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# Habitat use and spatial niche overlap of sympatric savannah tortoises at multiple spatial scales in South Sudan

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## ABSTRACT

Tortoise ecology is poorly studied in East Africa. Here, using two terrestrial Testudinidae (*Stigmochelys pardalis* and *Kinixys belliana*) as study models, we (i) present basic demographic characteristics (sex-ratio, and density),  (ii) describe correlates of their presence at two spatial scales (micro-habitat and macro-habitat), (iii) evaluate the effects of rainfall on their seasonal activity patterns, and (iv) analyze abundance patterns in relation to macro- and micro-habitat characteristics. We also describe an experiment, using tortoise shells, that can allow to control, and eventually correct, the reliability of observed data by taking into account the detectability of the study species in the wild. On the basis of a suite of statistical analysis and GIS-based elaborations, we confirmed, and further uncovered, the remarkable ecological differences existing between *S. pardalis* and *K. belliana.* The habitat use was different interspecifically, with *K. belliana* being much more linked to dense vegetation spots, often nearby waterbodies, whereas *S. pardalis* being an habitat generalist, at both micro- and macrohabitat scale. Nonetheless, juveniles of both species were observed in areas with significantly higher % soil covered by vegetation taller than 200 cm than adults of both sexes. This different habitat selection is hypothesized to be due to antipredatory reasons.  Overall, our data suggests that interspecific competition should be minimal between these species.

*Keywords: Tortoises; Habitat selection; Ecology; East Africa*

## 1. Introduction

Worldwide, there are currently approximately 360 recognized species of extant and recently extinct turtles and tortoises (Order Testudines), a much lower number than that in any other vertebrate group of similar body size (Luiselli, 2006a). Given the low species richness of terrestrial chelonians typically found in any locality, in most assemblages there are from 2 to 4 sympatric taxa (Iverson, 1992). In Africa, most regions contain just 1 or 2 sympatric species (e.g., Hailey & Coulson, 1995), however, in other localities (i.e., South and West Africa) up to 4 sympatric species can be found (Iverson, 1992; Luiselli, 2003).

Natural assemblages of tortoises are considered not to exhibit interspecific competition, with species-specific eco-physiological characteristics being more important (Luiselli, 2006a). This characteristic of the group may be related to the very low number of sympatric species, coupled with the typical life-history characteristics of chelonians: long-life span, delayed maturity, generalist omnivorous or herbivorous habits (Luiselli, 2006a). Nonetheless, because the available information on tropical terrestrial chelonians is scarce, it is difficult to understand patterns of coexistence. One of the main reasons for this lack of data is the elusive behaviour of free-ranging tortoises in hot tropical climates. As a result, it is often difficult to determine whether observed patterns are affected by small sample sizes, are exacerbated by the complicated landscape in which the species occur, or by the effect of interspecific differences in elusiveness and therefore detectability (de Solla et al., 2005; Mazerolle et al., 2005; Watkins et al., 2010).

In Africa, coexistence studies of tortoise species have been undertaken in savannahs of Zimbabwe (e.g., Hailey & Coulson, 1995; Coulson & Hailey, 2001), in West African Sahel (Petrozzi et al., 2020), and in West African Guinean forests (Luiselli, 2003, 2006b; Luiselli et al., 2008), but only anecdotal observations are available from the other regions of the continent (Branch, 2008). In this paper, we investigated the coexistence of two savannah tortoises (family: Testudinidae) in South Sudan (East Africa): the leopard tortoise (*Stigmochelys pardalis*) and Bell's hinge-back tortoise (*Kinixys belliana*) (Figure 1). Here, we (1) present the basic demographic characteristics (sex-ratio, and density) of these two species, (2) describe correlates of their presence at two spatial scales (micro-habitat and macro-habitat), (3) the effects of rainfall on their seasonal activity patterns, and (4) analyze abundance patterns in relation to macro- and micro-habitat characteristics. We also describe an experiment, using tortoise shells, that can be easily replicated in other tortoise studies, that may allow ecologists to control, and eventually correct, the reliability of observed data by taking into account the detectability of the study species in the wild.

