × 10 m area surrounding the turtle sighting or capture location into three categories: predominantly rocky, predominantly sandy, or predominantly muddy (Akani et al. 2018). (c) We recorded bank vegetation along the bank of the waterbody where each individual turtle was sighted, and classified it into four categories: bare (no vegetation, often due to overgrazing/trampling), grassy (low grasses with no secondary vegetation), bushy (low lying shrubs and bushes but no trees), and forested (gallery forests). (d) We classified aquatic emergent vegetation into one of the following three categories: no aquatic vegetation (when there was less than 10% of the waters surface was covered by aquatic plants); scarce aquatic vegetation (11-30%), and abundant aquatic vegetation (> 30%). We calculated % aquatic vegetation cover by eye using a 10 m radius from where the turtle was sighted or captured. We also recorded the method of capture/sighting: (i) visual transect, (ii) in funnel-traps, (iii) fishers nets or bushmeat markets, (iv) brought to us by local people.

No animals were injured during this study; when possible, individuals captured by fishers were bought and released unharmed at their point of capture. When the original point of capture was not provided, we did not use that individual in the analyses. Data on individual turtles observed/captured during the reconnaissance surveys in 2014 (Cote d'Ivoire and Liberia) were also not considered in the analyses.

Statistical analyses

Due to a lack of precise field effort data and standardized trapping in Nigeria and Ghana, we separated these countries from the analyses of populations from Liberia and Cote d'Ivoire (although multivariate comparisons were still carried out, see below for more details).

We used expected-versus-observed χ^2 tests to assess whether the adult sex-ratio departed from equality in each of the study areas, and to investigate interseasonal differences in the frequency of sightings/captures (James, 1991). We also used expected-versus-observed χ^2 tests to analyze the frequency differences between countries and among age-classes/sexes (males, females, juveniles) regarding their usage of the various habitat categories, including (i) river width, (ii) substrate type, (iii) bank vegetation type and (iv) amount of emergent aquatic vegetation. For Nigeria, we evaluated the differences in inter-seasonal activity during the ten years of sampling by calculating the difference in the mean number of observed individuals during the wet versus the dry season using a Mann-Whitney U-test (due to the non-normal distribution of the data).

Niche breadths for numerical data, including (i) river width, (ii) substrate type, (iii) bank vegetation type, and (iv) emergent aquatic vegetation were calculated using Simpson's (1949) measure of niche breadth. This index assumes that increasing values suggest increased ecological generalism along each ecological niche axis. Niche breadth analysis was only performed for data from Liberia and Cote d'Ivoire, as the lack of standardization (for instance, uneven field effort between seasons) may introduce biases in these calculations for Ghana and Nigeria. In order to evaluate microhabitat similarities amongst *T. triunguis* individuals among the four countries, we performed two sets of multivariate analyses. Firstly, to ordinate the main habitat factors (for each of the four microhabitat categories) for the sparse data matrices of the species in the four countries, we carried out a Detrended Correspondence Analysis (DCA, Hill & Gauch, 1980) that typified the arrangment of each turtle population (Ghana, Nigeria, Cote d'Ivoire and Liberia) across the gradients in each microhabitat category. For this DCA, we used the log-transformed frequency of occurrence of each population in each microhabitat category. Second, we carried out a UPGMA analysis (with Euclidean similarity index and 40 bootstraps for tree branching) to ordinate the various turtle populations in relation to their dissimilarity in terms of microhabitat type (Podani & Schmera, 2006). In this case, we used the log-transformed frequencies of occurrence recorded in the field for each population in each microhabitat category. All statistical analyses were carried out with PAST 4.16 software, with alpha being set at 5%.

Results

Sourcing

Overall, our study is based on 793 turtles observed in the four study countries. There was a remarkable heterogeneity in the frequency of the individuals coming from the various capture sources in each country (χ^2=354.7, df = 12, P < 0.0001) (Online Supplementary Table S1). When standardized field surveys were carried out, most of the recorded individuals came from fishers (45.4% of individuals in Cote d'Ivoire and 43.3% in Liberia) and traps (37.3% of individuals in Cote d'Ivoire and 33.6% in Liberia), with few individuals seen during transects (we also found individuals being kept as pets in certain villages; Online Supplementary Table S1). There was no significant difference between these two countries in terms of percent of individuals obtained through the various methods (χ^2=2.9, df = 3, P = 0.491). For the opportunistic field surveys, most individuals were seen during either visual transects (Ghana) or in fisher's daily catches and markets (Nigeria).

Sample size, sex ratios and inter-seasonal activity intensity

Liberia

We recorded 104 individuals in Liberia. Adult sex-ratio was skewed towards males (1.76:1; χ^2= 22.9, df = 6, P < 0.001) (Table 1). Season played a significant role in the frequency of captures/sightings, with nearly two-thirds of our captures occuring during the wet season (68 versus 36; χ^2=9.8, df = 1, P < 0.01).

Cote d'Ivoire

We recorded 110 individuals in Cote d'Ivoire, and again the adult sex-ratio was skewed towards males (1.28:1; χ^2= 18, df = 6, P < 0.001) (Table 1). We recorded 41 individuals during the dry season and 69 during the wet season, with the frequency of recorded individuals also significantly higher during the wet season (χ^2=7.1, df = 1, P < 0.01).

Ghana

From Ghana, we recorded 56 individuals during the dry season and 31 during the wet season (differences between seasons were not computed because of uneven field effort, most of which occurred in the dry season; Online Supplementary Table S2). Though we did not record sex for individuals seen/captured in Ghana, adults significantly exceeded juveniles in our sample (χ^2= 29, df = 1, P < 0.01). The number of adults significantly exceeded juveniles during both the dry (χ^2= 10.3, df = 1, P < 0.01) and wet season (χ^2= 6, df = 1, P < 0.05).

