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

3

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20

**21 ABSTRACT**

22 Tortoise ecology is poorly studied in East Africa. Here, using two terrestrial Testudinidae  
23 (*Stigmochelys pardalis* and *Kinixys belliana*) as study models, we (i) present basic demographic  
24 characteristics (sex-ratio, and density), (ii) describe correlates of their presence at two spatial  
25 scales (micro-habitat and macro-habitat), (iii) evaluate the effects of rainfall on their seasonal  
26 activity patterns, and (iv) analyze abundance patterns in relation to macro- and micro-habitat  
27 characteristics. We also describe an experiment, using tortoise shells, that can allow to control,  
28 and eventually correct, the reliability of observed data by taking into account the detectability of  
29 the study species in the wild. On the basis of a suite of statistical analysis and GIS-based  
30 elaborations, we confirmed, and further uncovered, the remarkable ecological differences existing  
31 between *S. pardalis* and *K. belliana*. The habitat use was different interspecifically, with *K. belliana*  
32 being much more linked to dense vegetation spots, often nearby waterbodies, whereas *S. pardalis*  
33 being an habitat generalist, at both micro- and macrohabitat scale. Nonetheless, juveniles of both  
34 species were observed in areas with significantly higher % soil covered by vegetation taller than  
35 200 cm than adults of both sexes. This different habitat selection is hypothesized to be due to  
36 antipredatory reasons. Overall, our data suggests that interspecific competition should be minimal  
37 between these species.

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

**39 1. Introduction**

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

45 1995), however, in other localities (i.e., South and West Africa) up to 4 sympatric species can be  
46 found (Iverson, 1992; Luiselli, 2003).

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

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

69 that may allow ecologists to control, and eventually correct, the reliability of observed data by  
70 taking into account the detectability of the study species in the wild.

## 71 **2. Materials and methods**

### 72 **2.1 Study area**

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

82

83 The climate of the region is tropical, with a wet season in April – October (with an average  
84 of 100 mm rainfall per month) and a dry season between November – March (5-35 mm per  
85 month); during the dry season the hottest maximum temperature of 38°C is recorded in February.  
86 The typical vegetation is savannah, with small patches of dry forest and bushlands. The dominant  
87 trees in the park include *Acacia seyal*, *Azalia quanzensis*, *Balanites* spp., *Celtis* spp., *Calotropis*  
88 *procera*, *Combretum* spp., *Cassia* spp., *Dichrostachytus cinera*, *Erythrina* spp., *Euphorbia ingens*,  
89 *Euphorbia candelabra*, *Ficus* spp., *Kigerlia africana/aethiopica*, *Virtex doniana*, *Ziziphus* spp.,  
90 *Tamarindas indica*, and *Azadirachta indica*. The area also contains swamp meadows of dense low  
91 stoloniferous grasses such as antelope grass (*Echinochloa pyramidalis*) interspersed with patches of  
92 taller clump-forming grasses, as well as an understory of Jaragua grass (*Hyparrhenia rufa*). . The

93 park provides very fertile grazing lands for cattle as they are abundant and widespread across the  
94 area and they represent a source of food, a form of currency and a symbol of social status for the  
95 local inhabitants of this area (the Mundari, Pari and Bari tribes).

96

## 97 **2.2 Data collection**

### 98 *2.2.1 Tortoise detection experiment*

99 This experiment was performed during July – August (wet season) and October – November (dry  
100 season) of 2019. A total of 14 *S. pardalis* shells and 16 *K. belliana* shells were randomly placed in  
101 open spaces or hidden under bushes (simulating the “normal” habits of the study species) along  
102 300 m line transects (n = 3) in natural savannah habitats. Transects were laid out in three cover  
103 types of vegetation taller than 2 m: 1) 0-30%; 2) 31-60%; 3) >60% (Figure 2). Three experienced  
104 observers in tortoise field research (who were unaware of the location of the tortoise shells) were  
105 asked to walk slowly along these transects and locate as many shells as possible. This procedure  
106 was repeated three times, changing the position of the shells on each occasion (during three  
107 separate days) for each transect and for each season. We estimated the mean percentage of  
108 observed shells (by season and by vegetation cover category, i.e. open space and under bushes).