## 2. Materials and methods

### *2.1 Study area*

Data was collected at several sites in the Republic of South Sudan, a landlocked country in East-Central Africa. Most surveys were performed in the South Sudan Equatoria Region (including Central Equatoria and the Eastern Equatoria States), especially within and in the surroundings of the Bandingilo National Park. This protected area, near the White Nile River, encompasses aproximately 8,400 km$^2$ and is 40 km east of the main town of Mangalla in Jubek State. Most of the area is flat with occasional isolated large hills, and contains numerous rivers and lakes. Due to the low-lying land and predominantly clay-based soils, the park is prone to flooding during the rainy season. To the east, the soil is well drained sand looms,while black cotton soil occurs in the lower land, andis often waterlogged.

The climate of the region is tropical, with a wet season in April – October (with an average of 100 mm rainfall per month) and a dry season between November – March (5-35 mm per month); during the dry season the hottest maximum temperature of 38°C is recorded in February. The typical vegetation is savannah, with small patches of dry forest and bushlands. The dominant trees in the park include *Acacia seyal*, *Afzelia quanzensis, Balanites* spp., *Celtis* spp., *Calotropis procera, Combretum* spp., *Cassia* spp., *Dichrostachytus cinera, Erythrina* spp., *Euphorbia ingens, Euphorbia candelabra, Ficus* spp., *Kigerlia africana/aethiopica, Virtex doniana, Ziziphus* spp., *Tamarindas indica*, and *Azadirachta indica*. The area also contains swamp meadows of dense low stoloniferous grasses such as antelope grass (*Echinochloa pyramidalis*) interspersed with patches of taller clump-forming grasses, as well as an understory of Jaragua grass (*Hyparrhenia rufa*). . The park provides very fertile grazing lands for cattle as they are abundant and widespread across the area and they represent a source of food, a form of currency and a symbol of social status for the local inhabitants of this area (the Mundari, Pari and Bari tribes).

### ***2.2 Data collection***

#### *2.2.1 Tortoise detection experiment*

This experiment was performed during July – August (wet season) and October – November (dry season) of 2019. A total of 14 *S. pardalis* shells and 16 *K. belliana* shells were randomly placed in open spaces or hidden under bushes (simulating the "normal" habits of the study species) along 300 m line transects (n = 3) in natural savannah habitats. Transects were laid out in three cover types of vegetation taller than 2 m: 1) 0-30%; 2) 31-60%; 3) >60% (Figure 2). Three experienced observers in tortoise field research (who were unaware of the location ofthe tortoise shells) were asked to walk slowly along these transects and locate as many shells as possible. This procedure was repeated three times, changing the position of the shells on each occasion (during three separate days) for each transect and for each season. We estimated the mean percentage of observed shells (by season and by vegetation cover category, i.e. open space and under bushes).

#### *2.2.2 Field surveys for free-ranging tortoises*

We surveyed wild tortoises in the Equatoria State all year round from 2017 – 2019. We also used location data from additional records of tortoises from our unpublished research from 1989 onwards. A team of three researchers searched for tortoises from 0700 – 1800 (suspending searching during the hottest midday hours) within bush and grasslands, as well as in stony places and other potential tortoise habitats. Fieldwork was suspended during heavy rains. An average of 15 man-hours were spent in the field during each survey day. Field surveys consisted of slowly walking along a single randomly selected, separate, line transects (300 m long) throughout the survey sites in the study region. We walked a total of 416 transects, encompassing 124,800 m. The researchers were about 30 m apart each another, and the same transects were not repeated during the study period.

During each field survey, we recorded all individuals seen of *S. pardalis* and *K. belliana* .. We recorded date and time of each sighting, logged its GPS location, measured the size (curved carapace length) of the tortoise using a rope, noted its sex, and shell notched it for individual identification.

