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Article

Spatial Niche Expansion at Multiple Habitat Scales of a Tropical Freshwater Turtle in the Absence of a Potential Competitor

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Abstract: Resource partitioning, the division of limited resources by species to help avoid competition, has been observed in freshwater turtle assemblages in several natural systems but has rarely been studied in tropical African ecosystems. Here, we investigate habitat preferences of two congeneric species in the family Pelomedusidae, *Pelusios castaneus* and *P. cupulatta*, in riverine/wetland habitats in the southern Ivory Coast (West Africa). *Pelusios castaneus* is a widespread species across West-central African savannahs and open forests, whereas *P. cupulatta* is endemic to the Upper Guinean forest region in West Africa. The two species have a similar diet composition (mainly carnivorous) but diverge considerably in body size, *P. cupulatta* being much larger. We use hand-fishing-nets and fishing funnel traps to record turtles in 18 distinct sites and analyze habitat preferences by species at two spatial scales. At a macro-habitat scale, *P. castaneus* is captured mainly in marshlands, whereas *P. cupulatta* is found in both rivers and wetlands. The two species differ significantly in their use of: (i) banks (*P. castaneus* being found primarily in spots with grassy banks, whereas *P. cupulatta* is found in spots with forested banks), and (ii) aquatic vegetation (*P. cupulatta* prefers spots with more abundant aquatic vegetation than *P. castaneus*), but both species select sites with no or moderate current. Additionally, in sites where *P. cupulatta* is not found, *P. castaneus* expands its spatial niche at multiple habitat scales, notably invading waterbodies with forested banks. Our results suggest that these two Pelomedusid turtle species potentially compete in the freshwater habitats in the southern Ivory Coast.

Keywords: freshwater chelonians; *Pelusios*; habitat selection; niche partitioning; Ivory Coast; West Africa

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1. Introduction

Studies of freshwater turtle communities have primarily focused on microhabitat resource partitioning [1–4]. Some evidence suggests that spatial niche partitioning by turtles is, at least in part, determined by interspecific competition (see [5] for a meta-analysis of published research). Aggressive interactions, for instance, especially during basking, can result in competitive exclusion in some turtle assemblages [6,7]. Additionally, exploitation competition through (i) greater foraging efficiency of fast-moving highprotein prey, or (ii) greater digestive efficiency of plants and algae [8–12] can contribute to promoting interspecific competition among coexisting turtle species. Micro-habitat partitioning by sympatric turtle species, therefore, can reduce aggressive interactions and facilitate coexistence [5].

Interspecific competition in freshwater turtles has been studied mostly in temperate regions of North America and Europe (see [5] for a synthesis), whereas there is a dearth of information on tropical turtle systems. Regarding Africa, quantitative studies on whole freshwater turtle communities have been carried out in Nigeria [13–15] and Benin [4] or on selected species within a large geographic region [16].

Here, we analyze habitat partitioning, at different spatial scales, of two sympatric Pelomedusid turtles (*Pelusios cupulatta*, endemic; *Pelusios castaneus*, wide ranging) in the southern Ivory Coast (West Africa). We use location, habitat characteristics, and abundance/presence data to determine whether interspecific competition between these two congeners is evident and, also, to examine whether habitat preferences of a given species change in the presence or absence of a potential competitor. More specifically, we test the following key questions:

(1) Are the study species co-occurring in a same micro-habitat or do they exhibit apparent differences in habitat utilization?
(2) If the two species differ in their habitat utilization, are these differences found at multiple spatial scales?
(3) Are the eventual habitat differences due, at least in part, to interspecific competition?
(4) If so, do habitat preferences of either of these two species change when allopatric from a potential competitor?
(5) Is the assumption that *P. cupulatta* habitat use is similar to its sister species (*Pelusios niger*) confirmed by our field evidence?

These data are useful to better understand patterns and mechanisms of coexistence of turtles in freshwater tropical African ecosystems, and to promote science-based conservation actions for this group of increasingly threatened reptiles [17].

2. Materials and Methods

2.1. Study Species

The present study focused on two turtle species from the family Pelomedusidae: *Pelusios castaneus* and *Pelusios cupulatta*. These two species, though mostly aquatic, depend on aquatic and terrestrial habitats for different parts of their life cycle e.g., predator avoidance, feeding, courtship and mating, basking and nesting activities [1,2,18]. These two species have a similar, mainly carnivorous, generalist diet, but diverge considerably in body size, with *P. cupulatta* being much larger [18]. *Pelusios castaneus* is a widespread species across West-central African savannahs and open forests, ranging from Southern Senegal, Gambia, Guinea, Guinea-Bissau, Liberia, Sierra Leone, the Ivory Coast, Ghana, Togo, Benin, Southern Burkina Faso, Southern Niger, Nigeria, Cameroon, Southwestern Chad, and the Northern and Western Central African Republic [19]. To contrast, *P. cupulatta* is endemic to the Upper Guinean forest region in West Africa, from Liberia to Western Ghana, and occurs only within the coastal forest zone [18]. *Pelusios cupulatta* has been considered as a conspecific of *P. niger* for a long time, but recently has been described as a distinct species [18].