Nigeria

Of the 492 individuals we observed in Nigeria, 302 were sexed. In this sample, we recorded 200 males and 102 females, showing a significant male-biased sex-ratio (χ^2= 31.8, df = 1, P < 0.0001). We also saw significantly higher activity during the wet season amongst the Nigerian population, with the mean number of sighted individuals per year (n = 10 years of sampling) being 31.7 ± 12.6 during the average wet season and 17.5 ± 5.8 during the average dry season (Mann-Whitney U-test, U = 7.5, z = 3.518, P < 0.0001).

Overall, our results were consistent across countries, showing that (i) males were more abundant (or more capture prone) than females and that (ii) activity, or the frequency of sightings, is more intense during the wet season.

Microhabitat analyses

Liberia and Cote d'Ivoire

We analyzed these two countries together because the sampling methodology applied in each country was identical and thus the results were directly comparable without any statistical adjustment. In both countries, *T. triunguis* preferred large rivers, with no statistical difference between Cote d'Ivoire and Liberia (χ^2=0.08, df = 1, P = 0.994). However, there were slight inter-country differences; in Cote d'Ivoire turtles were most often sighted in rivers >15 m wide, whereas in Liberia, rivers with a width between 10.1-15 m were the mostly commonly used (Fig. 3a). Further examining the use of various river widths by sex and age, we found that there were significant differences between juveniles and adults in both Cote d'Ivoire (χ^2=18, df = 6, P < 0.01) and Liberia (χ^2= 22.9, df = 6, P < 0.001) with adults preferring wider rivers and juveniles using rivers in the <5 m or 5.1-10 m categories (70% of juvenile sightings in Cote d'Ivoire and 91.7% of juvenile sightings in Liberia were in these two categories; Fig. 4a). In terms of river width niche breadth, populations from the two countries differed considerably. In Cote d'Ivoire, the juveniles were slightly more generalist (B = 1.85) than both females (B = 1.54) and males (B = 1.39), which was the opposite of what we found in Liberia, where juveniles (B = 1.67) were much less generalist than both adult sexes (males B = 3.01; females B = 3.41). Overall, we saw greater generalism in regard to river width in the Liberian population.

Trionyx triunguis in both countries used muddy substrates most often (Fig. 3b), with no detectable differences between juveniles, males, or females (Fig. 4b), or between countries (Table 2). In terms of substrate type, in Cote d'Ivoire the niche breadth values were similar among males (B = 1.63), females (B = 1.46) and juveniles (B = 1.72), however, in Liberia, the males (B = 2.1) appeared more generalist than both females (B = 1.73) and juveniles (B = 1.6).

The two populations differed in their bank vegetation preferences, with individuals in Cote d'Ivoire being found more frequently in areas with gallery forest along the banks versus bushy vegetation, which was used more often in Liberia (χ^2 = 6.02, df= 2, P < 0.05). Both groups tended to avoid baren or grassy bank vegetation areas (Fig. 3c). In Cote d'Ivoire, there were no differences between the sexes or age classes in bank vegetation use (χ^2 = 4.37, df= 2, P = 0.11), with a clear preference for forested and bushy banks by all ages and sexes. However, in Liberia these differences were highly significant (χ^2 = 6.02, df= 2, P < 0.05), with juveniles differing from both males and females (χ^2 = 75.7, df= 3, P < 0.0001) in showing little preference for any particular bank vegetation type while both adult sexes showed clear preference for forested and bushy banks (Fig. 4c). Concerning the niche breadth estimates for bank vegetation type, in Cote d'Ivoire, males exhibited a lower level of generalism than females and juveniles (males B = 1.46; females B = 2.03; juveniles B = 1.92), and in Liberia, juveniles were more generalist (B = 4.32) than males (B = 3.57) and especially females (B = 2.86). Interestingly, the Liberian population overall showed greater levels of generalism when compared to the Ivorian population, as seen for the river-width niche.

The two populations were similar in their usage of abundant emergent vegetation (Fig. 3d), with no significant differences between Cote d'Ivoire and Liberia (χ^2 = 5.2, df= 2, P = 0.073). In Cote d'Ivoire, there was no difference between the sexes in regard to emergent vegetation use (χ^2 = 1.11, df= 2, P = 0.57), with a clear preference for abundant emergent vegetation (χ^2 = 28.2, df= 2, P < 0.0001) (Fig. 4d). Adults did however differ significantly from juveniles (χ^2 = 9.7, df= 2, P < 0.01), being much more generalist than the juveniles, which were only found at sites with abundant emergent vegetation. In Liberia, there was also no difference between males and females (χ^2 = 0.6, df= 2, P = 0.74), but there was a significant difference between adults (after pooling males and females) and juveniles (χ^2 = 5.97, df= 2, P < 0.05; Figure 4d; Table 3). Based on the emergent vegetation niche breadth, juveniles (B = 1.00) were clearly less generalist than both males (B = 2.32) and females (B = 2.68) in Cote d'Ivoire and in Liberia (juvenile B = 1.60; male B = 2.89; female B = 2.75). Overall, there were no differences between Ivorian and Liberian populations in terms of microhabitat niche generalism along the emergent vegetation niche axis.

Ghana

In terms of river width, there were statistically significant differences in the frequency of use among the four categories (χ^2= 60, df = 3, P < 0.0001): 57.5% of the individuals (total n = 87) were found in rivers >15 m, 24.1% in rivers of 5.1-10 m, and 18.4% in rivers <5 m wide. Most specimens (n = 50 out of 87) were found in muddy substrates, 16 in sandy substrates and 21 in rocky substrates (χ^2= 27, df = 2, P < 0.0001). Ghanaian individuals significantly (χ^2= 67.8, df = 3, P < 0.0001) preferred bushy banks (57.5% of the observed individuals) compared to grassy (32.2%) and forested banks (10.3%), and significantly preferred (χ^2= 9.6, df = 2, P < 0.05) areas with abundant emergent vegetation (47.1% of the recorded individuals) over those with scarce (28.7%) or no (24.1%) aquatic vegetation.

