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Macrohabitat and Microhabitat Usage by Two Softshell Turtles (*Trionyx triunguis* and *Cyclanorbis senegalensis*) in West and Central Africa

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Abstract*.—No field studies have been conducted characterizing the habitat characteristics and eventual spatial resource partitioning between softshell turtles (family Trionychidae) in West and Central Africa. Here, we analyze the macrohabitat, microhabitat (along four variables), and apparent population abundance of Nile Soft-shelled Terrapin (*Trionyx triunguis*) and Senegal Flap-shelled Terrapin (*Cyclanorbis senegalensis*) by collating 22 y of data (1995–2017) from 11 countries in West and Central Africa. We found that the carapace length of *T. triunguis* was significantly larger than *C. senegalensis*. Qualitative observations on the apparent population abundance suggests that the smaller species was relatively common in most of the sampled sites, whereas the larger species was often rare or even very rare. We found the two species in a variety of macrohabitats, and a clear difference between them was not apparent in our data. Instead, at the microhabitat scale, the two species differed significantly in all the four microhabitat variables considered in this study. Overall, the data we present are consistent with a general pattern of resource partitioning previously highlighted for freshwater turtle communities worldwide, where sympatric species tend to partition the microhabitat resources and not the available macrohabitats. Because *T. triunguis* seemed rare in most of the surveyed sites, we suggest that more field investigations should be undertaken to understand whether the current status of Vulnerable is suited for this species, or if a more highly threatened category on the Red List should be adopted.

Key Words.—conservation; ecology; habitat selection; Trionychidae; West-Central Africa.

Introduction

Resource partitioning has been one of the most intensely studied processes in ecology since the mid-1900s (e.g. Pianka 1986), and has been investigated in a suite of reptiles, including freshwater turtles (e.g., Luiselli 2008 for a review). A meta-analysis of the available data from different continents (especially Europe and North America) and habitats (rivers, lakes, marshlands, ponds, etc.) has shown that the micro-habitat resource (especially basking site typology) is partitioned in nearly 80% of the freshwater turtle communities studied so far, followed by the food resource dimension (nearly 70%), whereas macro-habitat and time were clearly less important (Luiselli 2008). Some freshwater turtles are large-sized carnivores (particularly chelydrids and trionychids) and may be near the top of some food chains in their natural pond and river habitats (Pritchard

