Tortoise ecology in the West African savannah: multi-scale habitat selection and activity patterns of a threatened giant species, and its ecological relationships with a smaller-sized species

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ABSTRACT

The status of most vertebrates in the African Sahel is not well known. Among these, the African spurred tortoise (*Centrochelys sulcata*), a charismatic but also one of most threatened vertebrates in the Sahel, is still poorly studied. We investigated the status of this species, its potential distribution, habitat selection (at multiple spatial scales) and activity patterns in Mali and Burkina Faso, two countries within the tortoise' known range. We employed field surveys and villager interviews in 23 sites to determine the presence of the species. In these surveys and interviews, we also included the Western hinge-back tortoise (*Kinixys nogueyi*), a sympatric chelonian also suspected of being in decline. Age-stratified interviews revealed that *C. sulcata* is widespread in Mali, but since there was a statistically higher frequency of older respondents that remembered *C. sulcata* present around their village, compared to younger respondents, it is likely that the species has been declining throughout the study area. We encountered a total 77 *C. sulcata* and 20 *K. nogueyi* individuals during our field surveys. Most *C. sulcata* were found along areas of intermittent streams and stabilised dunes, known locally as *koris*. *Centrochelys sulcata* individuals were more likely to occur in sandy dry savannah areas that were further away from human settlements, and which contained inland waters or were closer to these. *Kinixys nogueyi* exhibited instead an allopatric distribution, with no ascertained sympatry with *C. sulcata* at the microhabitat scale. Cattle incidence was negatively correlated with the presence by *C. sulcata*. Our results also indicate that aboveground activity of *C. sulcata* is limited to the wet season and has a clearly bimodal diel activity cycle, with most sightings in the early morning hours. We provide suggestions on how best to survey this species in the wild while advancing new information on its distribution and biology. These data are invaluable to assess the status of this species as part of future conservation planning efforts.

Keywords: ecology; phenology; conservation; Sahel; West Africa; *Centrochelys sulcata; Kinixys nogueyi*

1. Introduction

The African spurred tortoise (*Centrochelys sulcata*) is among the most charismatic but also one of most threatened vertebrates in the African Sahel (Vetter, 2005; Petrozzi et al., 2016). The Sahel is the semi-desert transition zone in Africa between the Sahara to the north and the Sudanian Savanna to the south. This tortoise, one of the largest terrestrial chelonians (adult males reaching more than 100 kg in weight), was originally widely but patchily distributed across the Sahel (Branch, 2008). Despite being common in captive collections, because it is easy to maintain and breed (e.g., Vetter, 2005; Burney et al., 2012) and has been introduced into California and Hawaii (Burney et al., 2012), the species is declining in the wild (Branch 2008). The World Conservation Union (IUCN) currently lists the species as 'Vulnerable' (IUCN 2017), its habitat threatened by overgrazing by cattle and other domestic animals, as well as from anthropogenic seasonal fires (Petrozzi et al. 2017a). Moreover, the species is drafted as "Endangered" by the IUCN/SSC Tortoises and Freshwater Turtles Specialist Group (assessment made in Lomé continental meeting, August 2013), but this red-list assessment has not yet been officially published in the IUCN red list (available at www.iucnredlist.org).

Densities of the African spurred tortoise are currently estimated to be lower than for most other terrestrial chelonians (Petrozzi et al. 2018). Its distribution range is characterised by wide gaps and discontinuities, not only due to anthropogenic impacts, but also as a result of the species' preference for sites with intermittent streams (known as *kori*) and stabilised dunes (Petrozzi et al. 2017b). Studies of the genetic variability of this species (Ballasina, 2002) suggest that there are some significant differences between Eastern and Western populations (Devaux, 2000).

The survival of the African spurred tortoise in the wild has been, and still is, interwoven with the cultural and religious beliefs of the mainly nomadic Islamic peoples living in the Sahel. For centuries, these tribes have not consumed tortoises because all reptiles are *haraam* (= forbidden) food by Islamic law (*Sharia*). However, in recent decades, the human population in the Sahel has increased dramatically, with drought, poverty, and famine triggering movements of many and different peoples throughout the region. As a consequence, non-Muslim communities, who do consume tortoises, are more numerous, as witnessed in northern Nigeria. Likewise, pastoralists together with their accompanying livestock have also increased significantly (Burney et al., 2012). Consequently, overgrazing and encroaching desertification are likely to cause widespread population losses of tortoises in the region. Additionally, the lucrative trade of live animals for export to global pet markets by locals, an activity not prohibited by *Sharia* law, places even more pressure on wild tortoise populations (Burney et al., 2012). It is customary to keep tortoises in rudimentary captive conditions within households before their sale, where they sometimes even breed. Some individuals have been known to escape back into the wild.

Knowledge of the ecology of the African spurred tortoise is patchy and insufficient to be useful in action planning for managing the remaining wild populations. Conservation Action Plans are designed to help develop and implement strategies to conserve species and habitats (IUCN – SSC Species Conservation Planning Sub-Committee, 2017). IUCN has compiled action plans for species and habitats, and these documents have become among the world's most authoritative sources of species-related conservation information available to natural resource managers, conservationists and decision makers around the world (e.g. Ross, 1998).

A fundamental element for any action plan is data on the distribution of the target species, its ecology and if possible, abundance (IUCN – SSC Species Conservation Planning Sub-Committee, 2017). Although for many species our current knowledge on the distribution and abundance has greatly improved during the last two decades, there are still countless taxa for which we know little, particularly those in the tropical and subtropical regions (Mallon et al., 2015).