2.2. Study Sites

We studied turtles in 18 different localities along the coastal region in the Southwestern Ivory Coast, West Africa (Figure 1). These sites represented a random selection of potential aquatic habitats in the Southwestern Ivory Coast, though sites were chosen due to ease of access. The landscape was forest adjacent to the sea, crossed by vegetated hills, and intersected by valleys of different widths (Figure 2). The region is characterized by a subequatorial climate of two rainy seasons, influenced by the Intertropical Front (ITF) that extends from East to West. This zone has the highest rainfall in the country, with an average annual rainfall >1800 mm. However, the coastal area between Sassandra and Jacqueville receives less rainfall (between 1600 and 1800 mm). The human population density along the entire coastal area is relatively high, mostly in urban environments. Economic activity is dominated by agriculture, fisheries, and mineral extraction. Other uncontrolled activities provoke further pressure on the environment of this area. These activities include clearing of coastal vegetation, expansion of makeshift buildings to accommodate the increasing human population, as well as emerging tourism, removal of sand, and dam building on rivers for agriculture or energy production.

Five biome types are found within the study area: (1) coastal forest; (2) swamp forest; (3) mangrove; (4) prelagunar savannas and (5) coastal savannas. The coastal forest is an evergreen forest formation. By 1955, the dense humid forest and mangroves which accounted for >13 million hectares along the coast and its immediate hinterland, had fallen to <900,000 hectares by 2000. This amounts to nearly 94% of forest lost in 45 years and replaced by plantations or fallows. Mangrove ecosystems have been similarly affected by anthropogenic factors due to the overexploitation of mangrove wood (*Rhizophora racemosa*) for construction, fishing, tanning, cooking food, and smoking fish or crustaceans.