Nigeria

In terms of river width use, the Nigerian population did not show any sexual, age-based or seasonal differences (in all cases P ≥ 0.15; χ^2 test), with the overall population exhibiting a statistical preference for rivers >15 m and secondarily rivers between 10.1-15 m wide (χ^2= 44.3, df = 3, P < 0.0001; Figure 5a). The vast majority of individuals were found using muddy substrates (n = 423 out of 492; 86%), with only a few using sandy substrates and none using rocky substrates (χ^2= 628.1, df = 2, P < 0.0001). Again, we found no difference between the sexes, or based on age or season (in all cases P ≥ 0.33; χ^2 test; Figure 5b). Error bars indicated very little variation in the observed pattern (Figure 5b). We found a clear use of either forested

(50%) or bushy (33%) bank vegetation types in Nigeria (χ^2= 270.7, df = 3, P < 0.0001), with no statistically significant difference between seasons, sexes and age classes (in all cases P ≥ 0.221; χ^2 test). Seventy-five percent of all individuals observed in Nigeria were seen in areas with abundant emergent aquatic vegetation (χ^2= 384.4, df = 2, P < 0.0001), irrespective of age or sex (in all cases P ≥ 0.441; χ^2 test; Figure 5d). Error bars again indicated very little variation in the observed pattern (Figure 5d).

Multivariate analyses

A DCA (eigenvalue 1 = 0.0464, eigenvalue 2 = 0.0037) showed that all populations of *T. triunguis* were positioned similarly in the multivariate space in relation to the gradients of the various microhabitat categories (Figure 6). A UPGMA revealed that turtle populations from Cote d'Ivoire and Nigeria were most similar to eachother in terms of microhabitat use, with Liberia and especially Ghana being less similar (Figure 7).

Discussion

Overall habitat use by *T. triunguis* in this study was similar to that found for the species in a previous, multi-species study spanning eight countries (including Ghana and Nigeria) in West Africa (Akani et al. 2018) as well as in Togo near the Nangbeto reservoir (a lake habitat with muddy substrates, forested/bushy banks, and high amounts of emergent aquatic vegetation; Segniagbeto et al., 2022) and in The Gambia River in southeastern Senegal near Niokolo-Koba National Park (McGovern et al. unpub. data). All studies found *T. triunguis* to have a preference for larger rivers with muddy substrates, highly-vegetated banks, and abundant emergent aquatic vegetation, although data from Senegal is based on only five individual sightings due to the extreme rarity of the species in this country (individuals also seemed to inhabit areas with abundant rocks and underwater caves). It is speculated that this species was once more widespread in Senegal based on fisher interviews, however, rampant consumption of both targeted and opportunistically harvested individuals greatly depleted populations and has restricted remaining individuals to remote and semi-protected parts of the country (McGovern at al. unpub. data). The lack of data precludes our ability to ascertain whether current habitat use represents historic norms in this country, but we felt it important to highlight the plight this species is experiencing in parts of its range. Within the broader habitat preferences found amongst this and previous studies, we also found inter-country differences for both river width and bank vegetation type, with the Ivorian population using slighlty larger rivers and more vegetated banks (gallery forest) compared to individuals seen in Liberia (bushy (dense) banks used equally to forested banks) and Ghana (bushy banks followed by grassy banks and then forested banks). Our Nigerian sample revealed roughly equal use of 10.1-15 m and >15 m wide rivers and the majority of Ghanaian individuals used rivers >15 m wide.

Though we noticed overall preference of the above-mentioned habitat characteristics with slight country differences, we consider *T. triunguis* to have a wide tolerance in terms of the studied macro-habitat variables, with individuals seen/caught in rivers of all sizes, with all substrate types, and with nearly all levels of bank vegetation with the exception of completely bare banks. We also found *T. triunguis* to be active during both seasons, though activity was clearly increased during the wet season, with roughly two-thirds of all captures in each country occuring during this period despite nearly identical sampling effort (particularly in Liberia and Cote d'Ivoire) and trapping of perenial waterbodies. One possible explanation for the wide tolerance of habitats seen in this study, where all age-classes were sampled, may be a result of inter-age habitat partitioning. We found that juveniles were both more likely to use smaller rivers and be more generalist when considering bank vegetation type. Whether this is a result of competition with larger individuals, proximity to hatching sites, or an ecological preference (dietary, thermoregulatory, predator avoidance) is unknown, but it is clear that to monitor the juvenile age-class of this species, researchers must expand their surveys to include areas that may be considered less suitable when looking only for adult individuals. Our data also revealed the importance of trapping and fisher surveys/collaboration as methods for capturing elusive, seldom-basking species such as *T. triunguis*; 77.6% of all sightings/captures in this study resulted from these techniques.