Exploration of species in the arid savannahs and semi-deserts in the West African Sahel has been greatly hampered by the lack of adequate road networks, but more recently by the active presence of Islamic extremists throughout the region. As a result, most threatened species in the West African Sahel have been little studied in the last twenty years (Mallon et al., 2015). In this paper, we present new evidence on various aspects of the ecology and distribution of *C. sulcata* in two countries within its range (Mali and Burkina Faso), and on its ecological relationships with another tortoise species of smaller size, the West African hinge-back tortoise (*Kinixys nogueyi*). This latter is a omnivorous (mainly mushroom-eating) species that usually lives in bushy and relatively wet Guinea savannahs (Segniagbeto et al. 2015). Using a combination of field surveys and village interviews, we assess the habitat characteristics linked to the presence of *C. sulcata* at multiple spatial scales, as well as present data on diel and monthly activity patterns. This information is fundamental for the preparation of action plans in support of the conservation of the species.

2. Materials and methods

2.1. Study areas

Fieldwork in Mali was carried out during the wet season (Aug-Oct 2018) along the southern and south-western portions of the country. The main vegetation type in this area is Sudanian savannah with relatively thick scrubland along the main river courses. The area also contains degraded savannahs often affected by anthropogenic bush-fires and bushy savannahs with intermittent water bodies due to the heavy rainfall during the wet season peak. The climate is arid subtropical, with rain concentrated between July and September (170-230 mm per month) and <4 mm between November and March.

Fieldwork in Burkina Faso was undertaken from 2017 to 2019 in the Pama North region (0.704135 latitude, 11.256878 longitude) in the south east of the country. The main vegetation type in the area is Sudanian bushy savannah. The area has a semiarid subtropical climate, with rains concentrated between July and September (180-270 mm per month) and <4 mm between November and February.

2.2. Field data collection

Because of political instability and high security risks (e.g. terrorist attacks especially in Mali) survey sites were not selected randomly. A total of 23 sites in Mali and the Pama North area in Burkina Faso were considered relatively safe as well as easy to contact local police and military authorities in case of emergency. Within each site, a team of three researchers searched for tortoises from 0700-1800, Bamako time). Fieldwork was suspended during heavy rains. Every possible effort was made to explore each study site for the same number of field hours and using the same number of surveyors. On average, a total of 15 man-hours were spent in the field during each survey day.

We recorded all individuals of the two sympatric terrestrial chelonians i.e. *K. nogueyi* and *C. sulcata* found during field surveys. Tortoise (*C. sulcata*) tracks on the sand as well as burrows were also observed in eight of the Malian sites. For each live tortoise encountered we logged its GPS location, measured its size (curved carapace length) using a rope, and noted its sex.

To assess macro-habitat correlates of *C. sulcata* presence/absence we employed the location data for all tortoises found in Mali (the same was not possible in Burkina Faso because we collected field data from a single study area in the latter country; see above). However, we evaluated microhabitat selection using a subsample of tortoises found in Burkina Faso. For these animals, we recorded microhabitat characteristics within a 10 m and 200 m radius from the exact point of first sighting of the individual tortoise. The following three variables were measured in the field: (a) % soil covered by vegetation taller than 200 cm; (b) % sandy soil; (c) presence/absence of cattle (and signs of their presence). For variables (a) and (b), percentages were calculated by eye in ten randomly chosen 2 x 2m quadrats from which we calculated the median of all values.

2.3. Interviews

We conducted semi-structured interviews in 18 villages in south-west Mali (Figure S1). Interviewees (n = 116 retained; and additional 26 considered non-valid because of poor reliability) were farmers, hunters and shepherds (all males older than 21 years; no minors were included). They were asked whether they had ever seen *C. sulcata* in their area of activity, and asked if they had ever encountered the smaller *K. nogueyi*. Questions on the hinge-back tortoise were included to allow us to collect information on another little known chelonian, apparently in decline across West African savannahs (Segniagbeto et al., 2015), as well as lessen the attention on the African spurred tortoise. During interviews, we asked respondents to describe the shape and size of the tortoises instead of identifying them using photographs. This procedure was used so as to minimize wrong or false answers. Where possible, we independently interviewed young (21-40 years old; n = 69) and old (41-60 years old; n = 47) respondents, so as to determine historical trends of the species status from age-structured interviews (see Luiselli et al., 2020). Indeed, if for example in a given locality the interviewed elders report the species to be present whereas the young state that the species is not there, it is likely that the species has been extirpated or that its local populations are declining (Luiselli et al. 2020). This methodology has already been used with *C. sulcata* from elsewhere (Luiselli et al. 2020). Local assistants performed all interviews in the native language. In addition, we interviewed each person separately and independently in the same village. Since African spurred tortoises are popular pets in the Sahel region, we made it clear to interviewees that we referred exclusively to those specimens encountered in the wild.

2.4. Statistical analyses

2.4.1. Macro-habitat correlates

GPS coordinates for all tortoise records in Mali (n = 12 distinct sites) were imported into QGIS 3.4.00. We then created a number of 227 random points within the known range (IUCN's Extent of Occurrence) of the species (see Petrozzi et al., 2019 for the precise description of the methodology) to compare observations against a random background. We chose random points by using the Random Points algorithm. We created a buffer of 30 km around the most external presence sites of the convex polygon to enlarge its size to avoid any potential edge effect. Random points were created inside the increased minimum convex polygon shape file area. Within a 3km radius around each point we extracted the values for raster and shapefile for the following variables from various cartographic sources: (i) Estimated human population density (CIESIN, 2005); in eight classes (Table S1); (ii) road presence/absence (CIESIN, 2013); (iii) Human settlements (villages and towns) presence/absence (CIESIN, 2011); (iv) Inland water (lakes or perennial, fluctuating or intermittent water bodies including rivers and kori) presence/absence (http://worldmap.harvard.edu/data/geonode: Digital_Chart_of_the_World); (v) Inland water linear distance (in km) from the exact point of tortoise sighting; (vi) Linear distance (in km) of the nearest human settlement from the exact point of tortoise sighting; (vii) mean monthly rainfall (mm), and (viii) mean monthly air temperature (°C). Raster values (i) had a resolution of 2.5 arc-minute grid cell. Variable (iii) was a point shapefile; variable (iv) was both a line shapefile (perennial, fluctuating or intermittent water bodies including rivers and kori) and a polygon shapefile (lakes). Linear distances, for presence/absence of human settlements and inland water presence/absence, were obtained by using NNJoin plug in QGIS that joins two vector layers (the input and the join layer) based on the nearest neighbour relationships, to obtain precise distance. Data for road presence/absence, human settlements presence/absence, and inland water presence/absence were obtained by clipping the shape file of each variable with the 3-km-radius shape. Further details of the GIS procedure used are given in Petrozzi et al. (2019).