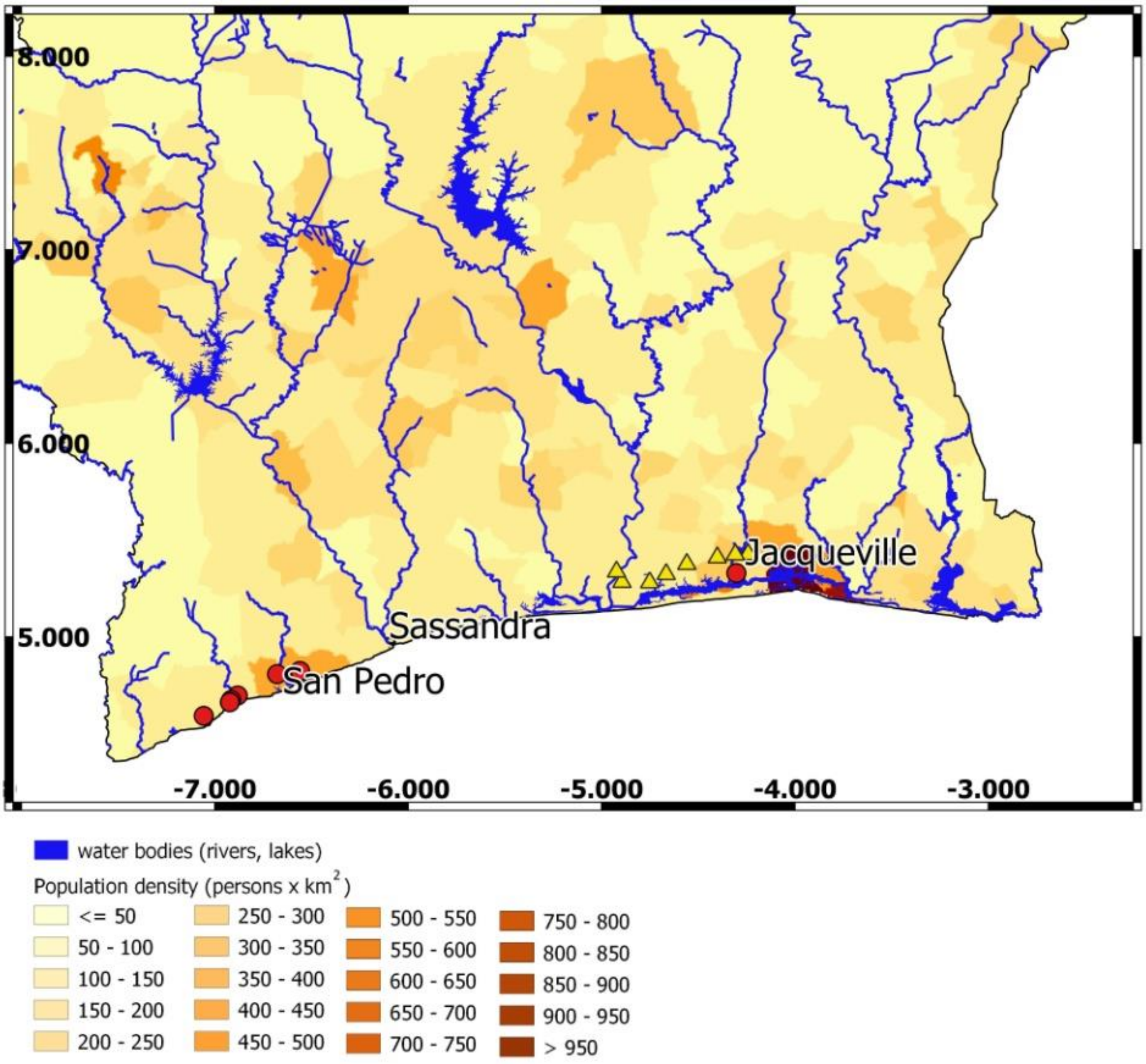

Figure 1. Map of the southern Ivory Coast showing the localities of the capture of sympatric turtles (red dots) and of allopatric *Pelusios castaneus* (yellow triangles), the water bodies, and the human population density.

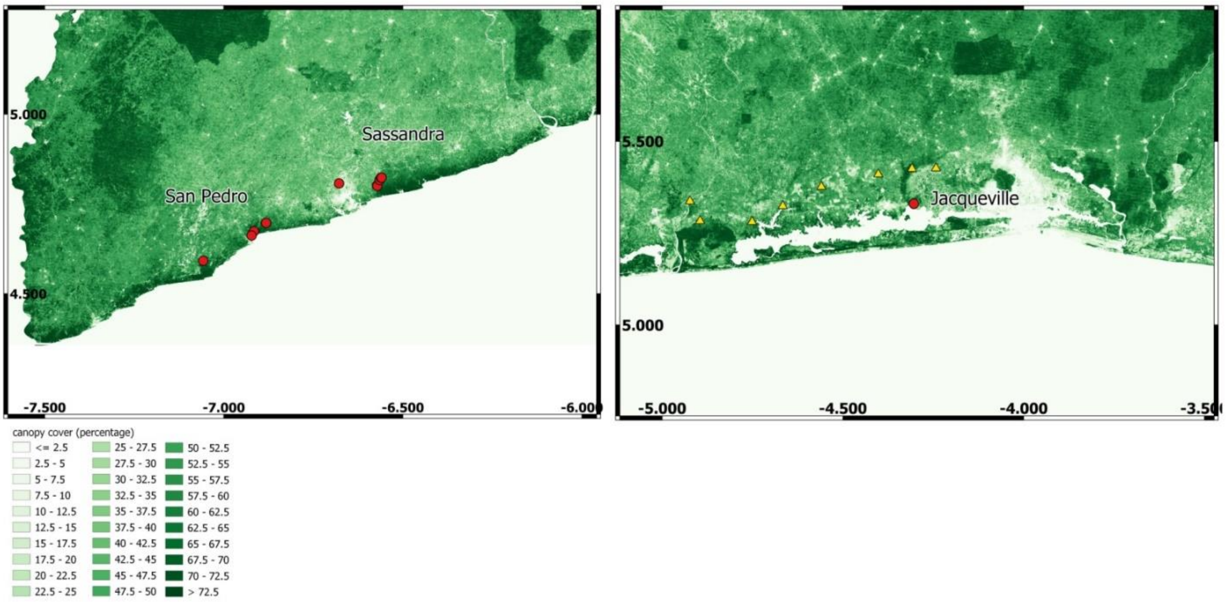

Figure 2. Smaller-scale map of the study areas, showing in more detail the vegetation characteristics (tree cover in shades of green). Symbols are the same as in Figure 1.

2.3. Protocol

We applied a field protocol similar to that used by [4] to study the coexistence ecology of turtles in Benin (West Africa). We surveyed each study site over a total of 10 field days during the wet season (May and June 2015, with additional data collected in September 2020).