Previous studies on sympatric softshell turtles have found habitat partitioning based on river depth and channel size, as well as water visibility and velocity (Barko and Briggler, 2006). Though we did not measure water depth, visibilty, or velocity in this study, it is possible that juvenile *T. triunguis* used smaller rivers and tributaries based on these variables, with larger individuals being better suited to cope with deeper, faster, or more turbid waters. However, disjunct populations of the same species may also differ in their habitat preferences, for example, False Map Turtles (*Graptemys pseudogeographica*) in the Middle Mississippi River were found to prefer shallow, slow-moving waters (Braun and Phelps 2016) whereas in the Tennessee River they were more often found in deeper, higher velocity waters (Lindeman 2000). These inter-population differences may point to the habitat generalism of some species or some populations. We found varying degrees of generalism across niche breadths and between countries, sexes, and ages for *T. triunguis*. Except for the emergent vegetation niche axis where we saw nearly identical levels of generalism between Ivorian and Liberian populations, the Liberian population in this study exhibited significantly higher levels of habitat generalism compared to individuals from Cote d'Ivoire. Though investigation of possible explanations for the increased generalism of the Liberian population was outside the scope of this study, possibilities include, a greater diversity of available habitats, higher *T. triunguis* abundance and competition (though we captured/sighted more individuals in Cote d'Ivoire), or lower food availability within any one micro-habitat (Berry, 1975; James, 1991), requiring individuals to expand into all available niches in search of resources. Interestingly, juveniles in both countries were found to be much more generalist in regards to river width and much less generalist along the emergent vegetation niche axis. It is possible that emergent aquatic vegetation may be acting as a predator buffer while also providing a reliable food source (small fish and invertebrates using the vegetation as cover and food) for younger, smaller individuals, whereas larger *T. triunguis* are less wary of predation and more reliant on larger rivers to provide the dietary resources they require. This in turn may be restricting adults to mostly larger rivers, but also allowing them to be more generalist in relation to the amount of emergent aquatic vegetation present. This is paricularly plausible given that softshell turtle prey type and size depend largely on the individuals relative body size (Pritchard 2001).

To better conserve a species, in-depth knowledge of space use and habitat requirements are paramount. However, there is a bias in the availability of species-habitat relationship data in the literature, with much of the data pertaining to common, North American or European species (e.g., *Chelydra serpentina*, Aresco and Gunzburger 2007, Lescher 2013; *G. Pseudogeographica*, DonnerWright et al. 1999, Lindeman 2000; *Trachemys scripta*, Braun and Phelps 2016; *Emys orbicularis*, Ficetola et al., 2004; Cadi et al., 2008; Vignoli et al. 2015; Luiselli, 2017; and *Mauremys* sp., Chelazzi et al., 2007), though recent studies are expanding outside of these regions (e.g. *Mauremys reevesii*, Bu et al., 2023). Though these studies have uncovered critically important habitat features that may dictate the presence or abundance of certain species, and while certain generalities may hold true across many turtle taxa, we must study each species to ensure that proper conservation measures are being enacted to safeguard each species long-term. These studies are especially pressing in areas where species are being exploited and habitats are being altered, both of which are occuring in all countries in this study. The four countries in the study are all experiencing >2% annual population growth and have each lost enough forest to cover at least 3% of their total land area since 2000 (with Nigeria and Ghana down to <25% forest cover and Cote d'Ivoire below 10%; data.worldbank.org). Sand mining continues to be a pervasive threat, with both nesting beaches and overall river ecology being disturbed by this extractive practice (Luiselli et al. 2024). Softshell turtles are also prized for their meat, rarely being released when captured by opportunistic fishermen (Luiselli et al. 2024). Perhaps most importantly, low levels of enforcement and weakly monitored protected areas have left *T. triunguis*, amongst other species, vulnerable to exploitation even in areas where they should be safest. Education in communities living alongside large rivers where this species may be encountered may be particularly vital. It is our hope that more precise microhabitat data and enhanced environmental education will allow researchers and enforcement teams to better monitor for this species and local communities to better manage and admire their local wildlife.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest or competing interests.

DATA AVAILABILITY STATEMENT

Data for this study are available from the authors upon reasonable request.

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Table 1. Total captures/sightings by sex for *Trionyx triunguis* in Cote d'Ivoire and Liberia between 2015-2022.

	Ivory Coast	Liberia
Males	41	44
Females	32	25
Juveniles	10	12
Adults of unknown sex	27	23
TOTAL	110	104

Table 2. Intersexual and age-based differences in substrate type used by *Trionyx triunguis* in Cote d'Ivoire and Liberia.

Inter-country comparisons		df:	P-value
χ^2	4.7676	2	0.092
Monte Carlo P-value	0.089		
Sex and age comparisons			
Cote d'Ivoire			
χ^2	0.36012	2	0.835
Monte Carlo P-value	0.902		
Liberia			
χ^2	3.2245	4	0.521
Monte Carlo P-value	0.531		

Table 3. Summary of microhabitat use differences among known male (m), female (f), and juvenile (j) *Trionyx triunguis* in three of the four studied countries. Sex was not recorded for *T. triunguis* in Ghana.

Microhabitat variable	Cote d'Ivoire	Liberia	Nigeria
River width	m≠f≠j	m≠f≠j	m=f=j
Substrate type	m=f=j	m=f=j	m=f=j
Bank vegetation	m=f=j	m=f≠j	m=f=j
Emergent vegetation %	m=f≠j	m=f≠j	m=f=j

Figure 1. Map of the Gulf of Guinea, showing the study areas in Nigeria, Ghana, Cote d'Ivoire and Liberia.