We analysed the selected variables potentially affecting the presence of the study species using logistic regression analyses (forward stepwise addition model; see Hosmer and Lemeshow, 1989; Teixeira et al., 2001). The dependent variable was the tortoise presence/absence (0 = absence, 1 = presence) and the selected predictors (i.e. variables i) to vi)) were the independent variables. There was a limited correlation between the environmental variables (Spearman r = 0.584), thus our modelling analysis was statistically valid (Teixeira et al., 2001).

2.4.2. Other statistical procedures

We used Spearman's rank correlations to assess the relationship: (i) between the number of observed tortoise tracks per site and the number of encountered tortoises per site, and (ii) between % of people reporting the presence of *C. sulcata* and % reporting the presence of *K. nogueyi* in each village. We used Pearson's correlation coefficient to determine the relationship between the monthly % frequency of observed tortoises and (i) mean monthly rainfall (mm), and (ii) mean monthly air temperature (°C). A Mann-Whitney U test was used to compare the median % of interviewees claiming the presence of *C.*

sulcata versus the % claiming *K. nogueyi* among villages, as well as the median differences in vegetation cover and sandy soil between sites at 10 m and 200 m radius from the tortoise sighting sites. Deviations from an expected 1:1 adult sex ratio were evaluated by observed-versus-expected χ^2 test. We used χ^2 test to evaluate the statistical differences in the frequency of respondents mentioning that *C. sulcata* was present in the surroundings of their village between 41-60 years old and 21-40 years old interviewees. Differences in: (i) the frequencies of sites with no sign of cattle presence between 10m and 200m radius, and in (ii) the monthly above-ground activity intensity (expressed as frequency of tortoise monthly records) in relation to field effort (number of field days per month), were also assessed by observed-versus-expected χ^2 test. All variables were tested for normality and homoscedasticity (using Shapiro-Wilk W test).

Alpha was set at 5%. In the text, means are presented ± 1 Standard Deviation (S.D.). All statistical analyses were performed with PASW version 11.0 software.

3. Results

3.1. Field records

In Mali, we recorded a total of 30 *C. sulcata* individuals (10 males, 14 females, and 6 juveniles) in 12 distinct sites (Figure 1). The number of tortoises observed per site ranged from 1 to 5 (mean = 2.50 ± 1.29). Although there was a tendency for the number of observed tracks to be positively correlated with the number of tortoises encountered in each site this was not statistically significant (r_s= 0.515, n = 15, P = 0.072). Geographic coordinates of the sites with tortoise presences, as well as the number and sex of individuals observed of *C. sulcata* are given in Table S2, and for *K. nogueyi* (n = 20 observed individuals) in Table S3.

In Burkina Faso, we encountered 47 *C. sulcata* individuals in the Pama North study area. The sex ratio of *C. sulcata* was even for both Mali and Burkina Faso individuals separately, as well as for all the data pooled (χ^2= 1.1, df = 1, P = 0.297).

Kinixys nogueyi exhibited an allopatric distribution in Mali, with no ascertained sympatry with *C. sulcata* at local scale (Figure 1).

3.2. Interview surveys

In Mali, a total of 63.8% and 69% of the 116 respondents indicated that *C. sulcata* (n = 74) and *K. nogueyi* (n =80) were present near their villages, respectively. In 61.1% of the 18 localities recorded, there was disagreement among interviewees concerning the presence or absence of *C. sulcata*, and the same level of discrepancy for *K. nogueyi* (Table 1). However, in 9 villages for *C. sulcata* and in 10 villages for *K. nogueyi*, the great majority or the totality of interviewees reported the occurrence of wild individuals of the species. Interviewees from two villages (Menantali and Sitakilly; Figure S1) reported that *C. sulcata* was absent but *K. nogueyi* was present, whereas in two other villages (Kolokani and Massantola; Figure S1) *C. sulcata* was considered present but not *K. nogueyi*. Only in a single village (Guenegore; Figure S1) was the presence of both species confirmed (Table 1). There was no correlation between the percentage number of people reporting presence of *C. sulcata* and those reporting *K. nogueyi* in each village (r_s = -0.382, n = 18, P = 0.118).

In terms of age classes (see table 2), there was a statistically higher frequency of 41-60 years old respondents stating that *C. sulcata* was present in the surroundings of their village than 21-40 years old respondents (χ^2= 15.54, df = 1, P < 0.0001), thus indicating a likely decreasing population abundance at the study areas.

3.3. Macro-habitat correlates

In Mali, presence of *C. sulcata* was positively related to: (i) increased linear distance from human settlements, (ii) the occurrence of inland waters and (iii) lesser linear distance from inland waters, but was negatively affected by cattle presence, with no other predictors having any influence (Table 3). The inland waters × cattle presence interaction fell just short of statistical significance for the presence of *C. sulcata* in Mali.

