CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group

Edited by

Anders G.J. Rhodin, John B. Iverson, Peter Paul van Dijk,
Craig B. Stanford, Eric V. Goode, Kurt A. Buhlmann, and Russell A. Mittermeier

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Centrochelys sulcata (Miller 1779) – African Spurred Tortoise, Grooved Tortoise, Sahel Tortoise, Tortue Sillonnée

Fabio Petrozzi[1], Emmanuel M. Hema[2], Gift Simon Demaya[3], John Sebit Benansio[3], Edem A. Eniang[4], Tomas Diagne[5], Gabriel Hoinsoudé Segniagbeto[6,7], and Luca Luiselli[6,7,8]

[1]*Ecolobby, via Aretina 142, 50136 Rome, Italy [fapetrozzi@gmail.com];*
[2]*Université Ouaga 1 Professeur Joseph Ki Zerbo/CUP-D, Laboratoire de Biologie et Ecologie Animales, Ouagadougou, Burkina Faso [hema.emmanuel@yahoo.fr];*
[3]*Department of Wildlife, University of Juba, South Sudan [gftsimon@yahoo.co.uk; sebitbenansio@gmail.com];*
[4]*Department of Forestry and Wildlife, University of Uyo, Uyo, Akwa-Ibom State, Nigeria [edemeniang@yahoo.com];*
[5]*African Chelonian Institute, BP 80 Joal, Thies 23015, Senegal [africanci@gmail.com];*
[6]*Laboratory of Ecology and Ecotoxicology, Faculty of Sciences, University of Lomé, BP 6057, Lomé, Togo [h_segniagbeto@yahoo.fr];*
[7]*Institute for Development, Ecology, Conservation and Cooperation, via G. Tomasi di Lampedusa 33, 00144 Rome, Italy [l.luiselli@ideccngo.org];*
[8]*Department of Applied and Environmental Biology, Rivers State University of Science and Technology, PMB 5080, Nkpolu, Port Harcourt, Rivers State, Nigeria*

Summary. – *Centrochelys sulcata*, the African Spurred Tortoise (Family Testudinidae) is one of the largest terrestrial chelonians in the world, the largest extant continental tortoise, and the largest tortoise in Africa. Males are larger than females, and may exceed 100 kg in body mass, with a straight carapace length of up to 86.0 cm in males and 57.8 cm in females, and a curved carapace length reaching 101.0 cm in males and 67.0 cm in females. The species has a wide geographic distribution across the arid savannahs of the Sahelian regions of sub-Saharan Africa, but with many gaps in its range, and reaches the southern tip of the Arabian Peninsula. The sex ratio is nearly equal and sexual maturity is reached at 10–15 years. The species is especially linked to habitat with periodic or intermittent streams and rivers, locally called kori in the Sahelian regions. In addition, African Spurred Tortoises can be found on slopes and hills, in particular on stabilized dunes, and sporadically in flat areas with semi-deciduous shrublands and high grasses. Cattle grazing has a negative effect on the presence of this species, especially when grazing areas are created with seasonal fires. The species is mostly herbivorous, but can feed on carrion on occasion and on garbage in the surroundings of human settlements. Males are highly territorial, with larger males winning sexual combats. The population density is among the lowest that has been observed so far in terrestrial chelonians. The species makes extensive use of deep and long burrows (up to 15 m long), occasionally used by more than one individual, and above-ground activity is mainly concentrated in the early morning hours and during the wet season (August). Reproduction is also seasonal, with matings occurring primarily in September to April. Nesting occurs from September to May, during which 2–3 clutches of 14–40 eggs (average egg ca. 52 x 44 mm, 55 g) are laid. The species is declining rapidly due to a plethora of reasons, including habitat loss, exploitation for eggs and meat as well as for the international pet trade, and the effects of climate change, but since it is easy to breed in captivity and is frequently bred by local communities, there is significant potential for reintroduction programs, some of which have already been initiated in Senegal.

Distribution. – Benin, Burkina Faso, Cameroon (likely extirpated), Central African Republic, Chad, Eritrea, Ethiopia, Mali, Mauritania, Niger, Nigeria, Saudi Arabia, Senegal, Sudan, and Yemen. Possibly previously present in Djibouti (extirpated?), Togo (extirpated?), and Somalia.

Synonymy. – *Testudo sulcata* Miller 1779*, Geochelone* (*Geochelone*) *sulcata, Geochelone sulcata, Peltastes sulcatus, Centrochelys sulcatus, Centrochelys sulcata, Testudo calcarata* Schneider 1784 (*nomen novum*)*, Chersine calcarata, Testudo radiata senegalensis* Gray 1831*, Geochelone senegalensis, Geochelone sulcata senegalensis, Testudo schoepfii* Rüppell *in* Gray 1873 (*nomen nudum*)*, Geochelone sulcata sudanensis* Ballasina, Vandepitte, Mochi, and Fenwick 2006 (*nomen nudum*).

Subspecies. – None currently recognized.

Status. – IUCN 2020 Red List Status: Vulnerable (VU A1cd, assessed 1996); TFTSG Provisional Red List: Endangered (EN, assessed 2013); CITES: Appendix II (as Testudinidae spp.).

Figure 1. Adult male *Centrochelys sulcata* from Katane, Senegal. Photo by Tomas Diagne.

Taxonomy. — The species was described as *Testudo sulcata* by Miller (1779). Through the years, it has been referred to by several subsequent designations: *Geochelone* (*Geochelone*) *sulcata*, *Geochelone sulcata*, *Peltastes sulcatus*, *Centrochelys sulcatus*, and finally *Centrochelys sulcata*. Its type locality was originally erronously designated as "India occidental" by Miller (1779), and further erroneously restricted to "West Indies" by Miller and Shaw (1796); Bour (2013) provided a detailed history of the description of the species. Subsequent synonyms of *Centrochelys sulcata* include *Testudo calcarata* Schneider 1784 (*nomen novum*), *Testudo radiata senegalensis* Gray 1831, *Testudo schoepfii* Rüppell *in* Gray 1873 (*nomen nudum*), and *Geochelone sulcata sudanensis* Ballasina, Vandepitte, Mochi, and Fenwick 2006 (*nomen nudum*).

No subspecies are currently recognized. Devaux (2004), studying the genetic differences between individuals in western and eastern Africa, defined two forms: the western populations (found from Mauritania to Niger, including Senegal), and the eastern populations (from Sudan to Ethiopia). However, Livoreil and Van Der Kuyl (2005), in an analysis of mitochondrial DNA variation in the species, found three closely related haplotypes, one from Sudan in the eastern range of the species, one from Senegal in the western range of the species, and a third common haplotype from Senegal, Mali, and Sudan.

The complete mitochondrial genomic analysis of *C. sulcata* revealed that the gene content included 13 protein-coding genes, 22 tRNA genes, two rRNA genes, and one control region (Shi et al. 2017). Otherwise, the lack of cytosine, as in other species of Testudinidae, was detected in arms of the tRNALys gene. In addition, an extra nucleotide adenine was discovered in the ND3 gene (Shi et al. 2017).

Description. — *Centrochelys sulcata* is one of the largest species of tortoise in the world and the largest in Africa (Branch 2008). Several insular tortoise species

Figure 2. Adult female *Centrochelys sulcata* in Kafta Sheraro National Park, northwestern Ethiopia. Photo by Håkan Pohlstrand.