To assess macro-habitat correlates of the presence/absence of the two study species, we used the location data for all tortoises found during our surveys and those in historical datasets collected since 1989. For each observed tortoise, we also recorded micro-habitat characteristics within a 200 m radius from the exact point of the first sighting of the individual tortoise (see also Petrozzi et al. 2020). For each observed tortoise, the following micro-habitats were measured in the field: (a) % soil covered by vegetation taller than 200 cm; (b) % sandy (not rocky or compact) soil; (c) presence/absence of waterbodies (even if small and temporary); (d) presence/absence of cattle (and signs of their presence). For variables (a) and (b), percentages were visually estimated in ten randomly chosen 2 x 2m quadrats from which we calculated the median of all values.

For macro-habitat characteristics, we used remotely accessed data using a GIS platform. We created a shapefile for each species containing all records, from which we created a minimum convex polygon shape file. We also enlarged this polygon by creating a buffer zone of 10 km to avoid any edge effects (Petrozzi et al., 2019). Using the Random Points algorithm, we created a second shape file with random points (n =100 both for *S. pardalis* and for *K. belliana*) inside the increased minimum convex polygon area (Petrozzi et al., 2019). We then merged presence and random points shapefiles into a single file, using UTM 31 N coordinates. We created a new shapefile (with coordinates WGS84) of buffer areas with 3-km radii around each presence and random point.

We extracted all information for the following variables within the buffer areas,  for the combined shapefile including  the presence records and the random buffer areas by using the zonal statistic tool:

a. Tree cover raster (Hansen et al. 2013) representing the percentage of forest; it ranges between 0 and 100 per output grid cell;

b. Land use raster (http://www.fao.org/geonetwork/srv/en/main.home) representing the characteristics of the land. All the categories of the variables are present in table S1;

c. Rainfall (Food and Agriculture Organization of the United Nations–United Nations Environment Programme 1984) representing the average annual rainfall, and is expressed in terms of millimetres (mm) per year;

d. IUCN Protected Areas of Africa data set (https://cmr.earthdata.nasa.gov/search/concepts/C1214603932-SCIOPS) representing 11 different types of parks, reserves and other unique areas which had some degree of protected status;

e. temperature (Harvest Choice 2015 a) representing the air surface temperature in °C ;

f. vegetation map of Africa (White, 1983).

All rasters were resampled at the same cell. Additionally, we uploaded the following shapefiles:

a. roads (Center for International Earth Science Information Network (CIESIN)/Columbia University, and Information Technology Outreach Services (ITOS)/University of Georgia 2013);

b. rivers (http://worldmap.harvard.edu/data/geonode:Digital_Chart_of_the_World);

c. lake (http://worldmap.harvard.edu/data/geonode:Digital_Chart_of_the_World);

d. human settlement (Harvest Choice, 2015b); including settlement population estimate

and we calculated the distances (in km) of all the above-mentioned layers from the presence and random points by using the 'QGIS NNJoin' plugin (Dharmawan, and Farda, 2017).

On the basis of the number of tortoise individuals, we calculated the kilometric index of abundance (KIA) (Maillard et al., 2001):

KIA = (number of individuals / numbers of kilometers covered).

In this formula, the number of kilometers covered represents the sum of the total distance of the transects.

### *2.3 Statistical analyses*

We employed Generalized Linear Models (GLZ, Hosmer & Lemeshow, 2000) to test the effect of season (dry vs wet season) and time of the day (morning vs evening) on the detectability of *S. pardalis* and *K. belliana* during the field experiment with shells. In every model, the season and the period of the day were used as dependent variables and the number of detected shells in plots with different vegetation cover (0-30%, 31-60%, 61-100%) as predictors. In all models, the logit link function and a binomial distribution of error were used (McCullagh & Nelder, 1989). We also ran a global GLZ model to test for the possible differences in detection of the two species.. In this global model we used the species, the season and the period of the day as dependent variables respectively, and the % of vegetation coverage as predictors. Also the joint effects between species, seasons and period of the day were analysed.

Generalized Linear Models (GLM, Hosmer & Lemeshow, 2000) were used to quantify the effects of habitat classes on the abundances of *K. belliana* and *S. pardalis* inside the study area. In the models, a best subset procedure was used to test the statistical significance of each variable. The abundance of species were used as a dependent variable and the number of contacts for each habitat types as predictors.