We started field surveys at 07:00 h and ended at 18:30 h. We caught turtles by hand-fishing nets (model Cormoran 6245, with 240 cm handle) and with fishing funnel traps. We constructed traps with non-stretch 2.5 cm fine-mesh to avoid turtles ensnaring their legs. Each trap, approximately 180 cm in size, 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 (none of the individuals died during the field study). We baited all traps with fish. The same number of traps (n = 30) were deployed at each site and each day; 10 traps were placed in each of the three aquatic vegetation categories (see below) at each site. Each trap was placed 50 m apart on average. Regarding each site, we visually estimated water current speed as well as the composition of bank vegetation (see below for the various categories) at each point where traps were placed. We visited each trap twice a day (around 10:00 h and 17:00 h). We removed captured turtles from the trap for further examination. Turtles were identified to species, sexed, and the curved carapace length and plastron length were measured. We individually marked all captured turtles by carapace scute notching so future captures of the same individuals were excluded without confounding our abundance/presence analysis. We released all individuals unharmed at the point of capture.

Similar to [4], and following other literature that indicates that presence/absence and local abundance of turtle species are largely determined by bank type and vegetation, aquatic vegetation, and current speed [20–22], we classified the microhabitat in which individual turtles were observed using the following three independent variables (Figure 3):

(a) Water current speed—within a 10 m radius around the sighting point of each individual turtle we evaluated the water current speed by eye in one of three categories: 0 = no current; 1 = moderate current; 2 = high current.

(b) Bank type—we described the type of bank linked to the water body where each individual turtle was sighted as: 0 = no bank vegetation (only organic substratum, bare); 1 = rocky banks (rocky); 2 = bank with mainly herbaceous vegetation (grassy); 3 = forested banks, i.e., when the bank vegetation consisted of a strip of gallery forest.

(c) Aquatic vegetation—classified as: 0 = no aquatic vegetation; 1 = moderate aquatic vegetation (1–25% covered by aquatic plants); 2 = high aquatic vegetation (26–50% cover); 3 = very high aquatic vegetation (>51% cover). The percentage of aquatic vegetation cover was evaluated by eye within a radius of 10 m around the site of sighting of each individual turtle. Since we grouped vegetation in four large categories based on the estimated percentage of vegetation cover, this design would have been problematic in cases where the percentage of vegetative cover was at the limit between two categories (such as 24% in one site and 26% in another site). These sites would have been categorized such that they were as different as two sites that had e.g., 2% and 49% cover. Although these were clearly not equivalent comparisons, we defined the three percentages of vegetative cover categories after having examined the distribution of sample sizes to verify that there were no such "threshold cases" in our samples.

Figure 3. Habitat types of sympatric *Pelusios castaneus* and *P. cupulatta* in the southern Ivory Coast and, Inset, a basket with several individuals of the two species just trapped during the present surveys. (**Upper left** photo): river spot with moderate current, forested banks (i.e., with bank vegetation consisting of a strip of gallery forest) and moderate aquatic vegetation. (**Upper right**): marshland spot with no current, forested banks, and high aquatic vegetation. (**Lower left**): marshland spot with no current, grassy banks and high aquatic vegetation. (**Lower right**): Marshland spot with no current, forested banks and no aquatic vegetation. Photos: L. Luiselli.

Regarding each surveyed site, we also categorized the macro-habitat according to the following typologies: (1) rivers; (2) lakes/dams; (3) wetlands; (4) urban/artificial. We also used Google Earth to calculate river width in the various study sites. Concerning marshlands we denoted an area of low water, often covered with tall grass, whereas a wetland was considered land covered mostly by water, with some marshy and soggy areas.

2.4. Statistical Analyses

Macro-habitat and micro-habitat measurements were treated as independent variables and, thus, were retained in all analyses after having checked for correlations among all possible pairs of variables ($p > 0.05$ in all pairwise comparisons). We divided the whole dataset into two subgroups: (a) data collected from sites where both the study species were captured at least once (hereby "sympatric" sites); (b) data collected from sites where only one species (*P. castaneus*) was observed (hereby "allopatric" sites). We performed all analyses independently for allopatric versus sympatric sites: concerning sympatric sites we compared the data for the two species, whereas for allopatric sites we compared the data on habitat use by *P. castaneus* in sympatry versus allopatry. Although we also surveyed a few sites where only *P. cupulatta* was found (see below for more details), we were not able to analyze this species due to the small sample sizes ($n < 6$). Regarding these sites, we did not consider the sample sizes adequate to exclude the presence of *P. castaneus,* thus these data were not included in any analyses.