Figure 3. Adult male *Centrochelys sulcata* in Arly, Burkina Faso, with forked gular scutes. Photo by Luca Luiselli and Fabio Petrozzi.

Figure 4. Adult male *Centrochelys sulcata* from Senegal with diverged gular scutes. Photo by Tomas Diagne.

Figure 5. Adult female *Centrochelys sulcata* in Kafta Sheraro National Park, northwestern Ethiopia. Photo by Håkan Pohlstrand.

(*Chelonoidis* spp.) in the Galápagos are larger, as are the *Aldabrachelys* taxa from Aldabra and the Seychelles. However, *C. sulcata* is the largest extant continental tortoise, all other larger continental tortoises having been driven into extinction by early humans (TEWG 2015).

Centrochelys sulcata typically has an adult body mass of 45–91 kg, but some male specimens reach sizes of more than 100 kg with a record specimen of more than 120 kg (Bour 2004). The straight carapace length (SCL) of males reaches to about 80 cm, with an exceptional male recorded at 83 cm (Lambert 1993; Vetter 2005) and one of 86 cm in Burkina Faso (Ardjima et al. 2020). Females are smaller and more rounded than males (Herz 2018). In Mali, Lambert (1996a) reported male SCL of 38.4–79.7 cm and female SCL of 33.6–57.8 cm. In Burkina Faso, in a total of 12 wild individuals measured for curved carapace length (CCL), males (mean = 78.4 ± 12.1 cm, range 73.0–97.0 cm, n = 7) were significantly larger than females (mean = 55.2 ± 5.7 cm, range 49.0–64.0 cm, n = 5) (Petrozzi et al. 2016a). In a captive sample from Burkina Faso, SCL in adult males measured 56.3 ± 10.6 cm (range 21.7–86.0 cm, n = 51) and in adult females measured 41.3 ± 10.6 cm (range 16.4–64.3 cm, n = 59) (Ardjima et al. 2020). In an introduced population in Costa Rica, the immature individuals, aged from 5 to 34 months, had a mean SCL of 8.31 cm, mean straight plastron length of 6.83 cm and mean maximum shell depth of 4.62 cm (Merchán et al. 2005).

Figure 6. Subadult *Centrochelys sulcata* from Senegal. Photos by Tomas Diagne.

Since *C. sulcata* may reach a very large size, SCL measurements are often difficult to obtain in the wild, and researchers are often forced to measure CCL (Petrozzi et al. 2016a). In the literature there are no available analyses that allow conversion of CCL into SCL, so we hereby provide an analysis based on tortoises we measured simultaneously for SCL (cm) and CCL (cm) in Burkina Faso. Based on our samples, the relationship for females (n = 59) and for males (n = 51) is:

$$Female\ SCL\ (cm) = 0.819CCL\ (cm) - 2.559$$
$$Male\ SCL\ (cm) = 0.925CCL\ (cm) - 7.389$$

Males also significantly exceed females in terms of body mass (Ardjima et al. 2020): in a sample of individuals from Burkina Faso, the mean male mass was 81.0 ± 54.6 kg (range 5.39–115 kg, n = 50) and the mean female mass was 37.1± 20.4 kg (range 1.81–52.2 kg, n = 59). In Mali, Hailey and Lambert (2002) reported an average body mass (including free-ranging juveniles) of about 33 kg, larger than in Burkina Faso (mean = 23.9 ± 37.4 kg, n = 230) (Ardjima et al. 2020). Lambert (1996a) reported that male body mass ranged from 11.8 to 93 kg and female mass 6.1–47 kg. A captive sample reported by Ritz et al. (2010) weighed about 27 kg on average.

According to Lambert (1993), the relationship between SCL (mm) and mass (g) for *C. sulcata* in Mali was:

$$Body\ mass\ (g) = 0.000922SCL^{2.755}$$

In Burkina Faso, the relationship between SCL (cm) and body mass (kg), after reanalyzing the raw data (n = 110) in

Figure 7. Hatchling *Centrochelys sulcata* from Senegal. Photos by Tomas Diagne.

Ardjima et al. (2020), and adding measurements from another 171 animals (total $n = 281$), is:

$$Body\ mass\ (kg) = 0.0294SCL^2 - 0.578SCL + 2.719$$

Except for growth lines and scute borders that are darker, the carapace and plastron have the same yellow-brownish sandy color. Hatchlings are more uniformly yellow than adults, and progressively take on a more contrasted coloration pattern with growth, developing darker coloration.

The carapace of this species is strongly convex and has five vertebrals, four pairs of costals, 11 marginals on each side with one supracaudal (all serrated, except those along the bridge, and the posterior ones upturned); there is no nuchal scute (Branch 2008; Trape et al. 2012). There are six pairs of plastral scutes.

The plastron is heavily concave in males and flat in females. Males have forked or diverged gular scutes and widely flared anal scutes; females have unforked gular scutes and narrowly flared anal scutes. The front limbs have five claws, with four on the rear limbs. All four limbs have distinctly pronounced scales (Herz 2018).

Distribution. — Determining the distribution of the species is problematic as some populations have originated from specimens escaped from captivity into the wild (Mallon et al. 2015). Moreover, social and political turbulence in much of the Sahel region often inhibits research on the species (Petrozzi et al. 2017), thus it is likely that the true distribution of this species may be underestimated.

The species has a wide range (Broadley 1989; Iverson 1992; Devaux 2000b; TTWG 2017), but also has a scattered distribution with many gaps, that may be due to a deep and generalized decline (Branch 2008; Petrozzi et al. 2016a). *Centrochelys sulcata* is native to the southern limit of the Saharan Desert and the Sahel, an ecoregion with typically semiarid grasslands, savannahs, and thorn shrublands. Its distribution includes, in alphabetical order, Benin (Vetter 2005), Burkina Faso (Petrozzi et al. 2016a), Cameroon (Vetter 2005), Central African Republic (Trape et al. 2012), Chad (Keith and Plowes, 1997; Trape et al. 2012), Djibouti (Vetter 2005), Eritrea (Largen 1997), Ethiopia (Vetter 2005), Mali (Perolini 1988), Mauritania (Arvy et al. 1997; Trape et al. 2012), Niger (Moore 1997; Trape et al. 2012; Petrozzi et al. 2019), Nigeria (Petrozzi et al. 2015), Saudi Arabia (Gasperetti et al. 1993), Senegal (Iverson 1992; Trape et al. 2012), Sudan (Cloudsley-Thompson 1970), and Yemen (Gasperetti et al. 1993). Because of the few historical data, and a shortage of field studies on habitat use and selection, it is difficult to assess if the gaps in distributional records are due to human harvesting and anthropogenic pressure on the species, or because of inadequate habitat characteristics and lack of survey efforts in many areas of its range (Petrozzi et al. 2015).

In Benin, the species occurred until about 20 years ago from Kandi to the Niger River course, in the extreme north of the country, and very likely on the Benin side of the W Regional Park. Interviewed shepherds showed shells of recently dead animals and confirmed its presence in the extreme north of the country, but no free-ranging animals were observed in 2002–2003 (Luiselli et al., unpubl. data).

In Burkina Faso the species is present in the northern and central-eastern part of the country (Petrozzi et al. 2016a); recently, the species has been recorded in Baraboulé, Pama North, Bogandé, Arly, Katchirga, Ouahigouya, Diapagà (Petrozzi et al. 2016a) and Fada (Petrozzi et al. 2020). In general, the species is rare in the country, and apparently confined to protected areas with well-preserved savannah habitat (Petrozzi et al. 2016a).