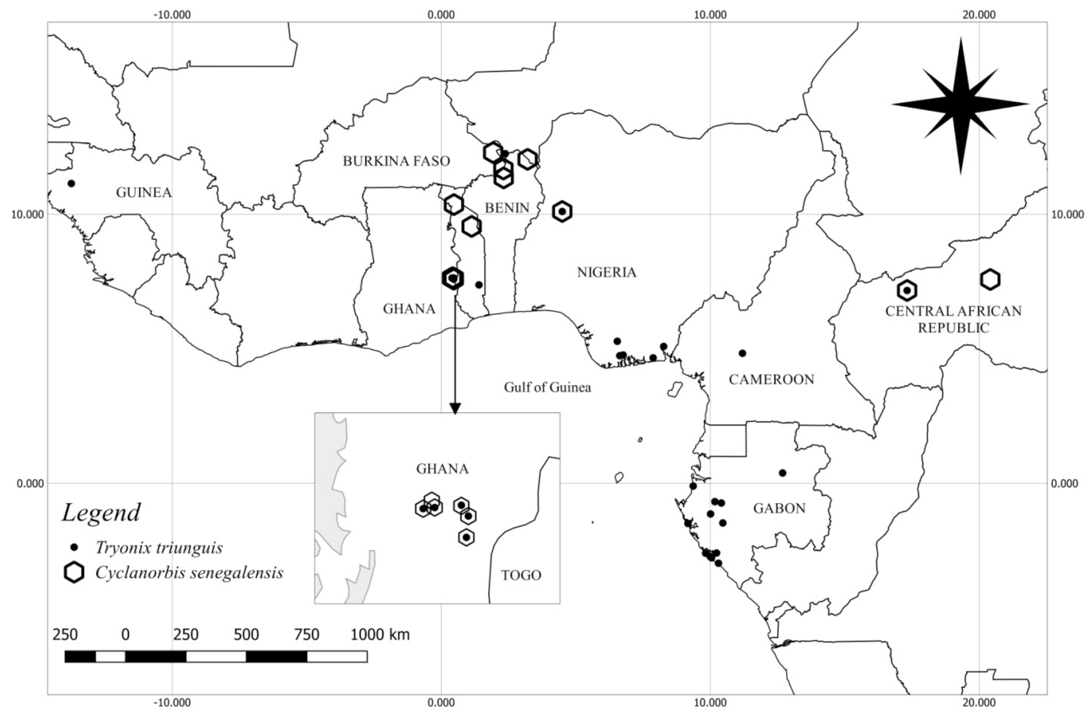

Figure 1. Map of West and Central Africa, showing the 32 study localities for Senegal Flap-shell Terrapin (*Cyclanorbis senegalensis*) and Nile Soft-shelled Terrapin (*Trionyx triunguis*). Note that the two species are sympatric in several localities.

2001). It has been suggested that the ecological role of these large carnivore turtles should be similar to that of snakes (Luiselli 2006), with a strong interspecific influence determining their coexistence dynamics (Pritchard 2001; Luiselli 2008).

Only a few field studies have been published on the community ecology of freshwater turtles in sub-Saharan Africa, with these being limited to West African swamp forest and mangrove regions (Luiselli and Akani 2003; Luiselli et al. 2004, 2006). Moreover, none of the studies provided quantitative assessment of the niche characteristics and resource partitioning patterns of Trionychidae species from Sub-Saharan Africa, despite the noteworthy case of coexistence between Senegal Flap-shelled Terrapin (*Cyclanorbis senegalensis*), Nubian Flap-shelled Terrapin (*Cyclanorbis elegans*), and Nile Soft-shelled Terrapin (*Trionyx triunguis*) in West and central Africa (Pritchard 2001; Branch 2008; Baker et al. 2015). The scientific knowledge on the ecology of *Cyclanorbis senegalensis* and *Trionyx triunguis* is still fragmentary (see a summary in Branch 2008) with quantitative data on the habitat characteristics and food habits of *Trionyx triunguis* available for the rainforest rivers of southern Nigeria (Akani et al. 2001; Luiselli et al. 2004, 2006) and with comments on natural history and distribution also for the wooded savannahs of the Dahomey Gap in Togo (Segniagbeto et al. 2014). The field ecology of *Cyclanorbis senegalensis* is nearly unknown and anecdotal comments are available only in general articles and books (e.g., Villiers 1958; Branch 2008; Trape et al. 2012; Segniagbeto et al. 2014). To contribute to the understanding of the coexistence dynamics of Afrotropical softshell turtles, we collate opportunistic data collected across 22 y on the macrohabitat and microhabitat use of *Cyclanorbis senegalensis* and *Trionyx triunguis* in several countries of Western and Central Africa. We focus on the differences in habitat use between species at the two spatial scales, on the respective body size differences, and we provide general comments on the patterns of ecological coexistence between these species.

Materials and Methods

Our study is based on opportunistic field data collected between 1995 and 2017 in 32 distinct localities (10 for *Cyclanorbis senegalensis* and 22 for *Trionyx triunguis*) of 11 African countries: Ghana, Benin, Togo, Nigeria, Burkina Faso, Cameroon, Guinea, Gabon, Central African Republic, Niger, and Burkina Faso (Fig. 1). The climate of these countries varies but is predominantly arid in the Sudanese zone and wet equatorial in the southern regions of Ghana, Nigeria, and Cameroon. The wet season, variably prolonged depending on the region, extends from April to September, with heavy rains concentrated only in August in the Sudanese zone

Figure 2. Measuring the curved carapace length of Nile Soft-shelled Terrapin (*Trionyx triunguis*) (a and b) and Senegal Flap-shell Terrapin (*Cyclanorbis senegalensis*) individuals. (Photographed by Luca Luiselli).