109

### 110 *2.2.2 Field surveys for free-ranging tortoises*

111 We surveyed wild tortoises in the Equatoria State all year round from 2017 – 2019. We also used  
112 location data from additional records of tortoises from our unpublished research from 1989  
113 onwards. A team of three researchers searched for tortoises from 0700 – 1800 (suspending  
114 searching during the hottest midday hours) within bush and grasslands, as well as in stony places  
115 and other potential tortoise habitats. Fieldwork was suspended during heavy rains. An average of  
116 15 man-hours were spent in the field during each survey day. Field surveys consisted of slowly

117 walking along a single randomly selected, separate, line transects (300 m long) throughout the  
118 survey sites in the study region. We walked a total of 416 transects, encompassing 124,800 m. The  
119 researchers were about 30 m apart each another, and the same transects were not repeated  
120 during the study period.

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

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

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

141 shapefile (with coordinates WGS84) of buffer areas with 3-km radii around each presence and  
142 random point.

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

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

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

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

153 d. IUCN Protected Areas of Africa data set

154 (<https://cmr.earthdata.nasa.gov/search/concepts/C1214603932-SCIOPS>) representing 11  
155 different types of parks, reserves and other unique areas which had some degree of protected  
156 status;

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

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

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

160 a. roads (Center for International Earth Science Information Network (CIESIN)/Columbia

161 University, and Information Technology Outreach Services (ITOS)/University of Georgia 2013);



162 b. rivers ([http://worldmap.harvard.edu/data/geonode:Digital\\_Chart\\_of\\_the\\_World](http://worldmap.harvard.edu/data/geonode:Digital_Chart_of_the_World));  
163 c. lake ([http://worldmap.harvard.edu/data/geonode:Digital\\_Chart\\_of\\_the\\_World](http://worldmap.harvard.edu/data/geonode:Digital_Chart_of_the_World));  
164 d. human settlement (Harvest Choice, 2015b); including settlement population estimate  
165 and we calculated the distances (in km) of all the above-mentioned layers from the presence and  
166 random points by using the 'QGIS NNJoin' plugin (Dharmawan, and Farda, 2017).

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

169 
$$\text{KIA} = (\text{number of individuals} / \text{numbers of kilometers covered}).$$

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

### 172 **2.3 Statistical analyses**

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

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

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

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

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

206 2001; Arntzen & Alexandrino 2004). We performed logistic regression analyses by SigmaPlot 14.0  
207 version PC software.

208 One-way ANOVAs (followed by Tukey HSD post-hoc pairwise tests) were used for testing, in  
209 each of the study species, the statistical differences between sexes and among adults versus  
210 juveniles in terms of the four micro-habitat variables mentioned above. Interspecific differences in  
211 terms of % sandy soil of the sighting spots and in terms of % soil covered by vegetation taller than  
212 200 cm were evaluated by Student t-test. Contingency table  $\chi^2$  test was used to evaluate (i) sex-  
213 ratio of the observed individuals of the two species, (ii) interspecific frequencies of sightings spots  
214 with nearby water and (iii) interspecific frequencies of sightings spots with nearby cattle.

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

### 219 **3. Results**

#### 220 **3.1 General data**

221 We observed a total of 107 tortoises, 63 *S. pardalis* and 44 *K. belliana*. The KIA index for *S. pardalis*  
222 was 0.504 individuals  $\times$  km<sup>-1</sup> and 0.00035 individuals  $\times$  km<sup>-1</sup> for *K. belliana*. Using a boundary strip  
223 of 8 m on both sides of each transect, we calculated a density of 0.315 individuals/ ha for *S.*  
224 *pardalis* and 0.22 individuals/ ha for *K. belliana*. All presence localities and randomly generated  
225 points for the two study species in South Sudan are given in Figure 3. For *S. pardalis*, our sample  
226 size consisted of 20 males, 39 females and 4 juveniles; sex ratio was not skewed from equality ( $\chi^2 =$   
227 3.1, df = 1, P = 0.094). In the case of *K. belliana*, we recorded 23 males, 15 females and 5 juveniles.  
228 Adult sex-ratio was even ( $\chi^2 = 0.9$ , df = 1, P = 0.339).

## 229 **3.2 Smaller-scale habitat use**

### 230 *3.2.1 Tortoise detection experiment*

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

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

### 243 **3.3 Micro-habitat characteristics of the tortoise records**

244 *Kinixys belliana*. The synopsis of the data is presented in Table 4. The various sex/age groups did  
245 not differ significantly in terms of % sandy soil of the sighting spots (one-way ANOVA.  $F_{2,40} = 0.45$ ,  $P$   
246 = 0.641), and in terms of % soil covered by vegetation taller than 200 cm of the sighting spots (one-  
247 way ANOVA.  $F_{2,40} = 2.65$ ,  $P = 0.08$ ). Interestingly, although these tortoises clearly selected well  
248 vegetated spots (with the mean percent of high vegetation cover being 77% for males and 82% for  
249 females), the juveniles appeared to select only highly vegetated spots (97% being the average high  
250 vegetation cover of their spots of sightings; Table 4). Cattle were observed in 4.6% of the sighting  
251 spots, whereas water was frequently found nearby the sighting spots (58.1% of cases [ $n = 43$ ]).