In Cameroon, the species is apparently extirpated: it was observed only at Bouba-Ndjidah (at 280 m a.s.l.) (Chirio and LeBreton 2007) and at Bénoué National Park southeast of Garoua (Vetter 2005). It should be searched for in Faro National Park (Chirio and LeBreton 2007).

In Central African Republic, there have been no recent field studies and a summary of the known localities was given in Chirio and Ineich (2006) and Trape et al. (2012).

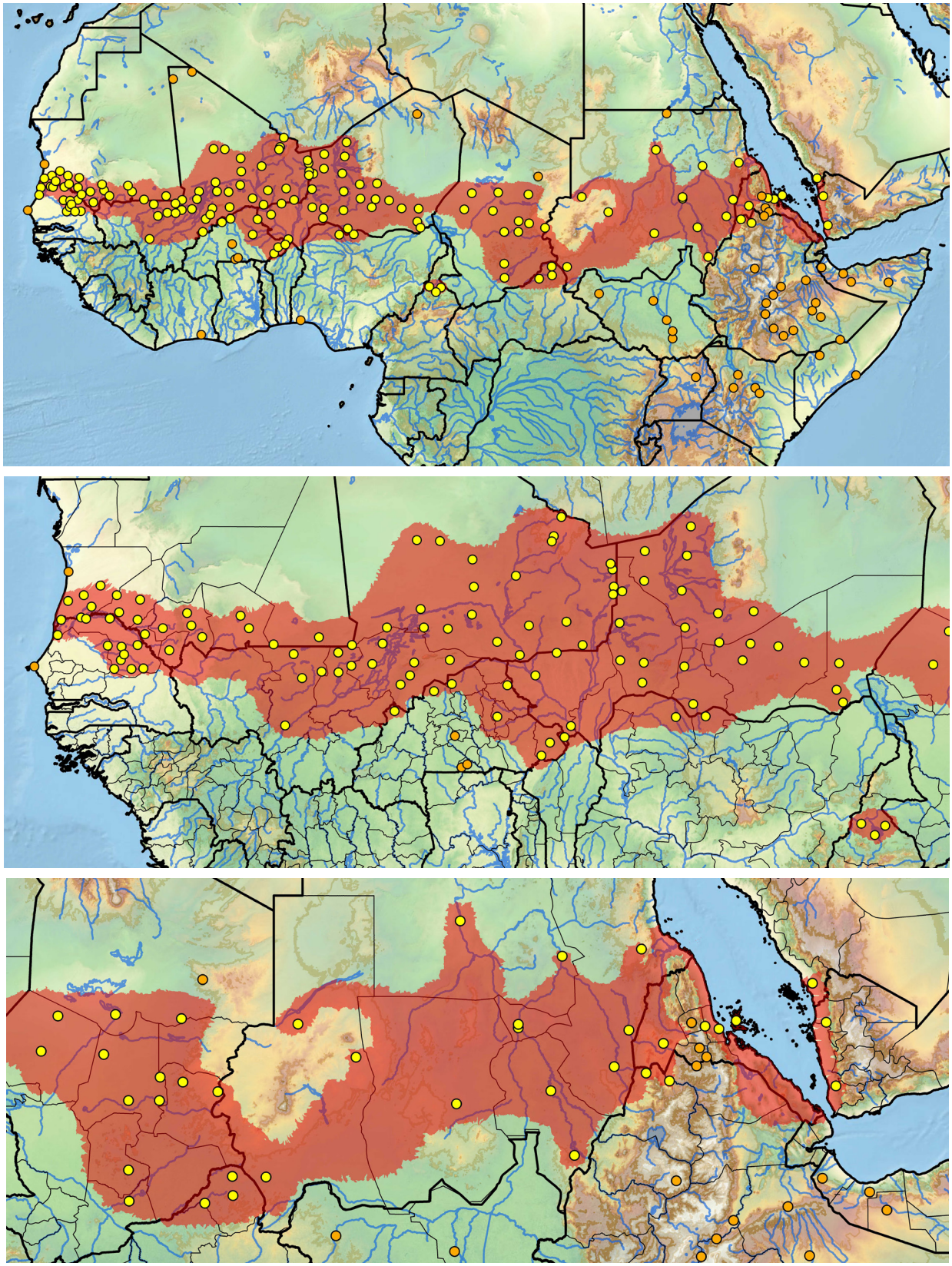

Figure 8. Distribution of *Centrochelys sulcata* in sub-Saharan Africa and the Arabian Peninsula. *Top*: Entire range, *middle*: western range, *bottom*: eastern range. Yellow dots = museum and literature occurrence records of native populations based on Iverson (1992) plus more recent and authors' data; orange dots = uncertain native or introduced or trade specimens (see Devaux 2000b); red shading = presumed indigenous range (see also Devaux 2000b). Distribution based on GIS-defined level 10 HUCs (hydrologic unit compartments) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs (Buhlmann et al. 2009; TTWG 2017), and adjusted based on authors' subsequent data.

Many individuals of this species were observed in the Vakaga area in the north of the country with thornbush savannah vegetation, and also in the Koumbala Reserve (Ndélé), in Birao (Chirio and Ineich 2006), and in Tiroungoulo, Gordil, Délembé, and Bamingui Bangoran National Park (Vetter 2005). Because of the difficult logistics in this country, it is well possible that the species is more widely distributed than actually confirmed.

In Chad, the species is apparently widely distributed across the southern and central regions (Trape et al. 2012), but there have been no recent field surveys to better evaluate its current distribution and abundance.

In Djibouti the species is probably extirpated, given the small size of the country and the high human density (Vetter 2005).

In Eritrea, the species is certainly present in the Asmara region, Barentu, and the Teseny Reserve (Vetter 2005; Trape et al. 2012). Historical records have come from Cheren from 1891, and from Godolefassi, Mareb River and Chenafena from 1928 (Del Prato 1891; Scortecci 1928; Largen 1997). In general, the species seems quite widespread across the country (Vetter 2005).

In Ethiopia, the species has been recorded from Dire Dawa and Addis Ababa, but these records were probably of captive individuals (Vetter 2005). The species is certainly present in Awash National Park, about 120 km east of Addis Ababa, but the population there may have originated from an introduction. The species is probably present along the border with Sudan, but there are no definite records of wild individuals from those regions where, however, field surveys are extremely difficult. Two adults were photographed in Kafta Sheraro National Park in northwestern Ethiopia along the border with Eritrea in 2018 (H. Pohlstrand, pers. comm.).

In Mali, the species has recently been observed in the southern portion of the country, more precisely at Abeibara, Tin Essako, Djoudj, Mopti, Menaka, Timbuctu, Youvarour, Niono, Tenenkou, and Ansongo, but was reported to be present by shepherds and villagers in a number of other villages (Petrozzi et al. 2020). Although likely in decline, it seems that the species is still relatively widespread across the southern regions and along the border with Burkina Faso (Petrozzi et al. 2020) and in the Dogons (Perolini 1988).

In Mauritania, the species is still found in the southern and southwestern regions (Arvy et al. 1997; Nickel 2006), Tagant (Lluch et al. 2004), Moudjéria, Trarza, Brakna, Gorgol, Assaba, Guidimaka, Hodh-ec-Chargui, Hodh-el-Gharbi, Rosso, and especially in the Diawling National Park (Nickel and Selah 2002; Vetter 2005; Padial 2006). In general, the species seems widespread in the country, and its populations are likely well connected to those occurring in Mali (Vetter 2005).