We standardized all variables to remove the effect of differences in the original scale of measurement. The standardization of values contains options to standardize all values of the selected variables used in the model. All values of selected variables are replaced by standardized values, which are computed as follows: Std score: (raw score – mean) /Std. Deviation using Statistica 6.0 software (www.statsoft.com). In all models, the identity link function and a normal distribution of error were used (McCullagh & Nelder, 1989).

We also performed a GLM to test the effect of months and macro-habitat on *S. pardalis* and *K. belliana* body size (male and female separately) using turtle body size as dependent variable and months and macro-habitat types as predictors. Pearson's correlation coefficient, between number of days per month and number of observed tortoises detected in each month, was used to assess the effects of rainfall on tortoises' above-ground activity patterns. In this case, due to the small sample sizes, we used pooled data of the two study species as a dependent variable.

We performed a logistic regression analysis to determine the effect of the various macro-habitat variables on the presence/absence of the two study species. The variables were entered as independent variables in the logistic regression analysis, with the presence/absence data for the tortoises as the dependent variable. Selection implied limited correlation between the environmental variables, with a Spearman correlation coefficient = 0.47 in our study cases. When the Spearman correlation coefficient is less than 0.8, this type of analysis is correct (Teixeira et al.

2001; Arntzen & Alexandrino 2004). We performed logistic regression analyses by SigmaPlot 14.0 version PC software.

One-way ANOVAs (followed by Tukey HSD post-hoc pairwise tests) were used for testing, in each of the study species, the statistical differences between sexes and among adults versus juveniles in terms of the four micro-habitat variables mentioned above. Interspecific differences in terms of % sandy soil of the sighting spots and in terms of % soil covered by vegetation taller than 200 cm were evaluated by Student t-test. Contingency table $\chi^2$ test was used to evaluate (i) sex-ratio of the observed individuals of the two species, (ii) interspecific frequencies of sightings spots with nearby water and (iii) interspecific frequencies of sightings spots with nearby cattle.

The spatial distribution of the various variables used for defining the ecological correlates of occurrence in the two study species are presented in the Supplemental Fig. S1 (*S. pardalis*) and S2 (*K. belliana*). All statistical analyses were performed by the software SigmaPlot 14.0 version, with alpha set at 5%. In the text, the means are followed by ± 1 Standard Deviation.

## 3. Results

### *3.1 General data*

We observed a total of 107 tortoises, 63 *S. pardalis* and 44 *K. belliana*. The KIA index for *S. pardalis* was 0.504 individuals × km$^{-1}$ and 0.00035 individuals × km$^{-1}$ for *K. belliana*. Using a boundary strip of 8 m on both sides of each transect, we calculated a density of 0.315 individuals/ ha for *S. pardalis* and 0.22 individuals/ ha for *K. belliana*.  All presence localities and randomly generated points for the two study species in South Sudan are given in Figure 3. For *S. pardalis*, our sample size consisted of 20 males, 39 females and 4 juveniles; sex ratio was not skewed from equality ($\chi^2$ = 3.1, df = 1, P = 0.094). In the case of *K. belliana*, we recorded 23 males, 15 females and 5 juveniles. Adult sex-ratio was even ($\chi^2$ = 0.9, df = 1, P = 0.339).

### *3.2 Smaller-scale habitat use*

#### *3.2.1 Tortoise detection experiment*

Overall, the results of the field experiment indicate that shells of *S. pardalis* were slightly easier to locate than those of *K. belliana* during the dry (respectively 73.8% versus 67.7% of the shells uncovered by surveyors) and wet season (respectively 65.5% versus 60.4%)(Table 1).