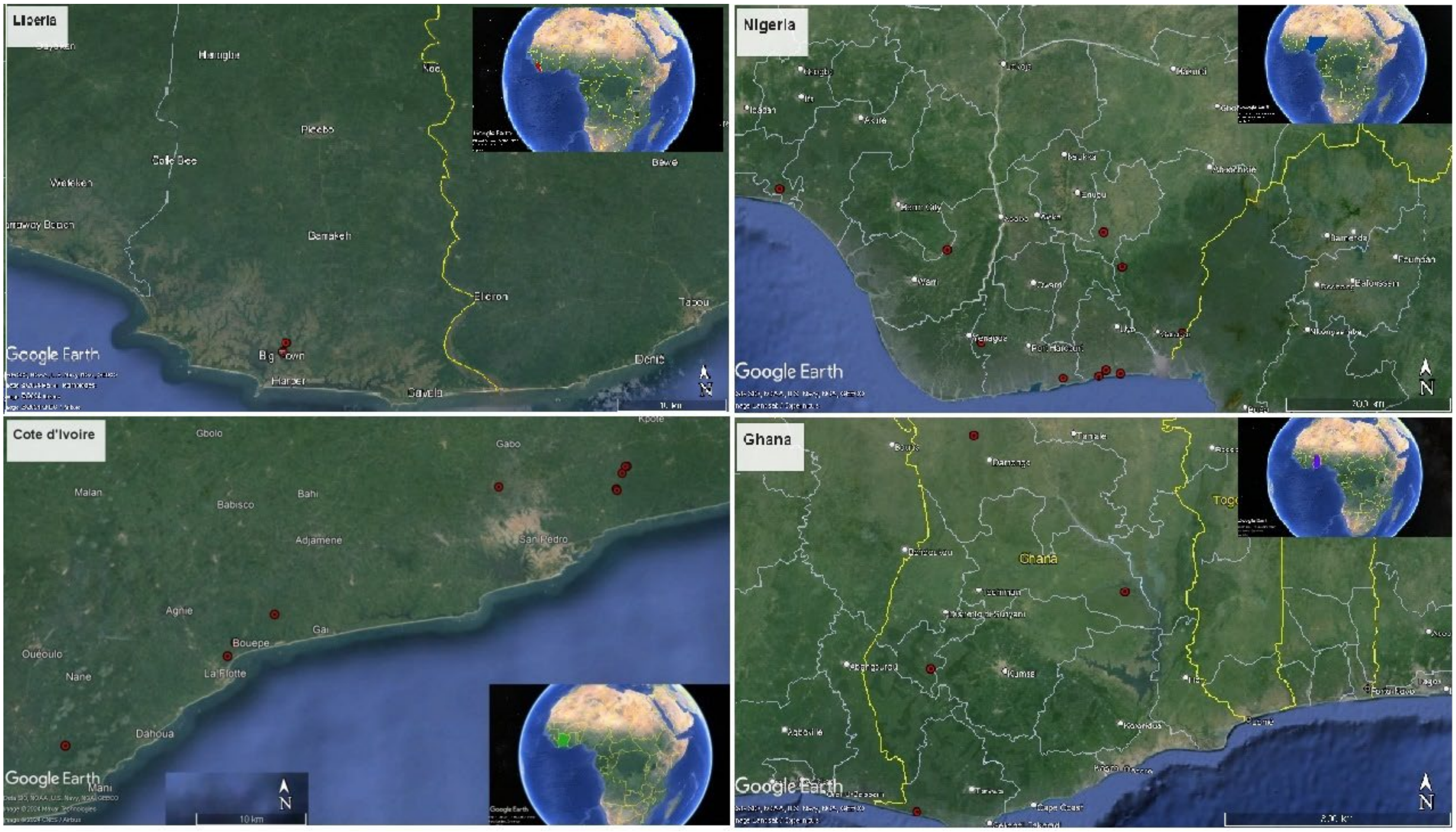


Figure 2. Some images of *Trionyx triun*guis and the setting of the traps for studying it at the study areas

Figure 3. Number of *Trionyx triunguis* individuals recorded using four microhabitat variables: (a) river width (m), (b) substrate type, (c) bank vegetation type, and (d) emergent vegetation % in Cote d'Ivoire and Liberia. Standard error bars are presented.

