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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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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    aproximately 8,400 km$^2$ 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, andis 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*, *Afzelia 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 ofthe 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);

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

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

171 of the transects.

### 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 ± 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 × km$^{-1}$ and 0.00035 individuals × km$^{-1}$ 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 (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      Logit P = -1.858 - (0.000157 × distance from water-body) + (0.0000154 × tree density).

300      *Stigmochelys pardalis.* The multiple logistic regression model (Likelihood ratio test statistic

301   = 13.739, P = 0.033; -2 log (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            Logit P = -3.079 + (0.0000923 × 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 × ha$^{-1}$ (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 × ha$^{-1}$ (McMaster & Downs, 1996), but was

330    less than that (0.85 individuals × ha$^{-1}$) 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 locationsy 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.