252 *Stigmochelys pardalis*. The synopsis of the data is presented in Table 4. There were  
253 significant differences among sexes/age classes in terms of % sandy soil of the sighting spots (one-  
254 way ANOVA.  $F_{2,60} = 3.66$ ,  $P < 0.05$ ), with juveniles being observed in spots with significantly higher  
255 % sandy soil than adult males (Tukey Honest significant post-hoc test:  $P = 0.013$ ). There were also  
256 inter-group differences in terms of % soil covered by vegetation taller than 200 cm of the sighting  
257 spots (one-way ANOVA.  $F_{2,60} = 10.21$ ,  $P < 0.001$ ), with juveniles being observed in spots with  
258 significantly higher % soil covered by vegetation taller than 200 cm, than adults of both sexes ( $P <$   
259  $0.001$ ), with males and females being very similar instead ( $P = 0.858$ ). Cattle were present in 6.3%  
260 of the sighting spots, and water was present in 9.5% of the sighting spots.

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

### 267 **3.4 Larger-scale habitat use**

#### 268 *3.4.1 Macro-habitat effects on sympatric tortoise abundances*

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

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

275 **3.4.2 Effects of months and macro-habitat on body size**

276 *Kinixys belliana*. The model highlighted a positive relationship with months (estimate = 0.394; Wald  
 277 = 5.216;  $p=0.00223$ ) and body size for the females, and a positive effects of months (estimate =  
 278 2.335; Wald = 18.132;  $p=0.00002$ ) and macro-habitat (estimate = 1.920; Wald = 9.001;  $p=0.00269$ )  
 279 for males.

280 *Stigmochelys pardalis*. Our model did not detect any effect of sex (estimate = 0.394, Wald =  
 281 0.194,  $P = 0.711$ ), months (estimate = 0.820; Wald = 1.185;  $p=0.276$ ) and macro-habitat types  
 282 (estimate = 0.472; Wald = 0.226;  $p=0.634$ ) on body sizes of these tortoises.

283 **3.5 Rainfall effects on sympatric tortoise records**

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

290 **3.6 Correlates of large-scale occurrence of the two species**

291 *Kinixys belliana*. The multiple logistic regression model (Likelihood ratio test statistic = 16.982,  $P =$   
 292 0.005;  $-2 \log(\text{likelihood}) = 76.094$ ; Hosmer-Lemeshow statistic = 7.69,  $P = 0.464$ ) resulted in two of  
 293 the variables being statistically significant: tree density (positively correlated to the probability of  
 294 presence of the species: coefficient = 0.0000154, standard error = 0.00000777, Wald = 3.948,  $P =$   
 295 0.047) and distance from the nearest water-body (negatively correlated to the probability of  
 296 presence of the species: coefficient = -0.000157, standard error = 0.0000869, Wald = 3.261,  $P =$

297 0.041). All the other variables were not significant (at least  $P = 0.110$ ). Thus, the logit equation was  
 298 as follows:

299 
$$\text{Logit } P = -1.858 - (0.000157 \times \text{distance from water-body}) + (0.0000154 \times \text{tree density}).$$

300 *Stigmochelys pardalis*. The multiple logistic regression model (Likelihood ratio test statistic  
 301 = 13.739,  $P = 0.033$ ;  $-2 \log(\text{likelihood}) = 101.402$ ; Hosmer-Lemeshow statistic = 11.114,  $P = 0.195$ )  
 302 gave a different outcome compared to the previous species. Indeed, only one variable was  
 303 statistically significant: distance from road (positively correlated to the probability of presence of  
 304 the species: coefficient = 0.0000923, standard error = 0.0000407, Wald = 5.15,  $P = 0.023$ ). All the  
 305 other variables were not significant (at least  $P = 0.102$ ). Thus, the logit equation for *S. pardalis* was  
 306 as follows:

307 
$$\text{Logit } P = -3.079 + (0.0000923 \times \text{distance from the nearest road}).$$