We evaluated the frequency differences of individuals captured by macro-habitat and micro-habitat variables, in sympatric sites (interspecific comparisons), and in allopatric sites (intraspecific comparisons) using contingency tables χ^2 tests. We set alpha at 5%, and performed all analyses using PAST 4.0 statistical software.

3. Results

3.1. General Data

Overall, we captured 149 *P. castaneus* (64 males, 66 females, 19 juveniles) and 91 *P. cupulatta* (43 males, 39 females, 9 juveniles) from 10 distinct sites where they co-occur in the same sites. We also captured 123 individuals of *P. castaneus* (52 males, 54 females, 17 juveniles) in eight sites where no *P. cupulatta* were found and we did not find any locations where only *P. cupulatta* was observed, apart from a few sites with numbers too low for any valuable analyses (Figure 2). Two other turtle species were observed within the surveyed sites: *Trionyx triunguis* and *Pelomedusa (subrufa) variabilis*. Both species were captured too unfrequently ($n = 3$ and $n = 11$ overall) for any meaningful analysis to be made and were not considered in our study.

3.2. Spatial Niche Characteristics in Sympatric Populations

Pelusios castaneus was captured mainly in marshlands, whereas *P. cupulatta* was recorded in both rivers and wetlands (Figure 4a); overall there was a significant interspecific difference in the frequency of individuals recorded in the different types of macro-habitat ($\chi^2 = 33.3$, df = 3, $p < 0.0001$).

Considering terms of bank-type we found a significant interspecific difference ($\chi^2 = 82.2$, df = 3, $p < 0.0001$). *P. castaneus* was found more in spots with grassy banks whereas *P. cupulatta* in spots with forested banks (Figure 4b).

Conversely, both species avoided a high current preferring a no or slow current equally, but we found no difference between species ($\chi^2 = 4.2$, df = 2, $p = 0.154$) (Figure 4c).

There was a clear and significant difference in the aquatic vegetation associated with each turtle species ($\chi^2 = 46.3$, df = 3, $p < 0.0001$), with *P. cupulatta* inhabiting spots with more abundant aquatic vegetation than *P. castaneus* (Figure 4d).

3.3. Spatial Niche Characteristics of Pelusios castaneus in Allopatry

There were significant differences in the frequency of observations of *P. castaneus* in allopatric versus sympatric conditions ($\chi^2 = 9.3$, df = 3, $p < 0.05$). There was a higher occurrence of the species in lakes/dams when allopatric (Figure 5a).