For *S. pardalis*, the GLZ results showed no effects of season or time of the day on the detectability of shells (Table 2). The plot with 0-30% of coverage was not included in the model because of no deviance. The GLZ results also showed no effects of season and time of the day on *K. belliana* shells detectability (Table 2). We found no significant effect of % vegetation coverage on the species' detection probabilities in the global GLZ model to test for the possible differences on the two species' detection (Table 3). Overall, since there were no statistical differences in the probability of detecting the two tortoise species in the field, despite their remarkable differences in coloration and size, we used the field data collected on the two species (see below) without statistical corrections.

### *3.3 Micro-habitat characteristics of the tortoise records*

*Kinixys belliana.* The synopsis of the data is presented in Table 4. The various sex/age groups did not differ significantly in terms of % sandy soil of the sighting spots (one-way ANOVA. $F_{2,40} = 0.45$, $P = 0.641$), and in terms of % soil covered by vegetation taller than 200 cm of the sighting spots (one-way ANOVA. $F_{2,40} = 2.65$, $P = 0.08$). Interestingly, although these tortoises clearly selected well vegetated spots (with the mean percent of high vegetation cover being 77% for males and 82% for females), the juveniles appeared to select only highly vegetated spots (97% being the average high vegetation cover of their spots of sightings; Table 4). Cattle were observed in 4.6% of the sighting spots, whereas water was frequently found nearby the sighting spots (58.1% of cases [n = 43]).

*Stigmochelys pardalis.* The synopsis of the data is presented in Table 4. There were significant differences among sexes/age classes in terms of % sandy soil of the sighting spots (one-way ANOVA. $F_{2,60} = 3.66$, $P < 0.05$), with juveniles being observed in spots with significantly higher % sandy soil than adult males (Tukey Honest significant post-hoc test: $P = 0.013$). There were also inter-group differences in terms of % soil covered by vegetation taller than 200 cm of the sighting spots (one-way ANOVA. $F_{2,60} = 10.21$, $P < 0.001$), with juveniles being observed in spots with significantly higher % soil covered by vegetation taller than 200 cm, than adults of both sexes ($P < 0.001$), with males and females being very similar instead ($P = 0.858$). Cattle were present in 6.3% of the sighting spots, and water was present in 9.5% of the sighting spots.

*Interspecific differences*. The two species did not differ in terms of % sandy soil of the sighting spots ($t = 1.51$, $P = 0.135$); however, % soil covered by vegetation taller than 200 cm of the sighting spots of *K. belliana* was significantly higher than that of *S. pardalis* ($t = 8.53$, $P < 0.0001$). In addition, the frequency of sightings spots with nearby water was significantly higher in *K. belliana* ($\chi^2$ test, $P < 0.001$), whereas there was no interspecific difference (at $\chi^2$ test) in terms of frequency of sightings spots with cattle presence (Figure 4).

### ***3.4 Larger-scale habitat use***

#### *3.4.1 Macro-habitat effects on sympatric tortoise abundances*

*Kinixys belliana.* The model showed that the abundance of this species increases with the increase of forested areas (estimate = 0.592; Wald = 2.068; p=0.0000) and savannah (estimate = 1.244; Wald = 9.121; p=0.0000).

*Stigmochelys pardalis.* The model showed that the abundance of this species increases with the increase of forest (estimate = 0.988; Wald = 5.450; p=0.0000) and decrease with shallow/inundated areas (estimate =-0.021; Wald = 2.938; p=0.0000).

### *3.4.2 Effects of months and macro-habitat on body size*

*Kinixys belliana.* The model highlighted a positive relationship with months (estimate = 0.394; Wald = 5.216; p=0.00223) and body size for the females, and a positive effects of months (estimate = 2.335; Wald = 18.132; p=0.00002) and macro-habitat (estimate = 1.920; Wald = 9.001; p=0.00269) for males.

*Stigmochelys pardalis.* Our model did not detect any effect of sex (estimate = 0.394, Wald = 0.194, P = 0.711), months (estimate = 0.820; Wald = 1.185; p=0.276) and macro-habitat types (estimate = 0.472; Wald = 0.226; p=0.634) on body sizes of these tortoises.