(not in Gabon where this period corresponds to the dry season).

For each of the sampled localities, we recorded the habitat characteristics of all softshell turtle individuals that were opportunistically observed, either free-ranging or just captured by fishermen. The surveys were time-constrained, and the number of observers was kept constant among surveys (two people at each site in each field day) to minimize bias in the results among sites and habitats. Due to socio-political instability in the region, we were unable to carry out rigorous representative surveys across the various countries. Instead, we focused our surveys on areas where the presence of these two species was already known (e.g., Trape et al. 2012).

We studied the habitat use of softshell turtles in these areas on a macrohabitat scale with description of the main vegetation characteristics of the areas surrounding the water basin where a given record was obtained, and on a microhabitat scale. We recorded microhabitat charactieristics of (1) Width of the river or water body (in m) in four categories (< 5 m, 5–15 m, 15–25 m, > 25 m). We estimated river width and then lumped a river within these categories. (2) Type of river-bed in three categories (predominantly rocky, predominantly sandy, or predominantly muddy). We evaluated each category within a 10 × 10 m area surrounding the spot of a sighting of turtle. (3) River banks vegetation type in four categories (empty banks, herbaceous banks, heavily vegetated banks dominated by shrubs, and heavily vegetated banks dominated by forest = gallery forest habitat). (4) Emergent aquatic vegetation in three categories (no emergent vegetation if > 90% of the water within a 10 × 10 m area surrounding the capture/observation point of a turtle was free, scarce vegetation if 50–89% of water was free, and abundant vegetation if < 50% of the water was free with many emergent vegetation patches are emerging from water). We estimated emergent vegetation categories by eye.

For all captured turtles, we measured curved carapace and plastron lengths (in cm; see Fig. 2) and we determined sex of turtles by examination of the shape of the cloacal region and tail. We measured and determined sex only of those individuals that were alive at the time of observation, whereas we identified several other individuals that were already dead when found (those captured and butchered by fishermen; see Fig. 3) to species but we did not measure them. In addition, we obtained qualitative estimation of the local abundance of each species by coupling our field observations with the information provided by by fishermen and local hunters. We categorized the apparent abundance of

Figure 3. A Nile Soft-shelled Terrapin (*Trionyx triunguis*) individual, just butchered by a local fisherman at Ndogo Lagoon near Gamba, southwestern Gabon. (Photographed by Olivier S.G. Pauwels).

turtles as Common when interviewed fishermen and/or field guides reported them to be abundant, and when we observed several individuals (e.g., as in the upstreams of the Kongou Falls along the Ivindo River, Gabon, where several individuals were killed by hunters and also seen in fishermen nets); Relatively Common when interviewed fishermen and/or field guides reported them to be abundant but we observed just one or two individuals at the site; Rare when interviewed fishermen and/or field guides reported them to be few and we observed just one or two individuals at the site; and Possibly Extinct when old shell remains were examined but the interviewed fishermen and/or field guides reported them to be extinct and we did not observe any individuals at the site during our surveys. These abundance categories are obviously approximate but may give preliminary information on the population status of these two species across the various sectors of their West and Central African range. In additional localities of known presence (i.e., Kédougou in Senegal and Archipel des Bijagos Egouba Hurricane in Guinea-Bissau for *T. triunguis*, and Kédougou in Senegal and Pendjari National Park in Benin; vouchers deposited at the African Chelonian Institute in Ngaparou / Mbour, Senegal), we could not collect data on their apparent abundance, and these localities are thus excluded from the analyses.