Mean monthly rainfall (mm) was significantly correlated with the % frequency of observed *C. sulcata* ($r = 0.68$, $n = 12$, $P < 0.05$; Figure 2). On the other hand, mean ambient temperature (°C) was not correlated with the % frequency of observed *C. sulcata* ($r = 0.413$, $n = 12$, $P = 0.181$).

3.4. Micro-habitat correlates

In Burkina Faso, a total of 21.8% (total n = 23) of *C. sulcata* individuals were observed in savannah habitat, 4.3% in bare sandy areas, 13% on vegetated stream banks, and 56.5% along a *kori*. In terms of microhabitat characteristics, African spurred tortoises were found in sites with 39.5 ± 20 % of soil covered by vegetation taller two metres, whereas mean coverage of the same type of vegetation within 200 m radius was 28.2 ± 12.5%. Although there was a positive correlation between % of soil covered by vegetation taller two metres at 10m and at 200m radius (Figure S2), in 78.3% of cases, percent vegetation coverage was higher at 10m radius than at 200m radius from the tortoise sighting site, whereas only in 8.7% of cases the vegetation was higher at 200m radius and in 13% of cases it was identical (Figure 3a). Median vegetation cover (%) in tortoise sighting sites was significantly higher within 10m than within a 200 m radius (Mann-Whitney U test: $z = -2.16$, $U = 166$, $P < 0.05$).

C. sulcata were also found in sites with 84.7 ± 22.6 % (10m radius) of sandy soil; in contrast the mean coverage of sandy soil within 200 m radius was 72.6 ± 26%. In 34.8% of cases, the soil at both 10m and 200m radius was wholly sandy. Excluding these cases, in the remaining cases (n =15) the percentage of sandy soil was generally higher at 10m radius than at 200m radius from tortoise sighting site (73.3%) or identical at the two scale radii (27.7%) (Figure 3b). Excluding the cases with entirely sandy soil at both 10m and 200m radius, median percentage of sandy soil of the tortoise sighting sites was significantly higher than within a radius of 200 m (Mann-Whitney U test: $z = -1.95$, $U = 66$, $P < 0.05$).

There was no sign of cattle presence in 65.2% of the survey sites (10m radius) and in 34.8% (200m radius). Frequencies of sites with no sign of cattle presence did not differ significantly between the 10m and 200m radius (observed-versus-expected $\chi^2 = 2.13$, df = 1, $P = 0.206$).

3.5. Activity patterns

African spurred tortoises exhibited a clearly bimodal diel activity cycle, with over 60% of the sightings (n = 47) occurring between 0600 and 0900 hours, and about 30% at twilight and early night (Figure S3).

Monthly activity (total records n = 47) had a significantly uneven distribution relative to field effort (number of field days per month) (observed-versus-expected $\chi^2 = 55.7$, df = 11, $P < 0.0001$). Above-ground activity of African spurred tortoises was significantly higher than expected from July to October, with the highest peak in August (Figure 4).

4. Discussion

The present study further confirms some aspects of our previous field research on *C. sulcata* in the African Sahel (Petrozzi et al. 2016, 2017a, 2017b, 2018, 2019), but we add considerably to our knowledge of this species and of *Kinixys nogueyi*. We also confirm the importance of *koris* for the survival of *C. sulcata* populations (see below for more details). Our study also provides a better understanding of the species’ micro-habitat requirements, daily and seasonal activity patterns, as well as its ecological relationships with *K. nogueyi.*

In addition, the present data on Mali are new since this country was not covered by previous studies by Petrozzi and associates.

The number of *C. sulcata* observed in two Sahelian countries in the present study was small despite our relatively extensive field coverage. Given these observations, it is likely that the population density of *C. sulcata* is among the lowest of any studied terrestrial tortoise in the world (Petrozzi et al., 2018), although, for instance, due to its decline, the Mojave Desert Tortoise (*Gopherus agassizii*) may in fact be lower densities in many parts of its range (<1/km^2) (Averill-Murray and Averill-Murray 2005). However, we are aware that our coverage may have suffered some bias because we were unable to survey some areas (especially those most remote) because of security reasons. In addition, absence data for this species may not reliable to assess macro-habitat correlates, since low densities make detection difficult, and false negatives are likely. Also, the study species' absence might be much more affected by factors unaccounted (e.g. hunting, cattle density, agriculture; see Petrozzi et al. 2017a) rather than macro-habitat conditions (Petrozzi et al. 2019). Nonetheless, our age-stratified interviews (sensu Luiselli et al., 2020) would suggest a clear trend of decline of the population abundance of *C. sulcata* throughout the range as only a minority of the young interviewees, compared to the greater majority of older interviewees suggested that the species was found in the surroundings of their village. This result agrees with similar interview campaigns conducted in three other West African countries (Burkina Faso, Niger and Nigeria) (Luiselli et al., 2020), and shows that this giant species may really be declining throughout its range.

We demonstrated that, at the macro-scale in Mali, the presence of water bodies (especially intermittent *koris*) were among the main determinants of the presence of *C. sulcata*. As mentioned above, the presence of *kori*s had been clearly demonstrated to be a crucial factor for the presence of these tortoises elsewhere (Petrozzi et al., 2017a, 2017b), and also our present data from Burkina Faso confirmed that most tortoise records occurred along *koris* (56.5% of cases). Petrozzi et al. (2017b) considered that *koris* are important for the survival of these tortoises in very arid environments because of the humidity that they assure and because, during the rainy season when their water current may be very strong, they carry substantial amounts of animal carrion and vegetation that can be opportunistically consumed by tortoises once deposited along the banks. Intermittent streams may also be selected in order to minimize mortality due to drought. Indeed, previous studies on desert tortoises showed that prolonged drought can greatly affect survival rates in the desert tortoise *Gopherus agassizii* (Longshore et al., 2003), since water balance is crucial for these arid zone reptiles (e.g. Wilson et al., 2001).