In Niger, the presence of this species has been recorded in the Niamey region, Tahoua, Zinder, W National Park area, in the Department Maradi at the border with Nigeria, and in Teneré-Termit (Claro 2003; Ineich et al. 2014; Petrozzi et al. 2018). Although in likely decline, the species is still relatively widespread in the country.

In Nigeria, the species is known only from a few localities of dry savannahs situated in the northernmost territories along the border with Niger (Ungongo, Kano State; surroundings of Katsina, Katsina State; Nkaé, Borno State; Petrozzi et al. 2015). Wild populations of this species appear to be extremely rare in the country. Instead, introduced non-native individuals (perhaps forming small reproductive populations) are found in a few areas in the southwestern part of the country (Olaniyi et al. 2016), including the Lekki area (Luiselli et al., unpubl. data).

In Senegal, the species was once very widespread in the northern part of the country, from Thiès to Saint-Louis, and towards the east and the border with Mali (Devaux 1993, 1998; Vetter 2005; Trape et al. 2012). Currently, the species has a relatively narrow distribution in the country, especially in the Departement Matam, not far from the border with Mauritania (Vetter 2005). A few wild specimens also occur in the Reserve de Faune du Ferlo Nord et Sud, near the Ranerou district.

In Sudan it has been observed in Al-Muglad, Barbar, Kassala, Dongola, Darfur, Wadi Halfa, and along the Nile river up to the border with Egypt (Devaux 2000a; Trape et al. 2012). The populations are probably connected with those of Chad, and the species is possibly more widespread in the country than currently determined (Devaux 2000a). However, the socio-political instability makes exploration of this country very difficult, and no recent surveys have been undertaken.

In Togo, Segniagbeto et al. (2014) did not include *C. sulcata* as a native species of the country. However, the habitat characteristics and the short linear distance from northern Togo to the Pama area in Burkina Faso, where wild populations of this species have been recorded (Petrozzi et al. 2018), would indicate that the historical presence of this species in extreme northern Togo (Oti-Keran area) is likely. However, because of the massive habitat degradation and exploitation by the human population, it is also likely that this species has been extirpated from Togo. Also its presence in Somalia is unlikely but not excluded, as there are localities where the species has been recorded, although they were all probably captive or introduced or trade specimens.

Many isolated specimens of *C. sulcata* recorded outside the Sahelian zone appear to represent introduced or escaped trade animals, with the numerous records immediately south of its native range in East Africa especially representative of this anthropogenic effect (Devaux 2000b). The species has also been introduced in various other extra-limital areas, including Catalonia in Spain (Massana and Martínez-Silvestre 2016), Hawaii (Burney et al. 2012), Costa Rica

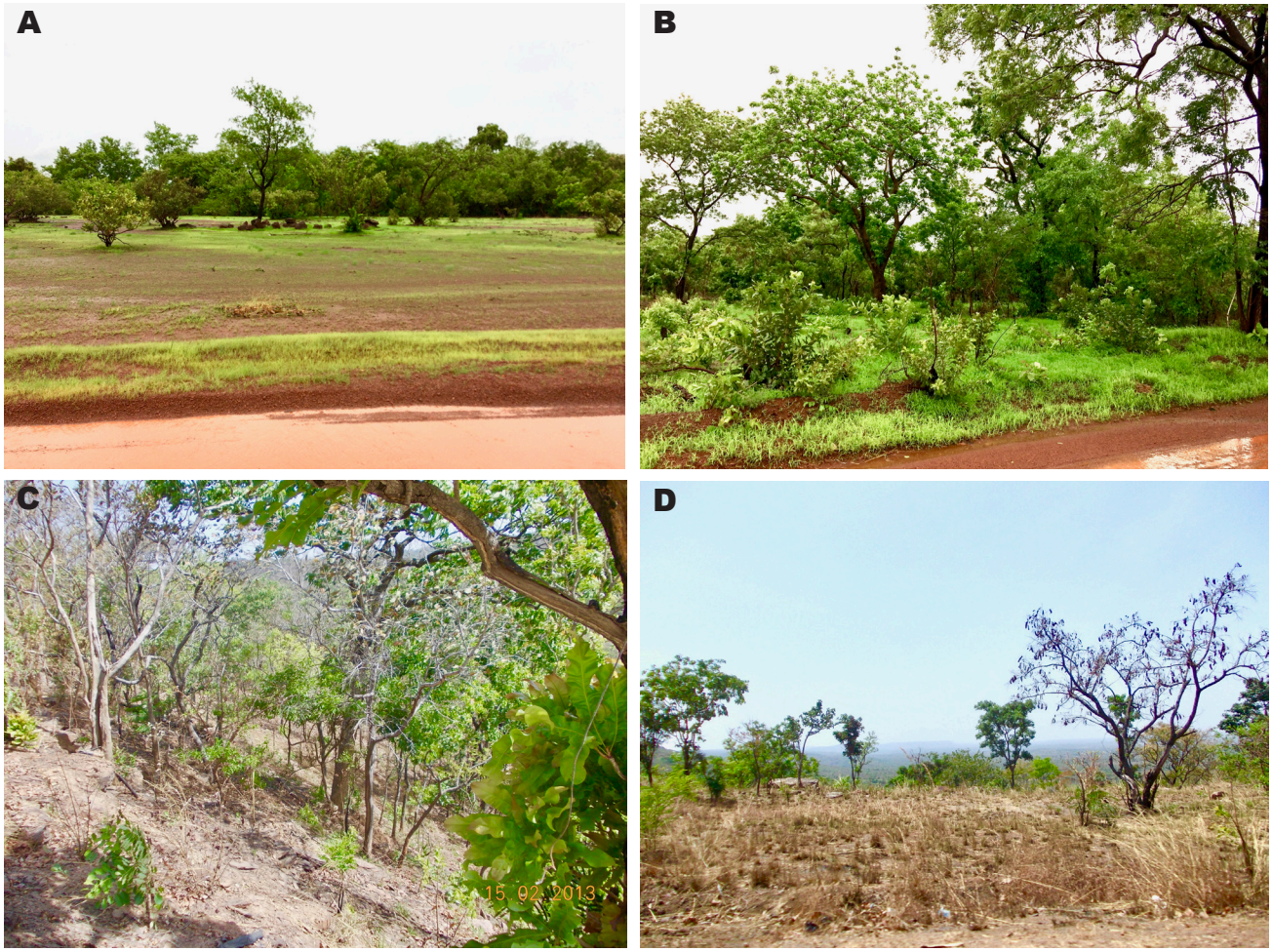

Figure 9. Typical habitats of *Centrochelys sulcata* in West Africa. **A–B:** savannah habitats in southern Mali, during the wet season. Photos by Luca Luiselli. **C–D:** dry savannah habitats in southeastern Burkina Faso, during the dry season. Photos by Fabio Petrozzi.

(Merchán et al. 2005), the Gambia, and possibly Saudi Arabia and Yemen (where it is likely to have been native in the past). Many escaped individuals can be observed in additional countries: for instance, we (Luiselli, Gonedele, et al.) observed a hatchling in Banco National Park, Abidjan, Ivory Coast.