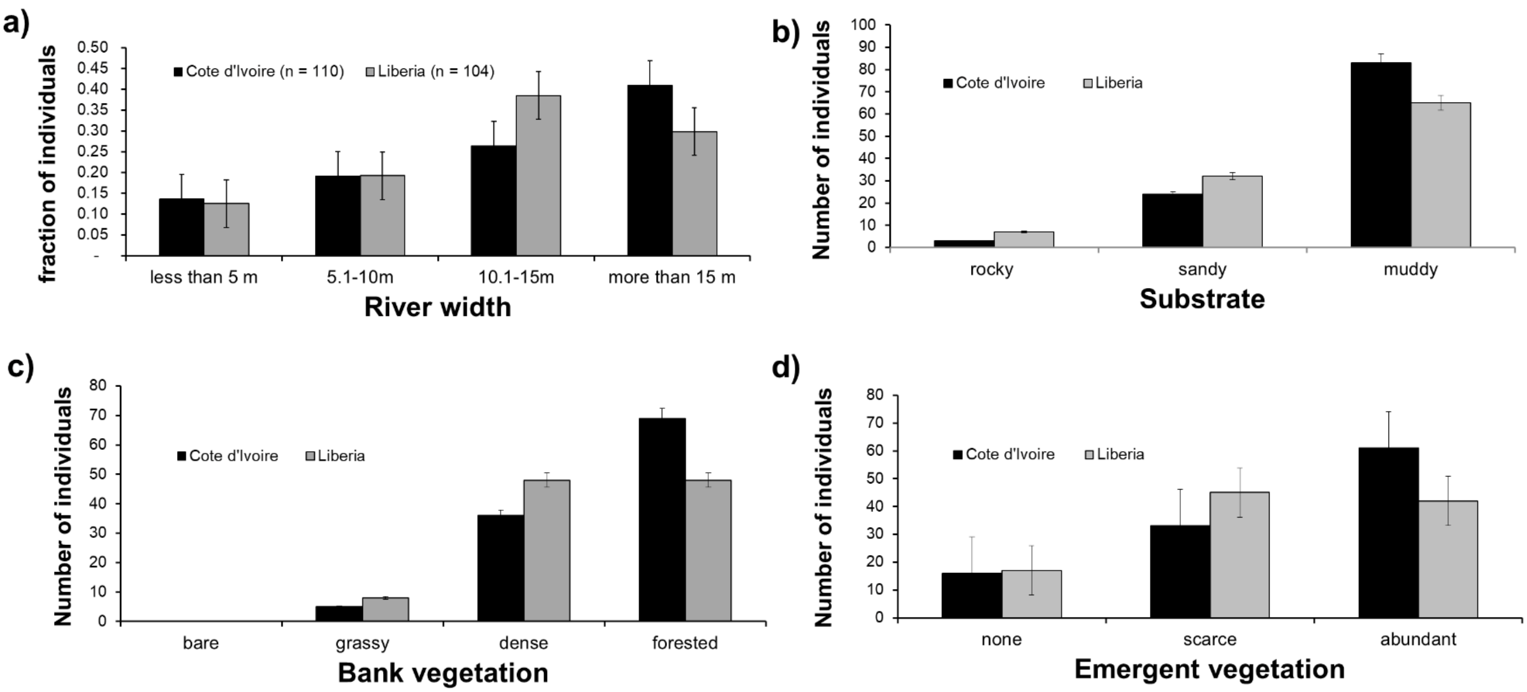


Figure 4. Intersexual and age-based usage of four microhabitat features by *Trionyx triunguis* in Cote d'Ivoire and Liberia. (a) River width (m), (b) Substrate type, (c) Bank vegetation type, (d) Emergent vegetation %. Standard error bars are presented.

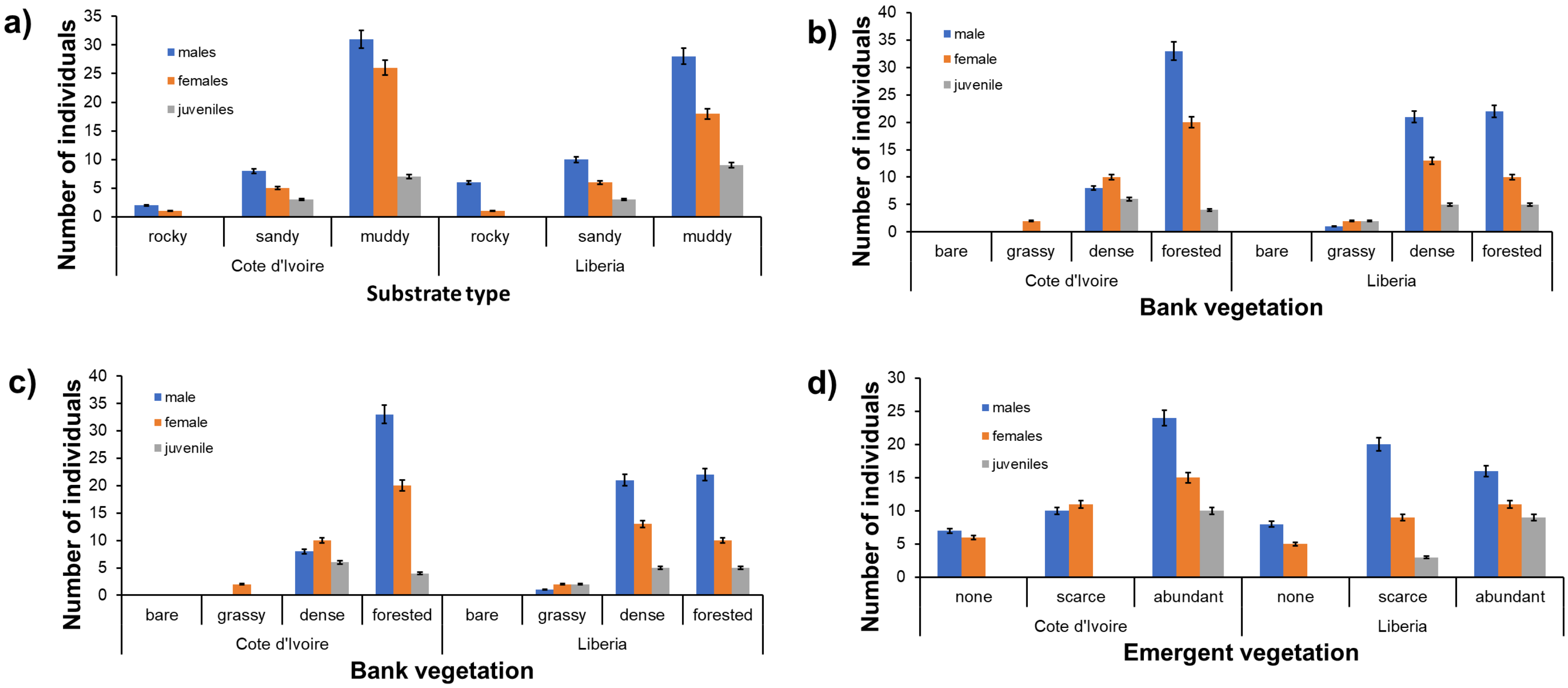


Figure 5. Sightings of *Trionyx triunguis* individuals in Akwa-Ibom State (south-eastern Nigeria), based on four microhabitat variables: (a) river width (m), (b) substrate type, (c) bank vegetation type, and (d) emergent vegetation %. Standar error bars are presented.