Our interviews also suggest that *C. sulcata* is likely to be more widespread in Mali than previously supposed (e.g. Vetter, 2005), as it is considered present in the wild by most interviewees in half of the surveyed villages.

Interestingly, the frequency of respondents considering *C. sulcata* present near their own village was similar to that relative to the smaller sized *K. nogueyi*, which in general is considered a more abundant species in the wild (Branch, 2008). This outcome may be counter-intuitive, and may be biased due to the fact that *C. sulcata* is a culturally important animal in the Sahel (Burney et al., 2012), and thus persons may tend to overestimate its occurrence. However, the fact that all respondents in various villages claimed the presence of only *C. sulcata* or *K. nogueyi* suggests that the ecological preferences of these two species are very different (Branch, 2008; Segniagbeto et al., 2015), but perhaps with some limited sympatry across Mali. Interviewees only reported a single area where both species were sympatric – we did not find any locality where the two species coexist in the wild (compare sites in Table S2 with those in Table S3). Generally speaking, we would suggest that because of the significant differences in body size, interspecific competition between *C. sulcata* and *K. nogueyi* is likely to be low , as seen in most terrestrial chelonian assemblages worldwide (Luiselli 2006). According to Luiselli (2006), terrestrial chelonians usually exhibit four almost universal ecological/life-history traits that may affect the role and the influence of interspecific competition: (i) low species richness, (ii) low population density, (iii) herbivorous/omnivorous dietary habits, and (iv) high longevity. The first three traits were clearly found in our studied ecological system, whereas the fourth may be fulfilled partly. Indeed, whereas *C. sulcata* is known to live long (several decades; see Vetter 2005; 54.5 years in captivity according to < http://genomics.senescence.info/species/entry.php?species=Centrochelys_sulcata>; last accessed 30 January 2020), *K. nogueyi* may normally live less than 16 years in the field (case study in Nigeria; Cayuela et al. 2019). Thus, the most likely explanation is that the two species are normally allopatric because they have divergent eco-physiological characteristics and ecological preferences (Branch 2008), without any community-level assembly rule being of any relevance.

The present paper adds further knowledge on the ecology of *C. sulcata*, its occurrence in different habitats, microhabitat correlates and activity patterns (both diel and seasonal). Data collected at 10m versus 200m radius clearly showed that *C. sulcata* were more likely to be found in vegetated sites within otherwise arid landscapes, in which sandy soils were common. On the other hand, cattle were not very important at the micro-scale. From a management point of view, it seems advisable to create and maintain patches of scrub within large arid sandy areas to increases the chances of survival of these chelonians. We also highlight that *C. sulcata* may not be found in its ideal habitat (because of human-made disturbances mentioned above), but in regions where there is less human pressure. Moreover, we could not dismiss that this is the case in the present study and in previously published research on this species.

Our results also indicate above-ground activity of these tortoises is limited to the wet season, with a strong positive correlation between monthly rainfall and frequency of tortoise field records. This result suggests that, in order to evaluate the population ecology and density of these reptiles, it would be advisable to undertake surveys only during the wet months (Petrozzi et al., 2018), as dry season surveys may substantially underestimate the real abundance of these tortoises in the wild. Also, the hour of the day during which surveys are undertaken may be important, as most individuals were observed during early morning hours, spending the rest of the day in their burrows. This pattern of diel activity, and especially the extensive use of burrows during the hottest part of the day, mirrors diel activity patterns exhibited by North American desert tortoises of the genus *Gopherus* (Zimmerman et al., 1994). The higher above-ground activity intensity during wet months and a bimodal diel activity pattern (with early morning peak) is not surprising since these patterns have been previously observed for other Afrotropical tortoises (Luiselli, 2003), especially from the arid environments (Hailey and Coulson, 1996).

In conclusion, our study shows that Mali is likely to be a country of significant importance for the conservation of the threatened *C. sulcata* as it seems more widespread and abundant there than in the other West African Sahelian countries. In addition, our study revealed that the presence and management of shrubs around the intermittent streams is important for the conservation of this species. As noted by Zimmerman et al. (1994) for North American desert tortoises, effective conservation efforts to preserve habitat of *C. sulcata* should focus upon managing variables associated with integrity of burrows.

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American Society of Ichthyology and Herpetology <www.asih.org/sites/default/files/documents/resources/guidelinesherpsresearch2004.pdf>. Since we did not capture or handle the observed specimens, no collection permits were required for carrying out the present study. Field surveys were authorized by the Ministère de l'Environnement, de l'Economie Verte et des Changements Climatiques, Ouagadougou (Burkina Faso), and by the Le Ministre de l'Environnement et de l'Assainissement du Mali, Bamako (Mali). Two anonymous reviewers significantly improved the quality of the submitted drafts.

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Table 1. Synopsis of the interview results in 18 human settlements in southern and south-western Mali. Presence = number of people reporting that a given species is present; Absence = number of people reporting that a given species is absent from their surroundings. Location of the villages are shown in Figure S1.

		C. sulcata		*K. nogueyi*	
Village	No. Interviewees	Presence	Absence	Presence	Absence
Fadougou	14	2	12	14	0
Kenieba	7	4	3	6	1
Kalaya	6	5	1	5	1
Guenegore	4	4	0	4	0
Samou	7	2	5	3	4
Bafoulabé	14	14	0	12	2
Koundian	7	6	1	4	3
Menantali	4	0	4	4	0
Mahina	3	2	1	3	0
Danaou	8	8	0	7	1
Oualia	6	1	5	4	2
Sebekoro	9	7	2	6	3
Kolokani	3	3	0	0	3
Massantola	4	4	0	0	4
Banamba	4	3	1	1	3
Diema	6	4	2	1	5
Sitakilly	4	0	4	4	0
Gory	6	5	1	2	4
TOTAL	116	74	42	80	36

Table 2. Synopsis of the interview results on interviewees divided by age groups, in 18 human settlements in southern and south-western Mali. Presence = number of people reporting that a given species is present; Absence = number of people reporting that a given species is absent from their surroundings. Location of the villages are shown in Figure S1.