We avoided pseudoreplication of data by not surveying the same site twice. Thus, we did not capture the same individual multiple occasions. We conducted a Chi-square to assess the differences in the frequency of observation of the softshell turtle species among the various categories of macrohabitats and we set alpha at 0.05 (Hammer 2012). We analyzed our microhabitat data in two ways. First, we used Generalized Linear Models (GLZs) to model the effect of different microhabitat types on the observed numbers of *C. senegalensis* and *T. triunguis* (Hosmer and Lemeshow 2000). The number of turtles in the four microhabitat types were the dependent variable and we used the identity link function and a normal distribution of error (McCullagh and Nelder 1989). We used parametric tests only after having verified the normality of data distribution by Shapiro-Wilk W normality test. While our GLZ models tested for habitat usage of each species, they did not allow for the identification of eventual niche differences between them due to insufficient statistical power. Thus, to uncover niche differences between species, we analyzed the distribution of the individuals of both species across the four microhabitat variables by Chi-square. We computed the significant variables for GLZs using the best subset procedure in Statistica 6.0 software. For all other statistical analyses, we used PAST 3.0 statistical software (Harper 2012).

Results

Our samples consisted of 196 *Cyclanorbis senegalensis* and 115 *Trionyx triunguis* from 32 sites. Of these, we measured 63 *C. senegalensis* and 57 *T. triunguis* for carapace length. These samples included also juvenile individuals for which sex could not be determined (n = 3 in each species). Adult sex ratio (1.14 F:1 M) was equal (χ^2 = 0.33, df = 1, P = 0.714) in *C. senegalensis* (32 females and 28 males). In *T. triunguis*, adult sex ratio (2.12 F: 1M) was skewed to females (36 females:17 males), but not significantly different than 1:1 (χ^2 = 3.55, df = 1, P = 0.059). We never observed or captured *Cyclanorbis elegans*, which is known to be exceedingly rare in the whole of its distribution range (Baker et al. 2015; Stanford et al. 2018). Carapace length of *C. senegalensis* (n = 63) averaged 23.3 cm (median = 24.0 cm; range, 12.0–34.2 cm) whereas that of *T. triunguis* (n = 57) averaged 28.6 cm (median = 28.7; range, 10.5–43.0 cm). On average, *T. triunguis* was significantly larger than *C. senegalensis* in terms of carapace length (t = -3.81, df = 118, P < 0.001).