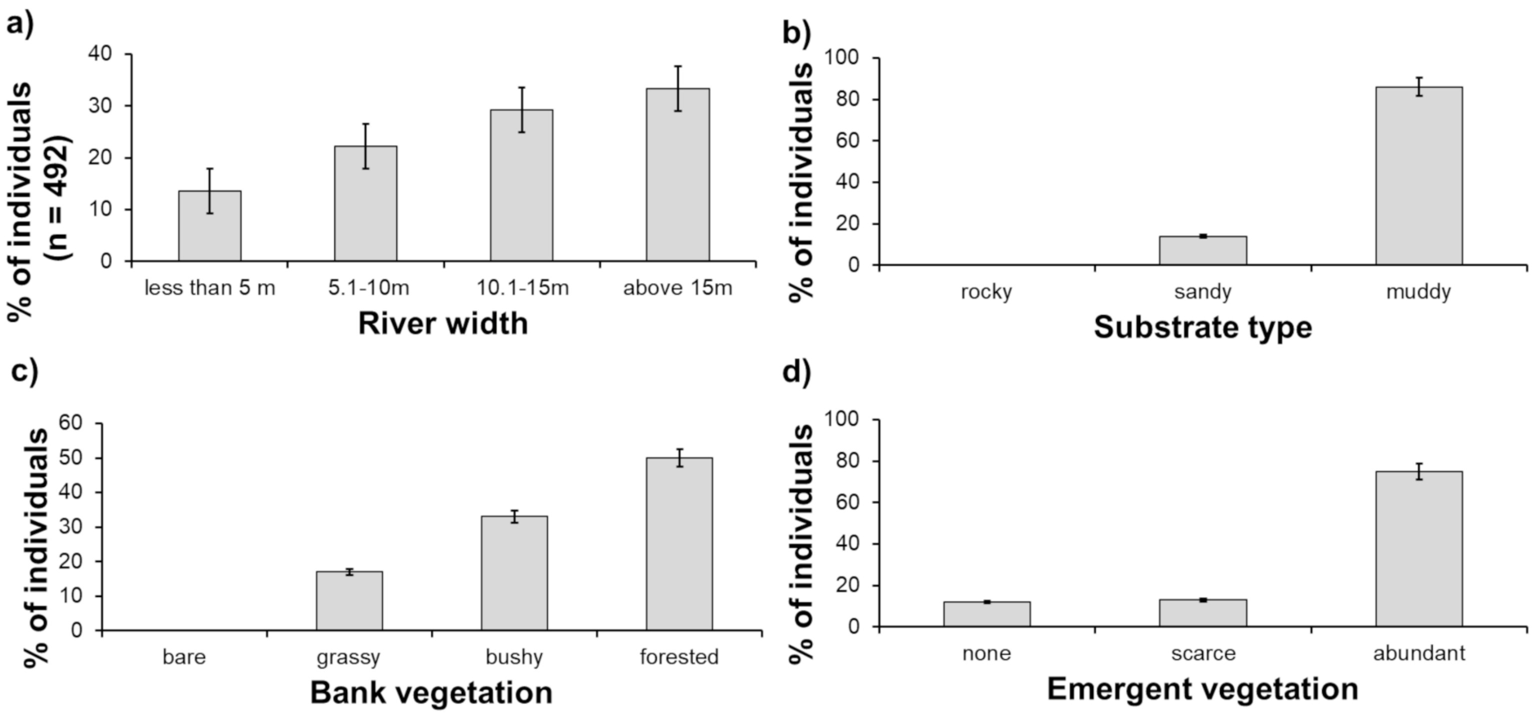


Figure 6. Detrended Correspondence Analysis (eigenvalue 1 = 0.0464, eigenvalue 2 = 0.0037) for all studied populations of *Trionyx triunguis*, showing widespread similarity amongst countries. Symbols: CI = Cote d’Ivoire; RWa-RWd = River width (four categories as described in the Methods); SBa-SBc = Substrate (three categories); BVa-BVd = Bank vegetation (four categories); Ava-AVc = Aquatic emergent vegetation (three categories).