		21-40 YEARS OLD		*41-60 YEARS OLD*	
Village	No. Interview-ees	Pres-ence	Ab-sence	Pres-ence	Ab-sence
Fadougou	14	0	12	2	0
Kenieba	7	1	3	3	0
Kalaya	6	2	1	3	0
Guene-gore	4	2	0	2	0
Samou	7	0	2	2	3
Bafoulabé	14	7	0	7	0
Koundian	7	4	1	2	0
Menantali	4	0	3	0	1
Mahina	3	0	1	2	0
Danaou	8	5	0	3	0
Oualia	6	0	3	1	2
Sebekoro	9	4	1	3	1
Kolokani	3	3	0	0	0
Mas-santola	4	1	0	3	0
Banamba	4	1	1	2	0
Diema	6	1	2	3	0
Sitakilly	4	0	4	0	0
Gory	6	3	1	2	0
TOTAL	116	34	35	40	7

Table 3. Synopsis of the statistical results (by logistic regression analysis) on the macro-habitat correlates of presence of *Centrochelys sulcata* in Mali (this study) and in comparison with previous studies at the general West African scale (Petrozzi et al. 2018). Symbols: = no significant effect of the given variable on the species' presence; + = significantly positive effect of the given variable on the species' presence; – = significantly negative effect of the given variable on the species' presence.

	This study						Petrozzi et al. (2018)	
Variable	Analyzed (Yes/Not)	χ^2	Odds ratio	-2log likelihood	P	Correlation response	Analyzed (Yes/No)	Correlation response
Estimated human population density	Yes	0.133	0.71	39.012	0.713	=		
Road presence	Yes	1.758	0.3	37.058	0.185	=	Yes	-
Presence Inland water	Yes	8.883	17.333	29.978	0.0029	+		
Inland water linear distance	Yes	4.14	0.843	34.671	0.041	-		
Land use	Yes	7.226	1.014	31.589	0.0072	+	Yes	+
Presence human settlements	Yes	0.164	0.72	38.652	0.686	=		
Linear distance (in km) of the nearest human settlement	Yes	7.51	1.016	31.297	0.0061	+	Yes	+
Presence of cattle	Yes	5.877	0.561	32.938	0.015	-		
Presence of cattle × Presence Inland water	Yes	2.89	0.773	32.313	0.053	=		
Rainfall	Yes	2.718	0.493	36.098	0.099	=	Yes	=
Average tree density	Not						Yes	=

Figure 1. Presence sites of *Centrochelys sulcata* and *Kinixys nogueyi* in Mali and Burkina Faso as mentioned in the present study.