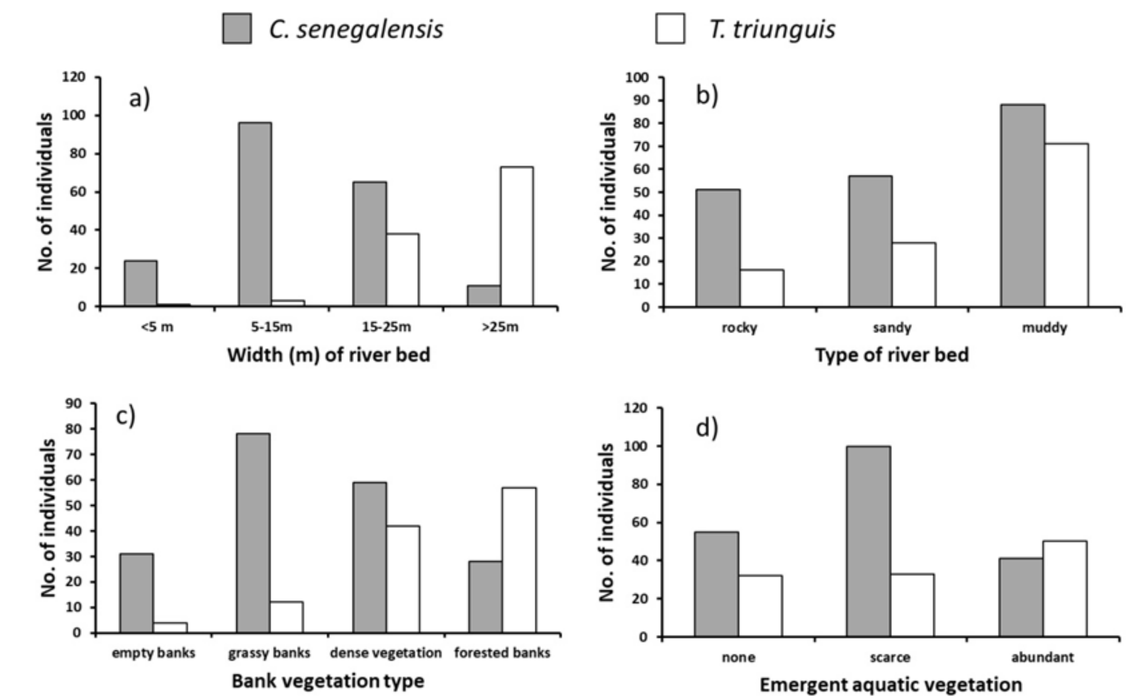

Figure 4. Abundance of Senegal Flap-shell Terrapin (*Cyclanorbis senegalensis*) and Nile Soft-shelled Terrapin (*Trionyx triunguis*) with various categories of microhabitat in west and central Africa.

Macrohabitat and apparent abundance of populations.—The two species were found in a variety of macrohabitats, with a preponderance of forest rivers and forest-savannah mosaic waterbodies in *T. triunguis*, and of Sudan savannah waterbodies in *C. senegalensis* (Table 1). *Trionyx triunguis* was also observed in lagoons and brackish water sites, and even along oceanic beaches (Table 1). In *T. triunguis*, several populations appeared relatively less abundant than those of *C. senegalensis*. Indeed, in the latter species, we estimated that only one of 10 populations was Rare (10%), whereas, in the former species, we estimated that nine of 22 populations were Rare and one was Possibly Extinct (45.45%) (Table 1). The frequency of Rare and Possibly extinct populations was significantly higher in *T. triunguis* than in *C. senegalensis* ($\chi^2 = 6.19$, df = 1, $P < 0.050$).

Microhabitat.—The numbers of individuals of *T. triunguis* increased with the increase of bank vegetation (from empty banks to gallery forest habitat: estimate = 0.0557; $P = 0.029$), the type of river-bed (from predominantly rocky, to predominantly muddy: estimate = 0.0329, $P < 0.001$) and the increase of emergent aquatic vegetation (from no emergent vegetation to abundant vegetation: estimate = 0.0880, $P < 0.001$). The numbers of observed individuals of *C. senegalensis* decreased with the increase of river width (from < 5 m to > 25 m: estimate = -0.3700, $P < 0.001$) and increased with the increase of bank vegetation (from empty banks to gallery forest habitat: estimate = 0.5924, $P < 0.0001$), from predominantly rocky, to predominantly muddy river-bed (estimate = 0.0595, $P < 0.001$) and with emergent aquatic vegetation (from no emergent vegetation to abundant vegetation: estimate = 0.0143, $P < 0.001$). Nonetheless, the GLZ showed a greater sensitivity of *C. senegalensis* to the river-bed width than *T. triunguis*.

There were significant differences in all the microhabitat variables between the two species (Fig. 4). *Trionyx triunguis* tended to inhabit waterbodies with larger width ($\chi^2 = 150.4$, df = 3, $P < 0.001$; Fig. 4a). *Cyclanorbis senegalensis* tended to inhabit waterbodies with sandy and rocky beds more frequently than *T. triunguis*, although still with a higher use of muddy beds ($\chi^2 = 9.600$, df = 2, $P < 0.010$; Fig. 4 b). *Trionyx triunguis* tended to inhabit waterbodies with densely vegetated and forested banks and *C. senegalensis* was frequently in waterbodies with empty or poorly vegetated banks (Fig. 4 c). *Cyclanorbis senegalensis* tended to inhabit waterbodies with scarce emergent aquatic vegetation ($\chi^2 = 21.11$, df = 2, $P < 0.001$; Fig. 4 d).