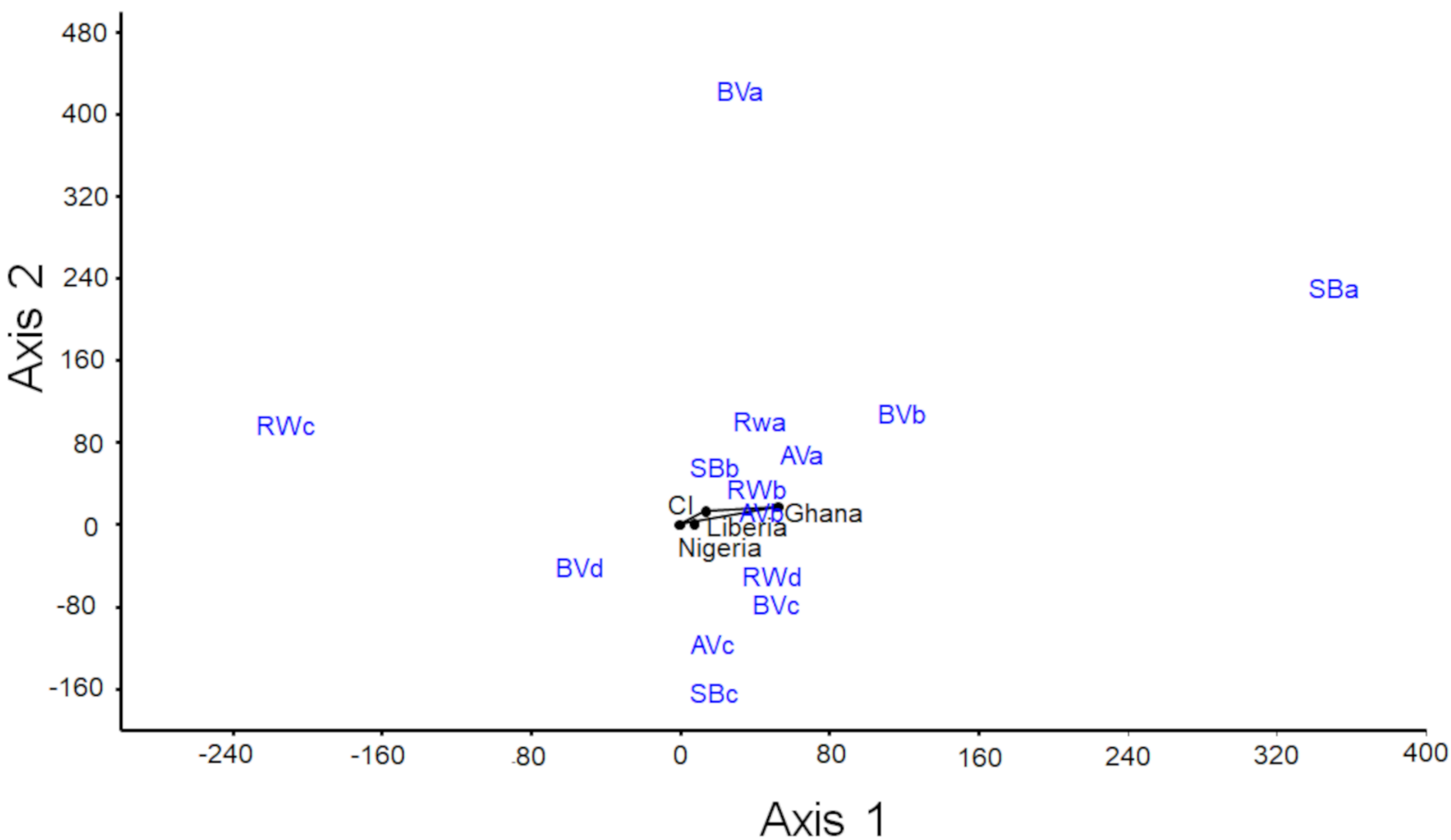
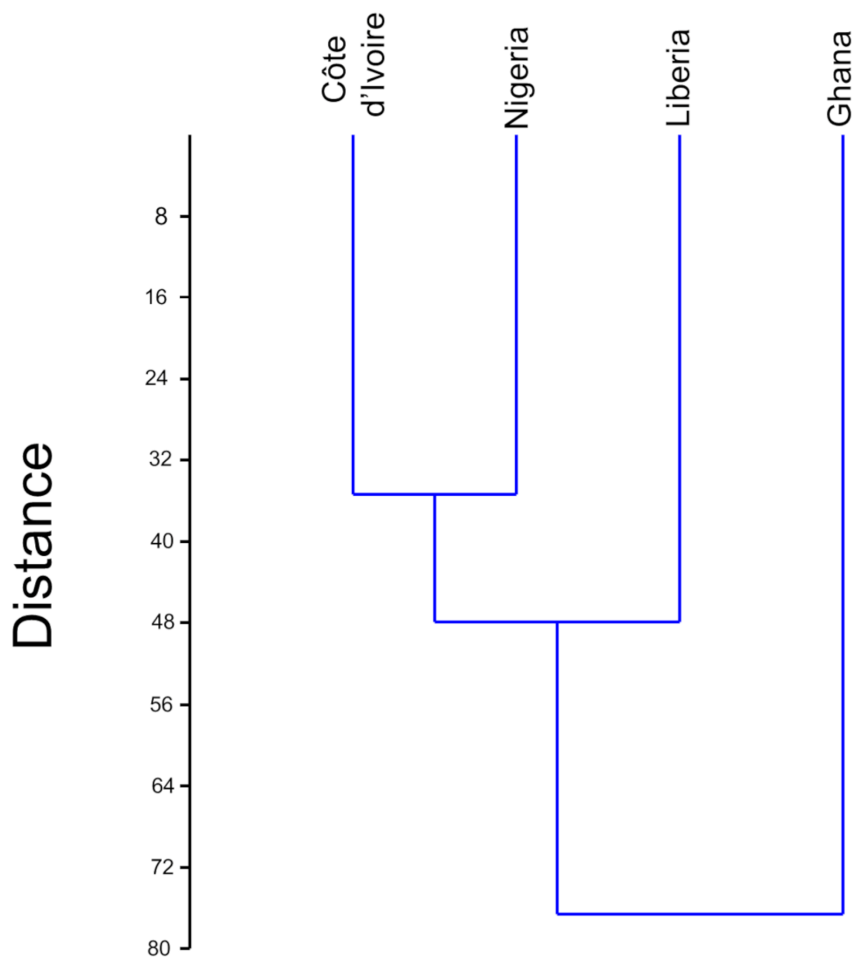


Figure 7. Dendrogram (UPGMA method, with Euclidean index and 40 bootstraps) showing the dissimilarities among countries in terms of the habitat use patterns by *Trionyx triunguis* in the studied sample.



ONLINE SUPPLEMENTARY MATERIALS

Table S1. Total number of captures/sightings for *Trionyx triunguis* in the four countries that were surveyed for this study, between 2015-2022 (Cote d'Ivoire and Liberia) and 2014-2023 (Nigeria and Ghana), separated by the type of method by which the various records were collected.

	visual transects/suryeys	fishers/markets	traps	rescued	TOTAL
Liberia	24	45	35	0	104
Cote d'Ivoire	19	50	41	0	110
Ghana	56	19	12	0	87
Nigeria	79	269	0	144	492
TOTAL	178	383	88	144	793

Table S2. Age-structure of *Trionyx triunguis* in Ghana by season and study area. For statistical details, see the text.

Site	age	2014	2017	2018	2021	2022	2023	TOTAL
dry season								
Digya Nat Park	Adults	0	4	0	5	4	7	20
	Juveniles	0	2	0	1	3	4	10
Amansuri wetlands	Adults	4	1	1	0	0	0	6
	Juveniles	0	3	0	0	0	0	3
Tano River	Adults	0	3	0	0	0	2	5
	Juveniles	0	0	2	0	0	0	2
Mole Nat Par	Adults	0	0	0	6	2	1	9
	Juveniles	0	0	0	1	0	0	1
wet season								
Digya Nat Par	Adults		2		1	1	2	6
	Juveniles		0		2	0	3	5
Tano River	Adults		0		1	2	1	4
	Juveniles		0		3	0	2	5
Mole Nat Par	Adults		3		1	1	3	8
	Juveniles		1		0	2	0	3