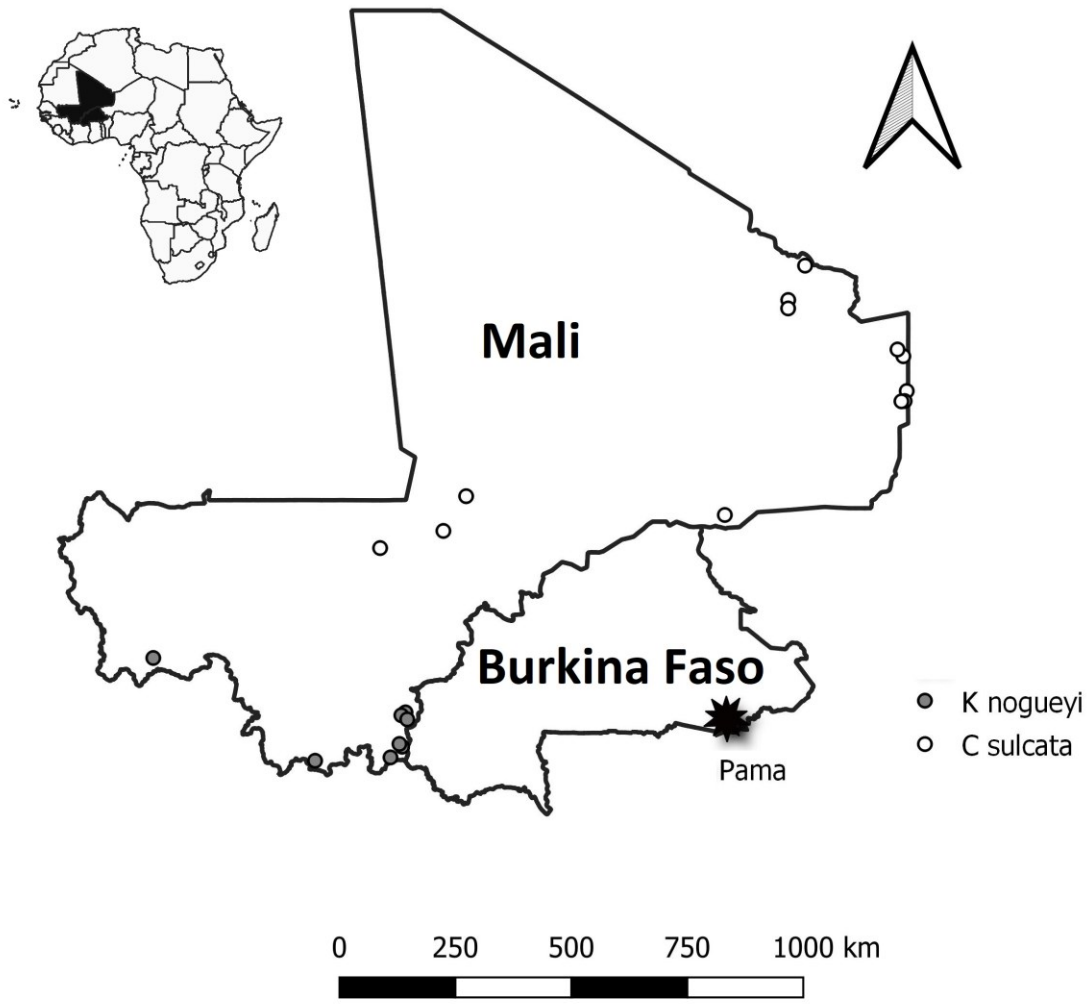


Figure 2. Correlation between monthly rainfall (mm) and % frequency of observed *Centrochelys sulcata* at a south-eastern locality in Burkina Faso. For statistical details, see the text.

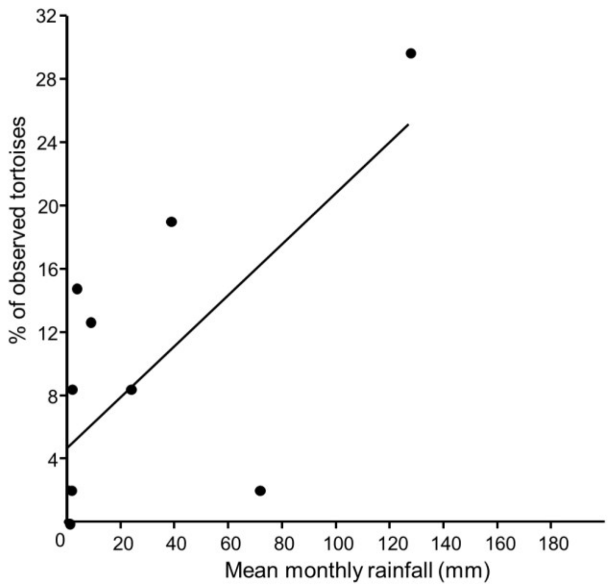


Figure 3. Microhabitat choice of *Centrochelys sulcata*. Distribution of the % coverage of vegetation taller than 2 m at 10m and 200 m radius from the exact sighting sites of African spurred tortoises (n = 23) recorded during the present study (graphic a); and distribution of the % sandy soil at 10m and 200 m radius from the exact sighting sites of African spurred tortoises (n = 23) recorded during the present study (graphic b).

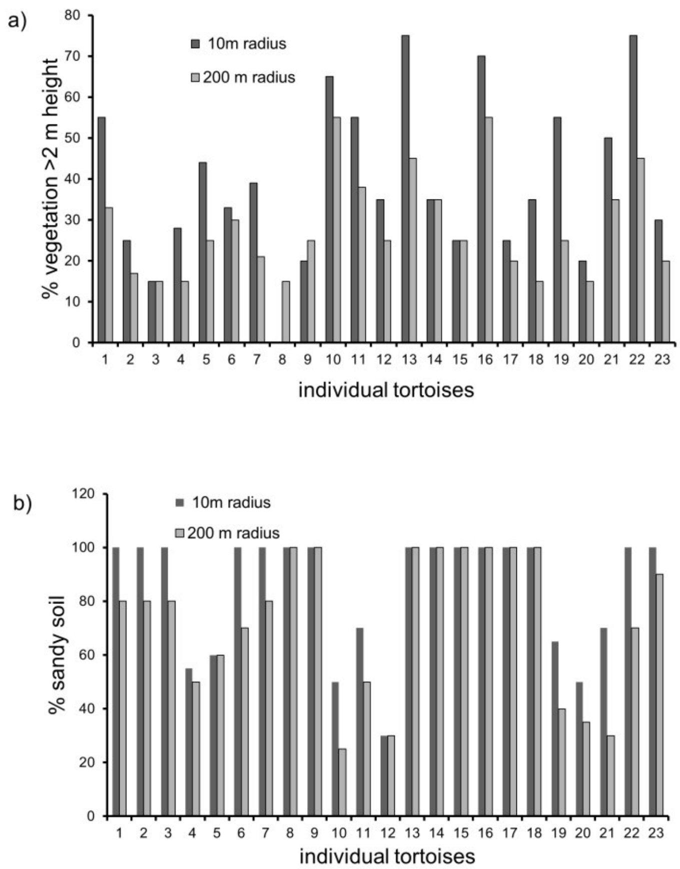
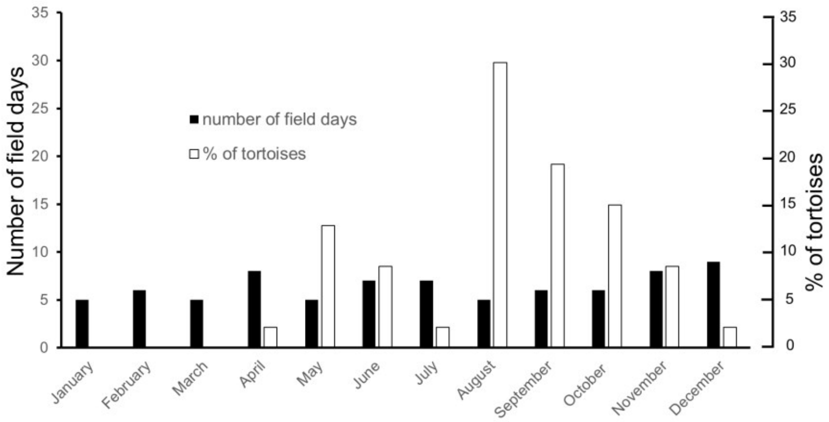


Figure 4. Monthly distribution of the % frequency of *Centrochelys sulcata* records (n = 47) in relation to the field effort (number of field days per month), at a south-eastern locality in Burkina Faso. For statistical details, see the text.