Discussion

Overall, our study confirmed that both *T. triunguis* and *C. senegalensis* have a wide tolerance in terms of macrohabitat usage, ranging from forested areas to rivers crossing throughout relatively arid savannahs (see also Chirio and LeBreton 2007; Branch 2008). Thus,

Table 1. Summary of the macrohabitat characteristics of each site of observation/capture of Senegal Flap-shell Terrapin (*Cyclanorbis senegalensis*) and Nile Soft-shelled Terrapin (*Trionyx triunguis*), including apparent abundance of the local turtle populations. Geographic coordinates are not given for conservation reasons but can be obtained on request from the authors. The abbreviation CAR = Central African Republic.

Species	Country	Locality	Habitat	Abundance
Cyclanorbis senegalensis	CAR	Kouki	Forest-savannah mosaic river	Relatively common
C. senegalensis	CAR	Sangba	Forest-savannah mosaic river	Relatively common
C. senegalensis	Benin	Chutes de Koudou	Sudan savannah river	Common
C. senegalensis	Benin	Bello Tonga	Sudan savannah river	Common
C. senegalensis	Benin	Keremou	Sudan savannah river	Common
C. senegalensis	Burkina Faso	Tapoa Djerma	Sudan savannah river	Common
C. senegalensis	Togo	Kara	Sudan savannah river	Relatively common
C. senegalensis	Togo	Mango	Sudan savannah river	Common
C. senegalensis	Nigeria	Kainji Lake	Sudan savannah lake	Common
C. senegalensis	Ghana	Digya National Park	Guinea savannah river	Rare
Trionyx triunguis	CAR	Kouki	Forest-savannah mosaic river	Rare
T. triunguis	Cameroon	Bafia, Sanaga river	Forest-savannah mosaic river	Relatively common
T. triunguis	Niger	W National Park, Mekrou river	Sudan savannah river	Rare
T. triunguis	Guinea	Kogon Lengere river near Sangaredi	Sudan savannah river	Possibly extinct
T. triunguis	Gabon	Tranquille	Forest river	Common
T. triunguis	Gabon	Lambaréné lakes	Forest river	Common
T. triunguis	Gabon	Koumouna Bouali	Forest river	Rare
T. triunguis	Gabon	Fernan Vaz	Lagoon (brackish water)	Common
T. triunguis	Gabon	Nyonié (7 km SE of -)	Forest-savanna mosaic stream	Rare
T. triunguis	Gabon	Ondimba, along Oguemoué Lake	Freshwater lake	Common
T. triunguis	Gabon	Between Gamba and Setté-Cama	Atlantic Ocean beach	Common
T. triunguis	Gabon	Gamba along Ndogo Lagoon	Lagoon (brackish water)	Common
T. triunguis	Gabon	Yenzi Lake	freshwater lake	Common
T. triunguis	Gabon	Mayonami	large river (Nyanga)	Common
T. triunguis	Gabon	Moukalaba-Doudou National Park	slow, clear forest river	Rare
T. triunguis	Gabon	Kongou Falls (a few km upstream -)	large river (Ivindo)	Common
T. triunguis	Togo	Lake Nangbeto	Guinea savannah lake	Common
T. triunguis	Nigeria	Eket	Forest river	Rare
T. triunguis	Nigeria	Sagbama (Orashi River)	Forest river	Relatively common
T. triunguis	Nigeria	Taylor Creek Forest Reserve	Forest river	Rare
T. triunguis	Nigeria	Akpabuyoh	Forest river	Rare
T. triunguis	Ghana	Digya National Park	Guinea savannah river	Rare

it is obviously difficult to highlight niche differences at a large spatial scale between these widespread and habitat generalist species; however, our microhabitat analyses scale uncovered patterns previously unreported. We found that the mean abundance of each species was influenced by similar microhabitat variables. For instance, the abundances of both species were positively associated with muddy river-beds and more vegetated banks. These similarities between species might explain the range overlap in West and