## 308 **4. Discussion**

### 309 ***4.1 Tortoise detection experiment***

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

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

#### 323 **4.2 Tortoise abundance**

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

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

#### 338 **4.3 Micro- and macro-habitat characteristics of the tortoise records**

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



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

362 In the case of *S. pardalis*, our study revealed a generalist habitat strategy (at both a micro-  
363 and macro-scale), where basically only the need of minimizing human disturbance (expressed by  
364 the distance from roads and paths) matters.. In Zimbabwe, *S. pardalis* was found to inhabit open  
365 riverine and large areas of pure mopane (*Colophospermum mopane*) bush habitats (Hailey and  
366 Coulson, 1995) but was considered an habitat generalist elsewhere (Greig & Burdett, 1976; Rall,

367 1985; Douglas & Rall, 2006), inhabiting even commercial farmlands (Drabik-Hamshare, 2016). In  
368 Tanzania, it was found frequently in short grass and along roads (not consisting with our findings),  
369 but also inside bushes and in medium tall grass, whereas it was rarely seen in tall grass and in the  
370 surroundings of waterbodies (Kabigumila, 1998, 2001c). Weatherby (1996) reported that these  
371 tortoises prefer open grassy areas, occasionally venturing into thick thornbush. Thus, overall our  
372 data mirrors those presented in the above-mentioned earlier studies, confirming that this species  
373 is a savannah habitat generalist that usually avoid high vegetation cover (just about 28% of our  
374 adult sample was found in highly vegetated spots). Based on this evidence, we would suggest that  
375 the distribution of this species in South Sudan is probably wide and continuous, especially in the  
376 central and eastern regions of the country.

377 As mentioned above, the juveniles of both species consistently revealed a much greater  
378 preference for very closed vegetation spots compared to adults. This is unlikely to be an outcome  
379 of small sample size (typically juvenile tortoises are very elusive; see also low encounter rates in  
380 Berry & Turner, 1986, and in Cayuela et al., 2019), as locating small tortoises is certainly much  
381 more difficult in closed vegetation than in open vegetated places. Instead, we think that this  
382 pattern reflects antipredatory adaptations in habitat selection by small tortoises. Malan & Branch  
383 (1992) reported cases of predation on *S. pardalis* hatchlings by birds of prey. In a radiotracking  
384 study on juveniles of an herbivorous tortoise species (*Gopherus agassizii*) from an arid  
385 environment, locations were more likely to be under the cover of perennial plants, , and in a  
386 greater number of small-mammal burrows. (Todd et al., 2016). In addition, juveniles of an  
387 omnivorous species (*Terrapene carolina bauri*) from a wetter area also preferentially used  
388 microhabitats with dense vegetation (Jennings, 2007), thus our data are very consistent with the  
389 few available studies on microhabitat preferences of juvenile turtles and tortoises from elsewhere..

#### 390 **4.4 Effects of months and macro-habitat on body size**

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

#### 403 **4.5 Rainfall effects on sympatric tortoise records**

404 Our data clearly revealed that the frequency of encounters with tortoises increases with the  
405 number of rainy days per month (a good proxy of the monthly rainfall). This is a general pattern  
406 with African tropical tortoises (Luiselli, 2003), and it has been already observed, for instance, in  
407 West African rainforest *Kinixys* species (e.g., Luiselli, 2003). In addition, in the dry savannahs of  
408 Swaziland, the above-ground activity of radiotracked *S. pardalis* was greater in the warm wet  
409 months compared with the cool, dry months (Monadjem et al., 2013). In another study in South  
410 Africa, there was a positive correlation between number of tortoises caught and rainfall per  
411 season, but activity levels and number of tortoises walking, and feeding was not correlated with  
412 seasonal rainfall (McMaster & Downs, 2013). There may be a phase of aestivation during the dry  
413 months in *S. pardalis* (Vetter, 2005), that cannot be excluded in our study populations (including *K.*  
414 *belliana*), given that no individual was observed between November and February. However,

415 further studies should confirm whether these tortoises really enter into prolonged estivation  
416 during the dry months in South Sudan. In general, we predict that the seasonal pattern observed in  
417 the two species at our study area will also be detected by additional studies on tropical tortoises  
418 throughout the world.

#### 419 **Conclusions**

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

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

575

576 **Figure 2.** The three cover types of vegetation taller than 2 m at the study areas in South Sudan : 1)  
577 0-30% (photos (a) and (b)); 2) 31-60% (photo (c)); 3) >60% (photo (d)). (All photos by G. S. Demaya)

578

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

581

582 **Figure 4.** Percentage of tortoise sighting spots with presence of cattle and presence of water-body within  
583 200m radius. For the statistical details, see the text.

584

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