### ***3.5 Rainfall effects on sympatric tortoise records***

The distribution of the number of observed tortoises across months is presented in Supplemental Figure S3. After pooling the data coming from the two study species, the highest numbers of individuals per month were found in July (n = 27) and August (n = 32). There was no sighting from November to February. Overall, there was a significant positive correlation between the monthly number of rainy days and the number of observed tortoise individuals (r = 0.636, n = 12, $P < 0.05$; Figure 5).

### ***3.6 Correlates of large-scale occurrence of the two species***

*Kinixys belliana.* The multiple logistic regression model (Likelihood ratio test statistic = 16.982, P = 0.005; -2 log (likelihood) = 76.094; Hosmer-Lemeshow statistic = 7.69, P = 0.464) resulted in two of the variables being statistically significant: tree density (positively correlated to the probability of presence of the species: coefficient = 0.0000154, standard error = 0.00000777, Wald = 3.948, P = 0.047) and distance from the nearest water-body (negatively correlated to the probability of presence of the species: coefficient = -0.000157, standard error = 0.0000869, Wald = 3.261, P =

0.041). All the other variables were not significant (at least P = 0.110). Thus, the logit equation was as follows:

$$\text{Logit } P = -1.858 - (0.000157 \times \text{distance from water-body}) + (0.0000154 \times \text{tree density}).$$

*Stigmochelys pardalis.* The multiple logistic regression model (Likelihood ratio test statistic = 13.739, P = 0.033; -2 log (likelihood) = 101.402; Hosmer-Lemeshow statistic = 11.114, P = 0,195) gave a different outcome compared to the previous species. Indeed, only one variable was statistically significant: distance from road (positively correlated to the probability of presence of the species: coefficient = 0.0000923, standard error = 0.0000407, Wald = 5.15, P = 0.023). All the other variables were not significant (at least P = 0.102). Thus, the logit equation for *S. pardalis* was as follows:

$$\text{Logit } P = -3.079 + (0.0000923 \times \text{distance from the nearest road}).$$

## 4. Discussion

### *4.1 Tortoise detection experiment*

Our experiment with tortoise shells clearly revealed that, despite their very different shell sizes, the detectability of the two species was not remarkably different in the field (although of course the smaller species was slightly less detectable than the larger species independent of season and time of day). This result is important because it shows that, the data relative on the coexistence ecology of these two species in the South Sudan savannahs may have not been due to detectability issues. This may also be typical in other terrestrial tortoise assemblages though differences in the behavioural elusiveness and the relative population density of the various sympatric species may influence the outcomes of the field research. Capture and sighting frequency of terrestrial tortoises are affected by sampling effort, time of day, season, size of the species as well as habitat type (Coulson and Hailey, 2001; Kabigumila, 2001a, 2001b; Willemsen and Hailey, 2001).

Moreover, previous experiments with shell models along line transects suggest that a large percentage of geometric tortoises could not be found during a census, as no observer was able to detect more than 50% of the models (Gardner et al., 1999).

### *4.2 Tortoise abundance*

Despite being considerably larger in body size (Hailey and Loveridge, 1998; Branch, 2008), the observed density of *S. pardalis* was far higher in our study area than that of *K. belliana*. For *K. belliana*, the observed density is consistent with data from other species of the same genus, *K. homeana, K. nogueyi, K. erosa*, and *K. spekii*, that ranged 0.15-2.85 individuals × ha$^{-1}$ (Coulson & Hailey, 2001; Luiselli, 2006). Density of *S. pardalis* was much higher in our study area than in South Africa's Nama-Karoo, where it was just 0.017 tortoises × ha$^{-1}$ (McMaster & Downs, 1996), but was less than that (0.85 individuals × ha$^{-1}$) that was recorded in Addo National Park, South Africa (Vetter, 2005).

In both species, the population was skewed towards adults, thus indicating a low hatchling recruitment (although juvenile elusiveness should be considered in this regard). The same was also observed in other *S. pardalis* from South Africa (McMaster, 2013) and in other *Kinixys* species from Nigeria (Cayuela et al., 2019). Adult sex-ratio was even in our study populations, and the same was true for *S. pardalis* from both Tanzania and South Africa (Vetter, 2005; McMaster, 2013) and *Kinixys* species from West Africa (Segniagbeto et al., 2015).