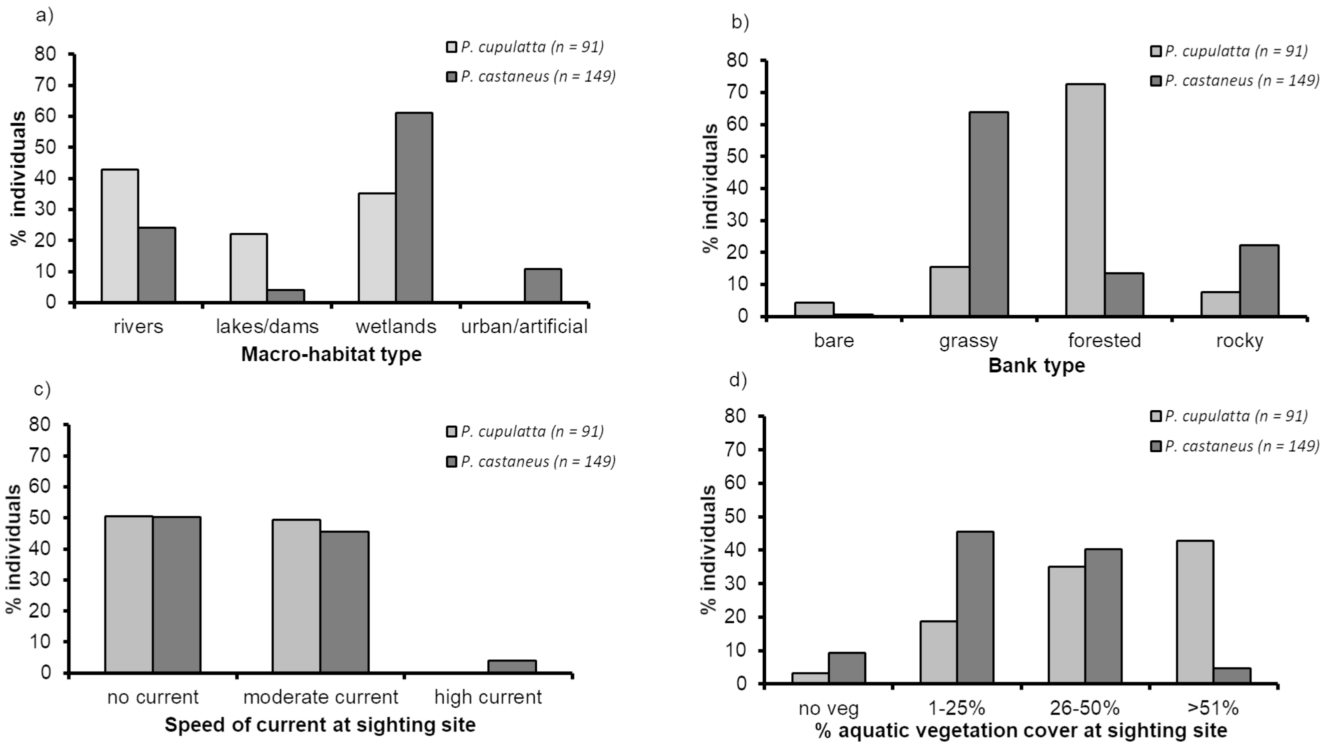

Figure 4. Distribution of the captures of turtle individuals by species and by macro-habitat (**a**), bank type category (**b**), current speed category (**c**), and aquatic vegetation category (**d**), in sites with sympatric populations of the two *Pelusios* species.

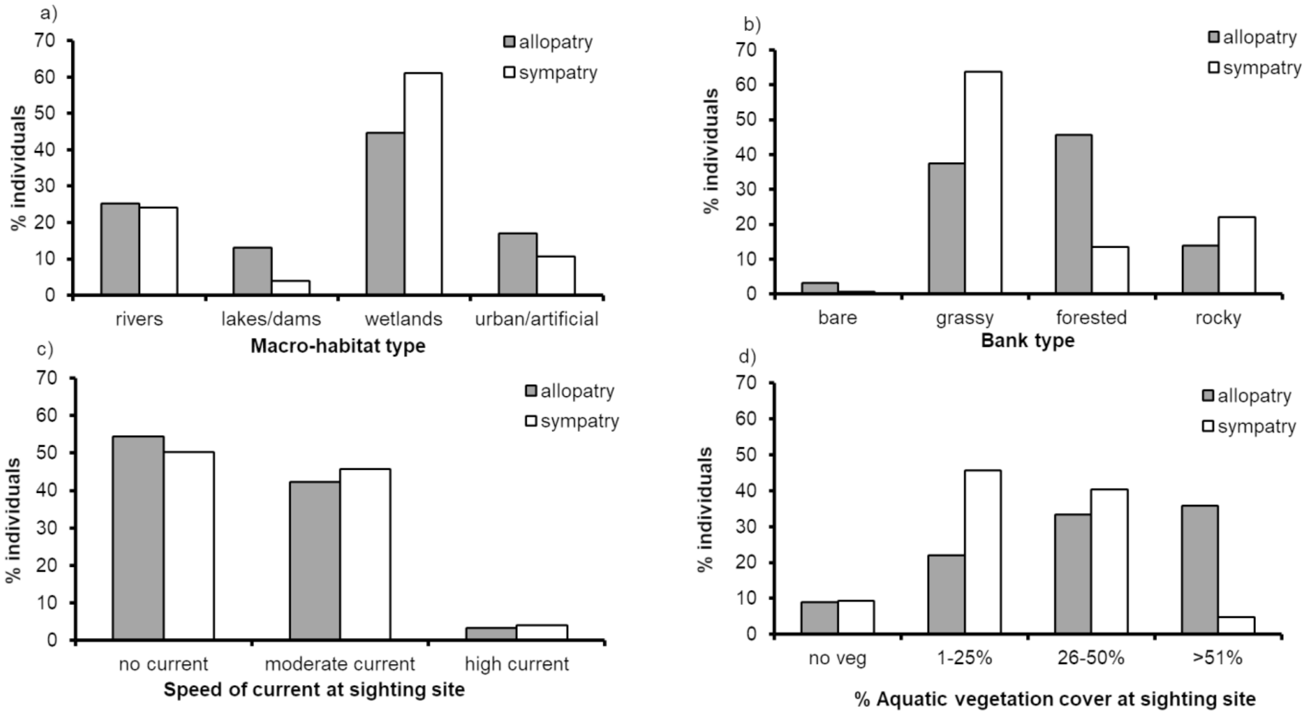

Figure 5. Distribution of the captures of *Pelusios castaneus* individuals (total $n = 123$) by macro-habitat (**a**), bank type category (**b**), current speed category (**c**), and aquatic vegetation category (**d**), in sites where it is allopatric versus sites in which it is sympatric with *P. cupulatta.*

Similarly, there was a significant intraspecific difference between allopatric versus sympatric conditions ($\chi^2 = 28.7$, df = 3, $p < 0.0001$), with *P. castaneus* clearly expanding its niche into forested banks when in allopatry (Figure 5b).