Habitat and Ecology. — For *C. sulcata*, there are not many available field studies on habitat use patterns at either local or regional scales. On a global scale, the species is found in the Sahel region, in areas where vegetation is scarce, and where there is a lack of water during the prolonged dry season, but running water during the wet season in August (Villiers 1958; Petrozzi et al. 2017). In particular, the species seems to occupy habitats where the diurnal temperatures may exceed 40°C and the nocturnal temperatures may decrease to below 15°C, as is the case in Mali (Cloudsley-Thompson 1970; Lambert 1996b). These areas are characterized by Sahelo-Sudanian vegetation (Boulweydou 2008; Branch 2008), e.g., *Acacia* spp., *Adansonia digitata*, *Grewia bicolor*, and annual plants, especially those present in the wet season (Vetter 2005). Moreover, *C. sulcata* seems to be associated with *Cenchrus biflorus*, an abundant plant species in the ephemeral Sahelian prairie (Scherman and Riveros 1989). In general, according to Lambert (1993), the savannah habitats occupied by this species in the Sahel optimally provide both shade from the sun during the hottest hours of the day and also green vegetation as food, e.g., *Eleusine indica* during the rainy season.

Although general reviews have considered that the species is a generalist in habitat selection (Vetter 2005), more detailed field studies, performed at a finer scale, have revealed that *C. sulcata* is not a generalist species, as it inhabits specific areas with distinctive landscape and vegetation characteristics (Petrozzi et al. 2019, 2020). One of the most important ecological variables for the species is the presence of periodic or intermittent streams and rivers, locally called *kori* in the Sahelian regions (Petrozzi et al. 2017). In addition, African Spurred Tortoises can be found on slopes and hills, in particular on stabilized dunes, and sporadically in flat areas with semi-deciduous shrublands and high grasses (Petrozzi et al. 2019). The species prefers stabilized dunes, because of their more abundant vegetation

(Petrozzi et al. 2017); during the wet season, annual herbs are present in high density and tortoises apparently select this habitat because of its bountiful availability of food (Petrozzi et al. 2017) and because stabilized dunes are optimal for digging burrows (Vetter 2005).

Adult Spurred Tortoises dig their own burrows (Pouvreau 1989; Jost and Jost 2005), the length of which can reach 15 m (Devaux 2004), but they may also use small mammal burrows: for example, Mill (2005) recorded a tortoise using the lair of a Cape Aardvark (*Orycteropus afer*). Burrows are crucial for the survival of individual tortoises, as they are occupied for long periods of time in order to avoid overheating (Petrozzi et al. 2017), and also for aestivating during dry season peaks (Vetter 2005). Hatchlings probably also seek the abandoned burrows of small mammals away from rocky outcrops in their natural habitats where the soil is light and sandy (Lambert 1993).

Whereas semi-deciduous shrublands and highly herbaceous areas are usually associated with presence of *C. sulcata*, bare areas (called *zipele* in the region) and cultivated areas are usually avoided (Petrozzi et al. 2017, 2019). In general, the species prefers areas where human activities are greatly limited, and areas with no cattle (Petrozzi et al. 2019).

Studies in Burkina Faso have revealed that the above-ground activity of *C. sulcata* is limited to the wet season (with the activity peak being in August and, to a lesser degree in September), and has a clearly bimodal diel activity cycle, with most sightings in the early morning hours (and a few in the evening) whereas it spends the rest of the day in its burrow (Petrozzi et al. 2020). In Mali, these tortoises retreat into their burrows when the ambient temperatures exceed 32°C, and they inhabit only regions with annual rainfall between 140–1098 mm (Lambert 1996a). Burrows are sometimes occupied by more than one individual (Petrozzi et al., unpubl. data), but often these are young individuals, as adults tend to reside alone in their burrow (Cadi 2004). Adults also exhibit a gender distribution pattern of males and females occupying separate but close burrows, between 100 and 200 m apart (Cadi 2004).

Cloudsley-Thompson (1970) observed in Mali that the basking behavior in this species is temperature-mediated rather than light-mediated. The higher above-ground activity intensity during wet months, and the bimodal diel activity pattern (with early morning peak), that are correlated with the temperature-mediated thermoregulation strategy, are not surprising since these patterns have previously been observed for other Afrotropical tortoises (Hailey and Coulson 1996; Luiselli 2003). However, according to Cloudsley-Thompson (1999), captive African Spurred Tortoises apparently show a different well-marked temperature-independent circadian activity rhythm.

Centrochelys sulcata is almost entirely herbivorous, with succulents, herbs, grasses, and withered parts of plants typically being eaten (Vetter 2005; Branch 2008). It is also among the tortoise species that has physiological specialization ensuring the fermentation of cellulose in the gastrointestinal tract (Baur 2003). However, very few data are available on the diet of free-ranging individuals. Among the plant species recorded as food for *C. sulcata* in the wild, we have noted the following: *Cassia obtusifolia*, *Commelina bengalensis*, *Dactyloctenium aegyptum*, *Digitaria ciliaris*, *Eleusine indica*, *Eragrostis tenella*, *Portulaca oleracea*, and *Leptadenia hastata* (Vetter 2005). In Djoudj and Mopti, Mali, the species has also been

Figure 10. Actively occupied *Centrochelys sulcata* burrow in Senegal. Photo by Tomas Diagne.

Figure 11. Adult *Centrochelys sulcata* inside its burrow in Mali. Photo by Fabio Petrozzi.

observed eating grasses and floating algae and plants on the water surface (Vetter 2005). In southeastern Burkina Faso, the scat of *C. sulcata* is typically formed of almost 100% grass fibers (Luiselli, Hema, and Petrozzi, unpubl. data). African Spurred Tortoises can also consume mushrooms (Elliott et al. 2019).

Occasionally, the species eats carrion, and it has been observed opportunistically feeding on corpses of goats and zebu (Vetter 2005). It is hypothesized that the preference of *C. sulcata* for *kori* habitat also depends partly on the fact that, by the wet season, the intermittent streams are full of water and consistently transport carrions of goats and other animals that can provide an additional food source (Petrozzi et al. 2017). In the surroundings of human settlements, these tortoises are also well known to feed opportunistically on garbage (Vetter 2005). In addition, *C. sulcata* is an important seed-disperser of savannah habitats (Burney et al. 2012; de Miranda 2017).

Males are highly territorial; the larger males win sexual combats (Grubb 1971; Stearns 1989). The anal scutes in full-grown males can be strongly and widely recurved, and sometimes even flared at the periphery (Lambert 1993). These thickened and generally strengthened anal scutes are probably associated with ramming and lifting the rear of the carapace of those females that resist mating (Lambert 1993).

In Burkina Faso and Niger, the estimated densities (by means of line transects with DISTANCE algorithm for determining population density) were in general apparently very low; median = 0.001 individuals × ha^{-1}, except in the Teneré-Termit region (Niger), where the estimated density was considerably higher (Petrozzi et al. 2018). The density of African Spurred Tortoises appeared, in general, to be lower than that observed in several other species of African tortoises (e.g., Hailey et al. 1988; Langtimm et al. 1996; Coulson and Hailey 2001; Kuzmin 2002).

The sex-ratio is even in Mali, and males are much larger than females (Lambert 1993). In Burkina Faso, the sex-ratio was slightly skewed towards males (1.3:1) (Petrozzi et al., unpubl. data). In Fada, Burkina Faso, the captive tortoise population was predominantly made up of adults (53%) and sub-adults (31%) and less by juveniles (16%); the adult sex ratio was 0.93 (13 males: 14 females), i.e., practically even (Ardjima et al. 2020).