### *4.3 Micro- and macro-habitat characteristics of the tortoise records*

Despite the small sample size, and supported by our shell detection experiment, we can confidently argue that our macro- and micro-habitat data were not biased for the two tortoise species. Thus, we can conclude that the collected data are indicative of the true habitat use patterns of the two study species.

At the micro-habitat scale, the two species clearly exhibited different preferences: *K. belliana* selected spots with high vegetation cover and with waterbodies in their surroundings, whereas *S. pardalis* was more of a generalist, showing no special preference for open/close vegetation or for presence/absence of waterbodies. However, in both species, juveniles inhabited spots with denser high vegetation than adults. For *K. belliana*, there is little published data available on its microhabitat use patterns apart from anecdotal information (e.g. Branch, 2008). However, some data on habitat selection by the closely related West African *Kinixys nogueyi* have been published (Luiselli et al., 2000; Segniagbeto et al., 2015), and can be used for comparisons. These studies documented that most *Kinixys nogueyi* specimens were found in Guinea savannah, but also inhabited rainforest patches and hilly forests. Another closely-related species, *Kinixys spekii*, was found to be associated with the dense riverine woodland along the Kove river, Zimbabwe (Hailey and Coulson, 1995). Thus, the fact that the closely-related and ecologically-similar *K. belliana* can select highly vegetated sites, nearby water, in a otherwise dry savannah habitat, cannot be considered surprising. Also, at the larger spatial scale, the distribution of *K. belliana* was positively influenced by the tree density and negatively by increasing distance from the nearest water-body, thus exactly confirming the pattern highlighted by our smaller-scale dataset. Based on these evidences and the locationsy of moist forests and dense bushlands/gallery forests in the country, we would suggest that the distribution of this species in South Sudan is scattered, and especially concentrated in the southern regions of the country.

In the case of *S. pardalis*, our study revealed a generalist habitat strategy (at both a micro- and macro-scale), where basically only the need of minimizing human disturbance (expressed by the distance from roads and paths) matters.. In Zimbabwe, *S. pardalis* was found to inhabit open riverine and large areas of pure mopane (*Colophospermum mopane*) bush habitats (Hailey and Coulson, 1995) but was considered an habitat generalist elsewhere (Greig & Burdett, 1976; Rall, 1985; Douglas & Rall, 2006), inhabiting even commercial farmlands (Drabik-Hamshare, 2016). In Tanzania, it was found frequently in short grass and along roads (not consisting with our findings), but also inside bushes and in medium tall grass, whereas it was rarely seen in tall grass and in the surroundings of waterbodies (Kabigumila, 1998, 2001c). Weatherby (1996) reported that these tortoises prefer open grassy areas, occasionally venturing into thick thornbush. Thus, overall our data mirrors those presented in the above-mentioned earlier studies, confirming that this species is a savannah habitat generalist that usually avoid high vegetation cover (just about 28% of our adult sample was found in highly vegetated spots). Based on this evidence, we would suggest that the distribution of this species in South Sudan is probably wide and continuous, especially in the central and eastern regions of the country.

As mentioned above, the juveniles of both species consistently revealed a much greater preference for very closed vegetation spots compared to adults. This is unlikely to be an outcome of small sample size (typically juvenile tortoises are very elusive; see also low encounter rates in Berry & Turner, 1986, and in Cayuela et al., 2019), as locating small tortoises is certainly much more difficult in closed vegetation than in open vegetated places. Instead, we think that this pattern reflects antipredatory adaptations in habitat selection by small tortoises.Malan & Branch (1992) reported cases of predation on *S. pardalis* hatchlings by birds of prey. In a radiotracking study on juveniles of an herbivorous tortoise species (*Gopherus agassizii*) from an arid environment, locations were more likely to be under the cover of perennial plants, , and in a greater number of small-mammal burrows. (Todd et al., 2016). In addition, juveniles of an omnivorous species (*Terrapene carolina bauri*) from a wetter area also preferentially used microhabitats with dense vegetation (Jennings, 2007), thus our data are very consistent with the few available studies on microhabitat preferences of juvenile turtles and tortoises from elsewhere..