Central Africa (Branch 2007); however, we found that the frequency of microhabitat useage between the two species was differentiated in all four variables considered in this study. Thus, it appears that while the overall macrohabitat useages based on variance in abundance are similar, there is an apparent partitioning of the microhabitat resources between species based on frequency of habitat useage. In addition, the significant difference in carapace length between these species increases the niche differences between species, which also likely differentiates their food niche because in softshell turtles, prey type and size depend mainly on the relative body size of the predator (Pritchard 2001).

In a meta-analysis of the data available on freshwater turtles across the world, Luiselli (2008) also pointed out that the microhabitat resource is the most important dimension for niche partitioning (it was partitioned in nearly 80% of the study cases), followed by the food resource dimension (nearly 70%), whereas macrohabitat and time were clearly less important. Thus, our results fit well with the general pattern highlighted in Luiselli (2008); however, among softshell turtles, some exceptions do exist. In North America, for instance, sympatric *Apalone spinifera* and *A. mutica* in the Middle Mississippi River, which also differ in body size, significantly partitioned the macrohabitat (Barko and Briggler 2006), unlike our study and the majority of turtle studies published so far (Luiselli 2008). In contrast, *A. spinifera* and *A. mutica* partitioned the microhabitat resource (i.e., basking sites) in another area of their range (Lindeman 2001) and both the microhabitat and the food resources in Iowa (Williams and Christiansen 1981).

Our study is based on independent data collected from distinct localities over a wide geographic region. Our study was not based on an experimental approach (for example, based on removal protocols, captivity experiments or longitudinal monitoring of single individuals; Cadi and Joly 2003, 2004) or on an observational approach on a single locality surveyed multiple times (e.g., Moll 1990; Lindeman 2000). Instead, our study was a comparative study based on the analysis of macrohabitat and microhabitat characteristics of a sample of free-ranging turtles originating from several African countries. Thus, our approach might have introduced some biases in the results, for instance, if the different sites were composed of very different microhabitat types and the turtles do exhibit temporal shifts in resources and habitat availablity so that we may be missing variability in habitat use. Nonetheless, we are confident that the outcomes of our study are not biased, because we analyzed a relatively large sample size, and in many of our study localities, both species occurred together and their apparent niche differences remained significant.

Conservation considerations.—Although our study was not specifically oriented towards studying the conservation ecology of these species, we found that in several of the studied localities that *T. triunguis* individuals are uncommon or even rare, whereas *C. senegalensis* individuals are in general common in most of the localities we surveyed. These different abundance patterns may reflect the fact that *T. triunguis* inhabits rivers and lakes from the most developed regions of West Africa, where intensive agriculture, modern fishing techniques, and heavy land reclamation practices are ongoing; whereas *C. senegalensis* is more linked to savannah watercourses where human density is lower and the economic development is much lower than in areas supporting *T. triunguis*. In addition, *T. triunguis* also inhabits heavily polluted areas being that are exploited by oil and natural gas exploration activities, as in the Niger Delta of southern Nigeria (Luiselli and Akani 2004; Luiselli et al. 2006).

It is likely that the general abundance patterns observed in our study sites reflect a global conservation status for both species in Western and Central Africa. Indeed, both species were listed as Vulnerable in the draft evaluation of the International Union for Conservation of Nature (IUCN) / Species Survival Commission Tortoise and Freshwater Specialist Group of the 2013 Specialist Group held in Lomé, but we suggest that, for *T. triunguis*, more field investigations should be done to better understand whether the status of Vulnerable is correct for this species, or if a higher threat designation in the IUCN Red List should be adopted. In this regard, it is noteworthy that Mediterranean populations of this species are already considered as Critically Endangered (Turtle Taxonomy Working Group 2017).

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