Sexual maturity is reached at about 35–50 cm SCL and at 15–20 kg body mass, corresponding to an age of about 10–12 yrs in females and 13–15 yrs in males (Vetter 2005). Herz (2014), however, reported that age of maturity is reached at 6 yrs in captive individuals, whereas Heimann (1999) reported a female who had her first brood at 5 yrs of age. Life expectancy in the wild is unknown, but in captivity it is at least 54 years (Biegler 1966) and is estimated to exceed 75 years (Walls 1997).

Figure 12. Wild *Centrochelys sulcata* mating in Senegal; male with forked gulars. Photo by Tomas Diagne.

Mating activity occurs from September to April (Vetter 2005); in Burkina Faso it has been observed in November (Luiselli et al., pers. obs.). In Sudan, mating activity has been observed from June until the end of March, but most frequently between September and November (Cloudsley-Thompson 1970). Males are anecdotally reported to search huge distances in order to find females: up to 10–20 or even 100 km, according to Vetter (2005). However, there are no quantitative field studies confirming these large distances, and no radiotracking studies on home range size for either males or females.

Egg deposition occurs from September through May, and the eggs, whitish and nearly ball-shaped, measure 52 x 44 mm on average (range 49–55 x 42–48 mm) and have an average mass of 55 g (range 25–70 g) (Vetter 2005). Mean egg mass was 40.3 g in Sudan (Cloudsley-Thompson 1970), 58.0 g in Chad (Mill 2005), and, in captivity, 35.0 g (Stearns 1989), 45.1 g (Herz 2014), or 53.4 g (Czernay and Praedicow 1988). The relative clutch mass (clutch mass/spent body mass) was 3.06% in Sudan (Cloudsley-Thompson 1970), 4.82% in Chad (Mill 2005), and, in captivity, 3.22% (Stearns 1989), 4.24% (Herz 2014), or 1.16% (Czernay and Praedicow 1988).

In captive individuals, egg clutches typically consist of 15–20 eggs, with a maximum record of 40 eggs (Vetter 2005). The average clutch size was 18.7 eggs in a captive sample from Nigeria (Boisson and Capon 1978), 17 eggs in Sudan (Cloudsley-Thompson 1970), 24.5 in a captive sample from Chad (Mill 2005). In a Burkina Faso sample, mean clutch size was 18.9 (standard deviation = 4.1, standard error = 1.53, range 14–21, n = 7; Petrozzi et al., unpubl. data). Data from captive individuals outside their natural range have indicated mean clutch sizes of 6.75 (Czernay and Praedicow 1988), 24.0 (Herz 2014), and 25.0 (Stearns 1989). Each female may oviposit up to 2–3 times

per year; according to Vetter (2005), the early clutches of free-ranging individuals (e.g., deposited in January) consist of fewer but larger eggs than subsequent clutches (e.g., deposited in April). Although *C. sulcata* females do not guard their eggs, a protective behavior of the nesting site has been observed to last several hours after oviposition (Czernay 1993).

Hatchlings measure 45 mm SCL on average (range, 36–60 mm), and have a mean body mass of 40 g (range, 20–75 g) (Vetter 2005). In Burkina Faso, the mean weight of juveniles was 145 ± 16.2 g (n = 120), and hatchlings weighed 31–46 g (n = 31) (Ardjima, Hema et al., unpubl. data).

Temperature-dependent sex determination (TSD) occurs in *C. sulcata*, with females produced at higher temperatures, males at lower temperatures, with the pivotal temperature at about 30.8ºC (Ligon et al. 2009). However, TSD in *C. sulcata* appears to no longer be evolutionarily adaptive, but persisting because selection against it and in favor of other sex-determining mechanisms is weak (Ligon et al. 2009).

There is a relationship between growth rate and weather conditions, especially the presence or lack of rainfall (Lambert 1993). This is manifest in the scute annuli in *C. sulcata*, in which clear, deep grooves (growth arrest lines) are formed during aestivation (Lambert 1993).

Adult individuals, larger than about 30 kg weight, are probably immune from predation (Coulson and Hailey 2001). There are no known data on predators of hatchlings or subadults. The Savannah Monitor Lizard (*Varanus exanthematicus*) was observed destroying an entire clutch of 28 eggs at Katane in Ferlo, Senegal (Diagne, unpubl. data). Nile Monitor Lizards (*Varanus niloticus*) are also surely predators of eggs where they coexist with *C. sulcata* (e.g., in southeastern Burkina Faso, W Regional Park, and southern Mali). Other potential predators may be mongooses (*Herpestes ichneumon*, *Ichneumia albicauda*), that are also usually sympatric with *C. sulcata*.

The African Spurred Tortoise inhabits regions where tortoise species richness is extremely low. It may co-occur with *Kinixys nogueyi* in West Africa or with *K. belliana* in central and east Africa (Trape et al. 2012). However, a field study recently conducted in Mali suggested that these two species do not occur in microsympatric conditions (Petrozzi et al. 2020). Nonetheless, in southern Egypt, where it no longer occurs, *C. sulcata* was historically apparently sympatric with *Stigmochelys pardalis* (Kowalski et al. 1993).

Population Status. — The species has anecdotally been considered in serious decline (Branch 2008), and indeed it is possibly the first reptile species that has been extirpated from Cameroon (Chirio and LeBreton 2007). It has also likely been extirpated from Djibouti (Vetter 2005), and perhaps Togo (Segniagbeto et al., unpubl. data). Local extirpations have occurred also in parts of northern Benin, northern Nigeria, central Burkina Faso (where the species was present also in the Ouagadougou region until about 50 years ago), in parts of Mali, Mauritania, and Senegal, and possibly elsewhere (e.g., Ogbonna et al. 2015).

In most sites where the species still occurs, only a few individuals can be observed (thus indicating small population sizes). Field work in Mali during 2018 in 12 distinct sites revealed that the number of tortoises observed per site ranged from 1 to 5 (mean = 2.50 ± 1.29; Petrozzi et al., in press). The same was also observed in Burkina Faso (Petrozzi et al. 2016a) and in Nigeria (Petrozzi et al. 2015). In general, *C. sulcata* seems to have a very scattered distribution also because of local extirpations (Devaux 2000b).

More recently, the decline of the species was quantified in three West African countries (Burkina Faso, Niger, and Nigeria) by interviewing 619 persons (hunters/farmers/cattle farmers) of different ages, with the interviewees being asked whether in their experience the tortoise was common, rare, or absent (Luiselli et al., in press). Their answers were stratified by age and analyzed; the probability of answering "common" increased with age in Nigeria and Burkina Faso, and the probability of responding "absent" declined with age in Nigeria and Niger. There were no significant effects of age for the answer "rare" in any country and no differences occurred between villages in any of the studied countries. Luiselli et al. (in press) extrapolated from these analyses that extirpation of *C. sulcata* may have occurred in 16.7% of the sites where old interviewees reported the species as common and young interviewees as absent.