ONLINE SUPPLEMENTARY MATERIALS

Table S1. Classes of Estimated Human Population Density (people per Km^2) and of Elevation (m a.s.l.) used for analyses in the present study

Class	Range
Human population density	
101	0-200
102	201-400
103	401-600
104	601-800
105	801-1000
106	1001-1200
107	1201-1400
108	>1400
Altitude	
101	0-290
102	291-580
103	580-780
104	870-1160
105	>1160

Table S2. Geographic coordinates of the sites of presence for *Centrochelys sulcata* in Mali as ascertained during the present study

Locality name	Coordinates	No. Observed	males	females	young	other notes
Abeibara	20.048241, 2.241333	1	1			tracks
Abeibara II	19.381973, 1.914380	1		1		tracks
Abeibara III	19.218373, 1.912379	3	1	2		tracks
Tin Essako	18.290784, 4.149378	2	2			
Tin Essako	18.421864, 4.035968	1		1		
Menaka	17.615752, 4.215415	4	1	1	2	tracks
Menaka II	17.420747, 4.174444	1		1		
Menaka III	17.415704, 4.112013	3		3		tracks
Timbuctu	24.187696, -6.206062	1	1			tracks
Timbuctu II	24.646594, -4.703365	2	1	1		
Youvarour	15.574957, -4.338818	5	1	3	1	tracks
Niono	14.568453, -6.008462	3	1	1	1	tracks
Tenenkou	14.901026, -4.780570	1	1			
Ansongo	15.210955, 0.683779	2			2	

Table S3. Geographic coordinates of the sites of presence for *Kinixys nogueyi* in Mali as ascertained during the present study

Locality name	Coordinates		males	females	young
Bafing National Park	12.435.789	-10.412.507	1 male		
Bougouni	10.441.530	-7.270.825	4 males	2 females	
Sikasso I	11.366.618	-5.533.010	1 female		
Sikasso II	11.380.750	-5.515.107	1 male		
Sikasso III	11.324.253	-5.596.600	2 males		
Sikasso IV	11.244.751	-5.481.976	1 male	1 female	
Kadiolo I	10.713.788	-5.581.546	2 subadults		
Kadiolo II	10.767.666	-5.634.295	1 female		
Kadiolo III	10.506.485	-5.807.627	2 males	2 females	

Figure S1. Map of Mali showing villages within which interviews were conducted. Village names: 1 = Fadougou, 2 = Kenieba, 3 = Kalaya, 4 = Guenegore, 5 = Samou, 6 = Bafoulabé, 7 = Koundian, 8 = Menantali , 9 = Mahina, 10 = Danaou, 11 = Oualia, 12 = Sebekoro, 13 = Kolokani, 14 = Massantola, 15 = Banamba, 16 = Diema, 17 = Sitakilly, 18 = Gory.

Figure S2. Correlation between % cover at two spatial scales (10m and 200m radius) for presence sites of *Centrochelys sulcata* at a study area in Burkina Faso.

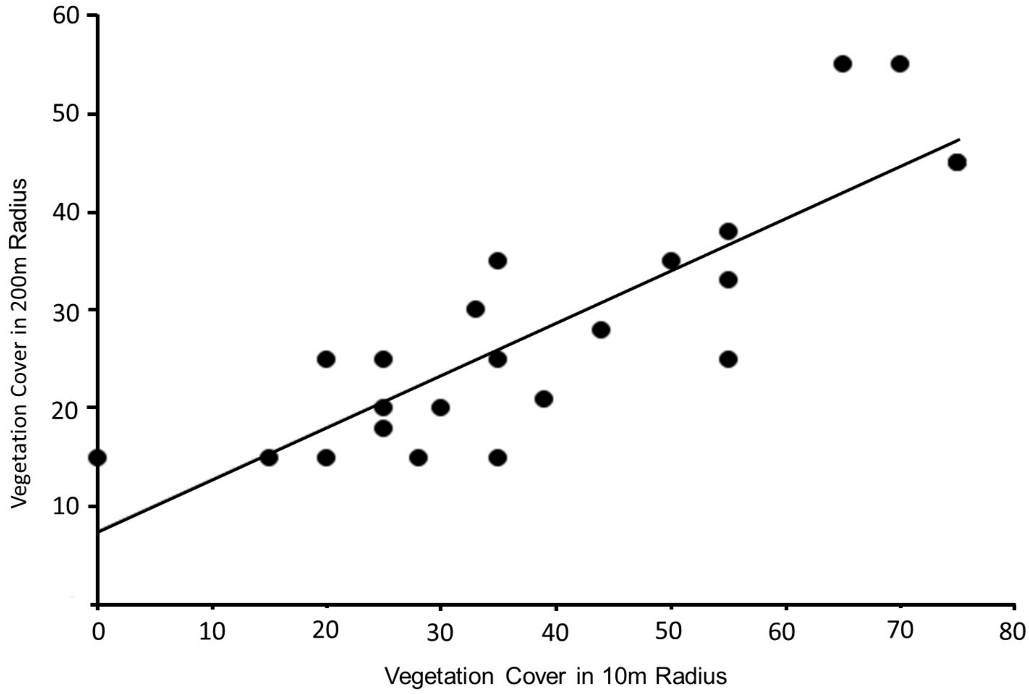


Figure S3. Bimodal diel activity cycle of *Cetrochelys sulcata* (n = 47) in Burkina Faso.