Pelusios castaneus individuals did not differ in allopatry versus sympatry in relation to the current speed ($\chi^2 = 0.4$, df = 2, $p = 0.819$) (Figure 5c). Instead, their utilization of aquatic vegetation changed significantly between allopatric versus sympatric conditions ($\chi^2 = 34.1$, df = 3, $p < 0.0001$), with these turtles clearly expanding their niche into highly vegetated spots (% of aquatic vegetation > 51%) when in allopatric conditions (Figure 5d).

4. Discussion

Our results suggest that *P. castaneus* and *P. cupulatta* exhibit differences in three of the four spatial niche characteristics considered in our study, notably macro-habitat and, in the case of micro-habitat characteristics, bank type and type of aquatic vegetation. Our analysis indicates that habitat partitioning occurs (possibly attributable, at least in part, to interspecific competition) in these two sympatric turtle species; this result is corroborated among three sympatric Pelomedusidae in seven study sites in southern Benin [4]. As previously noticed, the two species differed significantly in their maximum size (*P. cupulatta* being much larger; [18]). Given that body size differences are well known to minimize the strength of interspecific competition, at least from a theoretical point of view [23–25], we anticipate that the strongest competition should occur, if the resources are limited, between *P. castaneus* adults and *P. cupulatta* juveniles. Indeed, *P. castaneus* feed primarily on invertebrates during its whole life cycle [26] whereas *P. cupulatta* preys largely upon aquatic invertebrates during juvenile stages, but shifts to larger aquatic vertebrates (fish, frogs, and aquatic birds; Luiselli et al., pers. obs.) during the adult stage.

At a macro-habitat scale, *P. castaneus* was captured mainly in marshlands, whereas *P. cupulatta* was found in both rivers and wetlands. The two species differed significantly in their use of: (i) banks (*P. castaneus* being found mainly in spots with grassy banks and *P. cupulatta* in tracts of the waterbodies characterized by forested banks), and (ii) aquatic vegetation (*P. cupulatta* preferred spots with more abundant aquatic vegetation than *P. castaneus*), but both species selected sites with no or moderate current. Overall, the microhabitat preferences (bank and aquatic vegetation types) were consistent with the general distribution features of the two study species, as *P. castaneus* is distributed also in open-land waterbodies [4,18] whereas the same is not true for *P. cupulatta* [18]. However, because our data were collected over a short time period, we did not incorporate potential effects of seasonality that could have influenced habitat usage and location characteristics. During the dry season, for example, patches of land that are otherwise inundated are often dry and may become unsuitable for aquatic turtles. In this case, Pelomedusid turtles normally remain inactive in congealed mud, in shady and covered sites. Seasonal variations in habitat use have already been observed in West African aquatic reptiles [27] and, thus, could not be excluded in the case of turtles, especially in those marshlands and flooded banana plantation sites where water is available almost exclusively during the wet season.

Our study documented habitat partitioning between the two *Pelusios* species. Nonetheless, descriptive evidence of the occurrence of habitat niche partitioning may not be sufficient to conclude whether the two species do really compete when sympatric. To uncover whether interspecific competition may regulate the sympatric coexistence of potential competitors, comparisons of the patterns of resource use by a given species in the presence versus absence of the potential competitor may be instrumental [28,29]. Thus, the comparison of the patterns of habitat uses by *P. castaneus* in the sites where it was sympatric with *P. cupulatta* versus those where it was allopatric provided significant results. Obviously, the more conservative assumption is that the habitat use should not change between sympatric and allopatric conditions if only species-specific preferences and no-effect of interspecific competition are found, whereas the habitat use should change if an effect of interspecific competition is detectable [28,29]. However, we do not present data to demonstrate that the resources found in the areas of sympatry and allopatry are similar and, thus, the above hypothesis should be considered with caution. Interestingly, our study revealed that *P. castaneus* appeared to utilize intensely forested banks in sites where *P. cupulatta* was not found, whereas it avoided these habitats where *P. cupulatta* was present. We could not interpret this pattern differently from habitat shifts linked to interspecific competition release, with *P. castaneus* being the least strong competitor in sympatric conditions in the forest waterbodies of the southern Ivory Coast. Thus, the local distribution/abundance of *P. castaneus* may be constrained by that of *P. cupulatta*, a much bigger and certainly more aggressive species. Luiselli et al. [4] also observed in southern Benin that there were indications of habitat shifts in the presence versus absence of competitors among sympatric Pelomedusidae species. Thus, we would anticipate that (1) interspecific competition (for the spatial resource and perhaps for the trophic resource) may be a generalized component of the community interactions among Pelomedusidae species in tropical Africa, and that (2) mechanisms of spatial niche expansion may be widespread in these turtles when a given species occurs alone rather than in sympatry with other potential competitors.