Threats to Survival. — Habitat modification and the international pet trade are among the most important threats for the species (Petrozzi et al. 2016b). In many areas where the species is present, recent studies have shown that the density is very low, with the future survival of populations seriously at risk (Petrozzi et al. 2018). The presence of high density livestock and bushfires restricts the presence of *C. sulcata* (Petrozzi et al. 2016b), but in general, it seems that the species avoids areas with human activities or presence (or is simply no longer present in such areas). The presence of cattle was also negatively correlated with the presence of *C. sulcata* (Petrozzi et al. 2020). More specifically, Petrozzi et al. (2016b) found a significant negative correlation between the intensity of cattle grazing (expressed as density of cattle) and the presence of *C. sulcata*, and this negative effect increased when coupled with high fire intensity, whereas wildfires alone did not have a significant influence on the species' distribution on a global scale.

Traditionally, consumption of *C. sulcata* may have been minimal at the local community level, as the inhabitants

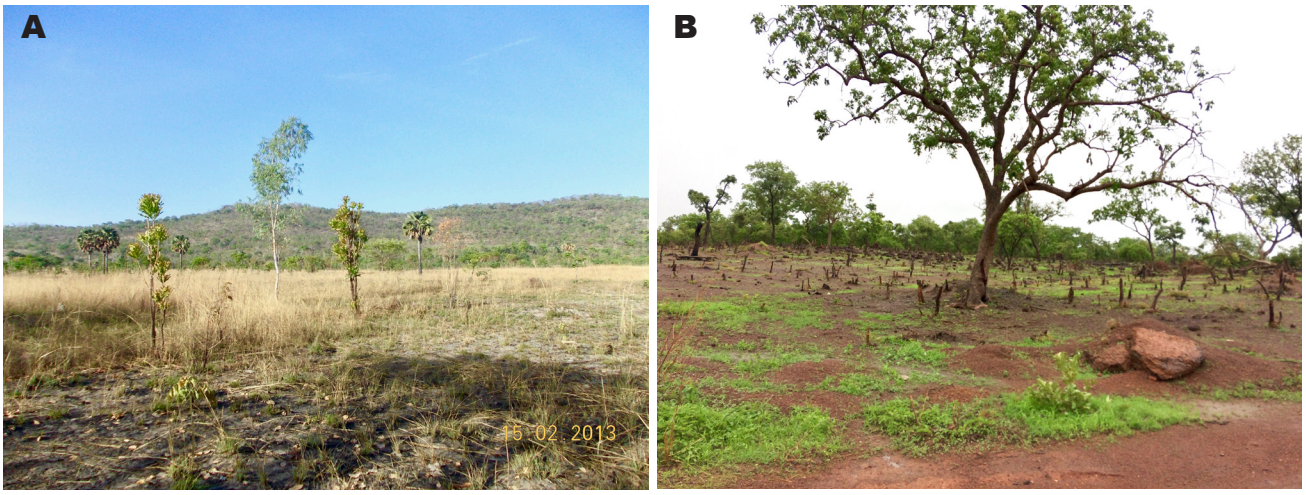

Figure 13. Degradation and loss of *Centrochelys sulcata* habitat. **A**: savannah being burned for conversion into plantations in Burkina Faso. Photo by Fabio Petrozzi. **B**: savannah being converted into plantations in Mali. Photo by Luca Luiselli.

of the Sahel region are primarily Muslims who have a religious prohibition against the consumption of turtle flesh (Broadley 1989; Klemens and Thorbjarnarson 1995). However, political instability, civil wars, and local famine may force human communities to consume individuals of this species and accelerate its decline, for instance, in Sudan (Siddig 2014).

Concerning the pet trade, data from CITES show that during 20 years (1990–2010) an annual average of 2000–2790 *C. sulcata* were traded. Of these specimens, 9132 in total (for a mean of over 900 individuals annually) were taken from the wild (Petrozzi et al. 2016b). On the origin of these specimens, recorded data are not often useful. In fact, many specimens were reported to come from countries where the species does not occur (e.g., Togo) or has been extirpated (e.g., Cameroon) (Chirio and LeBreton 2007). In some cases, specimens traded from countries where the species is not present probably came from the bordering countries (e.g., specimens traded from Togo originate in Burkina Faso, Niger, and Mali (Petrozzi et al. 2016a). Petrozzi et al. (2016b) observed a decrease in the annual export of wild individuals for the pet trade after the introduction of export quotas by country and by year, but trade data must be considered with caution. In Mali, in the Parc Zoologique of Bamako, the observed individuals were larger than those gathered by farmers in the Cercle de Nara area for the pet trade, suggesting that animals obtained and selected by trade tended to be of a smaller average size (Lambert 1993). Despite not being widespread, some local consumption does occurs, as *C. sulcata* meat is considered a delicacy by some Sahelian human populations (Warshall 1989; Petrozzi et al. 2017, 2018, 2019).

A recent assessment indicates that breeding farms in Togo are efficiently breeding this species for export (Segniagbeto et al., unpubl. data). However, the managers of these farms indicated that the parental breeding stock in Togo came from Mali and Niger, but were unable to indicate the period when the breeding specimens were acquired. However, most of the breeding farms started breeding the species at least 10 years ago and may have had a second generation (F2) by now. For this purpose, individuals exported from Togo come from the original breeding stock and are rarely more than one year old.

Overall, according to a recent evaluation, habitat fragmentation and loss has accounted for about 60% of the species' estimated percentage involvement of threats (*sensu* Stanford et al. 2020), with climate change accounting for about 25%, exploitation for local egg and meat consumption for ca. 10%, and exploitation for trade (pets, food, medicine) for about 5% (Diagne, McGovern, and Luiselli, in prep.). These values were determined by an expert-based evaluation of independent field researchers working throughout the African Sahel.

Conservation Measures Taken. — *Centrochelys sulcata* was assessed as Vulnerable for the IUCN Red List in 1996 and provisionally re-assessed for the Red List as Endangered by the IUCN Tortoise and Freshwater Turtle Specialist Group in 2013 (TTWG 2017; Rhodin et al. 2018). It has been listed on Appendix II of CITES since 1977 as part of the family listing of Testudinidae.

The species has been reintroduced in North Ferlo, Senegal (Garrigues and Cadi 2011), and there are captive colonies in several countries, both in Africa and elsewhere (e.g., Diagne 1996). In Ferlo, after four years of study on radiotracked reintroduced individuals, the survival rate was over 80%, which confirms the effectiveness of this method (Garrigues and Cadi 2011). In the Réserve de Bandia in Senegal, 8 individuals were introduced in 1993, and in 2002 the total number of observed individuals was 22 (Vincke et al. 2005), also showing the feasibility of these conservation measures.

In Senegal, in order to enhance the conservation prospects of the African Spurred Tortoise, Diagne in 1992 created S.O.S. (Save Our Sulcata), a non-profit conservation organization, and also co-founded and built the Village des Tortues in Noflaye, Senegal (Diagne 1996; Zwartepoorte 2006). The latter is a sanctuary and captive breeding facility for African Spurred Tortoises that now houses over 300 individuals; approximately 56 have been reintroduced back to the wild in Ferlo Nord Wildlife Reserve, Senegal (Devaux and Diagne, unpubl. data).

The African Spurred Tortoise is also one of the most popular and favored species for tourists and local people in northern Nigeria (Adefalu et al. 2015), thus showing the potential for effective conservation, based also on citizen science initiatives, in the Sahelian regions.