### *4.4 Effects of months and macro-habitat on body size*

Our GLM analyses showed that the body size of adult *K. belliana* males is larger in capture sites with higher percentages of bush and tree cover; and, for both sexes, body size tends to be larger in different time periods (i.e. from March to October), no pattern emerged for *S. pardalis*. This is possibly the most complicated pattern to explain in our study, and only tentative interpretations can be provided. Concerning the pattern of large males found preferably in high vegetation spots, we would suggest that this is an antipredatory strategy. In other turtles and tortoises, large males tend to have larger home ranges than smaller males and females (e.g., Rose & Judd, 1975; Geffen & Mendelssohn, 1988; O'Connor et al., 1994) so it is possible that males prefer to utilize closed canopy sites to minimize the increased costs of traveling due to predation, as increased movement presents greater risk (Lima & Dill, 1990; Fahrig, 2007). It is also possible that the males are resting in the shade of the plants as a means of thermal cooling after traversing their large homerange, or possibly that larger tortoises are easier to visualize in vegetation.

### *4.5 Rainfall effects on sympatric tortoise records*

Our data clearly revealed that the frequency of encounters with tortoises increases with the number of rainy days per month (a good proxy of the monthly rainfall). This is a general pattern with African tropical tortoises (Luiselli, 2003), and it has been already observed, for instance, in West African rainforest *Kinixys* species (e.g., Luiselli, 2003). In addition, in the dry savannahs of Swaziland, the above-ground activity of radiotracked *S. pardalis* was greater in the warm wet months compared with the cool, dry months (Monadjem et al., 2013). In another study in South Africa, there was a positive correlation between number of tortoises caught and rainfall per season, but activity levels and number of tortoises walking, and feeding was not correlated with seasonal rainfall (McMaster & Downs, 2013). There may be a phase of aestivation during the dry months in *S. pardalis* (Vetter, 2005), that cannot be excluded in our study populations (including *K. belliana*), given that no individual was observed between November and February. However, further studies should confirm whether these tortoises really enter into prolonged estivation during the dry months in South Sudan. In general, we predict that the seasonal pattern observed in the two species at our study area will also be detected by additional studies on tropical tortoises throughout the world.

## Conclusions

Our study showed that a relatively simple experiment as that presented in this paper may help in understanding the potential for biases in data recording with tortoise populations for which a high number of captures/contacts is not feasible. Our study also confirmed, and further uncovered, the remarkable ecological differences existing between *S. pardalis* and *K. belliana*, and suggests that interspecific competition should be minimal between these species, the same as in most of the terrestrial chelonian assemblages studied to date (Luiselli, 2006a). We would suggest that more detailed studies should be made for exploring the eventual conservation implications that may arise in the altered savannah areas where these two species do coexist in East Africa.

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**Figure 1.** The two study species in South Sudan: *Stigmochelys pardalis* juvenile (a) and adult (b) (photos by L. Luiselli); adult *Kinixys belliana* (c) (photo by G. S. Demaya); and shell of *Stigmochelys pardalis* (photo by J. S. Benansio)

**Figure 2.** The three cover types of vegetation taller than 2 m at the study areas in South Sudan : 1) 0-30% (photos (a) and (b); 2) 31-60% (photo (c)); 3) >60% (photo (d)). (All photos by G. S. Demaya)

**Figure 3.** Distribution of *Stigmochelys pardalis* (a) and *Kinixys belliana* (b) presence points in South Sudan, and randomly-generated points used for data analysis in the present paper

**Figure 4.** Percentage of tortoise sighting spots with presence of cattle and presence of water-body within 200m radius. For the statistical details, see the text.

**Figure 5.** Correlation between rainfall (expressed in terms of number of rainy days per month) and number of tortoises observed in the wild (*Kinixys belliana* and *Stigmochelys pardalis* pooled) at the study area in South Sudan.