Pelusios cupulatta appeared to be rather a habitat generalist at both spatial scales, although forested banks appeared the most important correlate of presence and abundance for this species. Considering that this species has been considered for a long time conspecific with *P. niger*, and that this latter species is a habitat specialist of rainforest waterbodies [4,30], this result is surprising and highlights that the two species may actually differ in terms of their ecological plasticity and ability to adapt to deforested sites. The hypothesis that *P. cupulatta* may be a habitat generalist in the southern Ivory Coast also is reinforced by the fact that it appears locally abundant in riverine/freshwater habitats nearby Abidjan, where the main forest has been cut for decades and where plantations (for instance, inundated old banana plantations) are now the dominant available habitat (Gonedele Bi and Luiselli unpublished). The conservation implications of this differential ecology between *P. cupulatta* and *P. niger* should be carefully assessed in the years to come. However, the definition of “generalist” still depends on the availability of habitat (a generalist should use habitat in proportion to its availability and not have any strong preferences). Since we did not collect data on the relative availability of each habitat type in the study area, we suggest that *P. cupulatta* may be a habitat generalist but this possibility certainly warrants further study.

We are aware that our study may suffer from some shortcomings that must be taken into account. Our inferences were made on the basis of locations where turtles were captured (presence-only data). Although these data clearly allowed us to define which habitats the turtles were using, both sampling characteristics (i.e., type of traps, length of the trapping phase, levels of human presence/disturbance around traps, seasonality, see below) and habitat availability (for instance, if differential trappability may characterize different habitat types or even different study areas) may have affected our results and may actually limit our interpretation of habitat preference and competition. Additionally, our actual statistical treatment would need an Non-metric Multidimensional Scaling analysis to consolidate our data; in this case, we preferred to wait for this additional analysis for when we will have more individuals and, moreover, access to an allopatric population of *P. cupulatta* to make the whole analysis more sound. Anyway, more focused field studies should be undertaken to explore in detail the potential biases arising from different sampling schemes/characteristics and by the effect of differential trappabilities by habitat type, as well as also precisely characterizing availability and use of each habitat type by turtles in each study site. Indeed, the choice of trapping method may have influenced sampling of the turtles [31], and the time of year also may have affected trapping. The ideal period for catching freshwater turtles is, in the savannah waterbodies of Ghana, the dry season (Gwebaa et al., submitted), but in the forest wetlands/marshlands of southern Nigeria it is the wet season [32]. Thus, it is not clear when the best trapping season is in our study area. Regarding seasonal ponds, aestivation during the dry season may occur, thus lowering turtle numbers [32], but this may not be the case in permanent waterbodies. The potential influence of sampling bias and habitat availability should be considered when interpreting the results herein presented. Additionally, studies on the trophic niche characteristics of the two species in sympatric versus allopatric conditions should be carried out, as interspecific competition and food niche partitioning often have been discovered in freshwater turtle communities from elsewhere, including West Africa [5,14,33].

Author Contributions: Conceptualization, L.L.; methodology, L.L., S.G.B.; validation, L.L., J.E.F.; formal analysis, L.L. and N.P.; investigation, F.P., D.D., L.L., S.N.A., S.G.B.; resources, L.L.; data curation, D.D. and F.P.; writing—original draft preparation, L.L.; writing—review and editing, S.G.B., N.P. and J.E.F.; supervision, L.L. and J.E.F.; funding acquisition, L.L. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement: Ethical review and approval were waived for this study, due to the fact that the two study species are free to catch and even to consume in Ivory Coast and do not need any capture and handling permit. In addition, no individuals were sacri-fied during the process of this study.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are reported in the figures and along the main text. Data not shown in figures/text are available on request from the corresponding author. The data are not publicly available due to ongoing longitudinal analysis.

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Conflicts of Interest: The authors declare no conflict of interest.

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