Although we are not aware of any specific conservation program for *C. sulcata* developed at the government level in any African country, the species is present in several protected areas: W Regional Park (Benin, Burkina Faso, Niger), Arly National Park, including Singou Reserve and Réserve Partielle de Pama, and Reserve Sylvo-Pastorale et Partielle de Faune de Sahel (Burkina Faso), Bénoué National Park and possibly Faro National Park (Cameroon, but now possibly extirpated), Koumbala Reserve and Bamingui Bangoran National Park (Central African Republic), Teseny Reserve (Eritrea), Kafta Sheraro National Park and Awash National Park (possibly introduced) (Ethiopia), Reserve Partielle de la Faune d'Ansongo-Ménaka (Mali), Diawling National Park (Mauritania), and possibly Oti-Keran National Park (Togo). In this latter protected area, urgent field surveys should be carried out in order to eventually confirm the presence of *C. sulcata* in Togo. It would also be very important to explore other protected areas in the species' range (for instance, in Chad) in order to evaluate whether it would be possible to create a viable network of potential protected corridors that may guarantee the wild survival of this species in the West African Sahel.

Conservation Measures Proposed. — Given that the species is easily bred in captivity (Stearns 1989; Wilson and Wilson 1997; Stauffer 2003), Ballasina et al. (2006) highlighted the needs of reintroductions of captive-bred individuals into the wild, and indeed this has already been done in a few cases (Garrigues and Cadi 2011). This conservation strategy may be easily feasible given that the species is often kept in captivity by local communities across the Sahel (Griaule 1952; Perolini 1988; Lambert 1996a, 1999), and that, in several cases, the captive individuals were either collected in the local surrounding regions or were the descendants of free-ranging individuals caught locally some decades earlier (Ardjima et al. 2020).

A captive tortoise census and interview study in two urban areas of Burkina Faso estimated a total 585–850 tortoises in Ouagadougou and 102–178 in Fada (Ardjima et al. 2020). In addition, tortoise owners in these urban areas revealed that "love and personal passion" for these reptiles was the motivational reason for 77.2% of interviewees for keeping them, and that most of them would be very happy to cooperate with eventual conservation programs for this species based on breeding and releasing the captive-born individuals (Ardjima et al. 2020). The Teneré-Termit region in Niger may represent a potentially critical area for the conservation of this species (Ineich et al. 2014), as *C. sulcata* density was considerably higher in this region than elsewhere (Petrozzi et al. 2018). Moreover, based on a series of interviews within the range of the species, it appears crucial that repatriation projects should involve the local population, in particular where the species is considered totemic. For instance, Ardjima et al. (2020) uncovered a significant potential to engage tortoise owners in Fada and Ouagadougou (Burkina Faso) to use their animals in a collaborative captive breeding programme to produce hatchlings for reintroduction, especially in the localities of eastern Burkina Faso where these tortoises have been extirpated.

From studies on the preferred habitat of this species, it would be possible to select suitable reintroduction sites within preferred habitats for the species. The reintroduction of African Spurred Tortoises in certain habitats may also encourage the proliferation of various savannah plants which depend on tortoises for their seed dispersal, as shown for conspecifics introduced in non-native habitats (Burney et al. 2012). Overall, the main challenge is to find suitable secure habitat (national parks or wildlife sanctuaries) to perform reintroduction activities for African Spurred Tortoises into their natural Sahelian native habitat and range.

Captive Husbandry. — The species is easy to raise and breed in captivity, and is one of the most intensely bred tortoise species in the world (Zwartepoorte 2006). In temperate regions, individuals should ideally be maintained in large outdoors enclosures in the summer, but must be indoors in the winter. The enclosures should be protected from predators (mostly small carnivores) and heavily planted with small ornamental scrubs and trees. Enclosures should also include rocky hiding places as well as additional shade areas. Since these tortoises dig huge and impressive burrows, it is essential to secure their outdoor environment, as they can easily escape enclosures by digging, and strong buried in-ground fencing is vital.

This species is apparently more abundant in captivity than in the wild. In 2002 Diagne performed a rapid census of the captive population in the United Sates with the help of the Turtle and Tortoise Preservation Group (Diagne, unpubl. data) and concluded that there were likely more specimens in the USA than in the entire natural range in Africa. Unfortunately, for taxonomic and health reasons, these abundant US-based captive-born specimens cannot readily be used for future reintroduction initiatives in the native range.

On average, life expectancy of African Spurred Tortoises in captivity is 50–80 years, up to a possible 120 years (Villiers 1958; Biegler 1966; Walls 1997)). When breeding occurs, females may lay up to 4 clutches a year with an average of 15–20 eggs deposited each time; eggs should be kept in vermiculite at 30ºC at 70–80% humidity, and emergence generally occurs after 85–100 days of incubation (Vetter 2005).

African Spurred Tortoises require a high fiber diet consisting mainly of broad leafy weeds and grass hay such as peanut hay. Other vegetables offered may include fruit, clover, plantain weed, sow thistle, dandelion, and spineless *Opuntia* cactus pads. Supplementing the diet with dark, leafy greens high in calcium and in vitamins A and C, such as dandelion greens, hibiscus leaves, and red leaf lettuce, is also important. In natural conditions these tortoises love to eat the leaves and flowers of *Leptadenia hastata*, an abundant plant in Sahelian habitat that appears to be nutritious for both hatchlings and adults. If kept in suitable captive conditions this species is quite resiliant, although some health problems may occur, including hypocalcemia and metabolic bone disease, prolapsus during mating, respiratory disease, dehydration, eye lesions, and carapacial pyramiding.

The carapaces of captive-raised African Spurred Tortoises often develop pyramidally-shaped osseous humps centrally under the horny plates. In an experimental study of captive animals where humps developed and blood values of calcium, phosphorus and haematocrit were measured, dry environmental conditions (24.3–57.8% and 30.6–74.8% relative humidity) produced taller humps than humid conditions (45–99% relative humidity), and hump formation was significantly different between tortoise groups kept under these different humidity conditions (Wiesner and Iben 2003). Variable dietary protein had a minor, positive impact on this pathological formation of pyramidal humps (Wiesner and Iben 2003). A high protein diet may contribute to the development of gout in this species when kept in captivity (Casimire-Etzioni et al. 2004).

In two urban centers of Burkina Faso (Ouagadougou and Fada), where these tortoises have been traditionally kept, 54.1% of the observed tortoises (n = 281) were fed an omnivorous diet (i.e., the owners fed the animals with almost everything they themselves ate), and 45.9% of animals were given a strictly herbivorous regime (Ardjima et al. 2020).

Current Research. — The conservation perspectives, population biology, and field ecology of this species have been studied since 2013 in Burkina Faso, Niger, Nigeria, and Mali by Petrozzi, Hema, and associates. These researchers are also investigating the potential for community participation and the creation of an inventory of the captive stock housed by local people in Burkina Faso. Diagne has been conducting field research and conservation programs on this species in Senegal for about 20 years. *Centrochelys sulcata* is also one of the target species of greater breadth research programs on the ecology of West African savannahs conducted jointly, since 2015, by IDECC-Institute for Development Ecology Conservation and Cooperation (Rome, Italy), the University of Lomé (Togo), the University of Dedougou (Burkina Faso), the University "Ouaga 1 Professeur Joseph Ki Zerbo/CUP-D", Ouagadougou (Burkina Faso) and the Manchester Metropolitan University (UK) (project leaders: Luiselli and John E. Fa).

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LITERATURE CITED

Adefalu, L.L., Omotesho, K.F., and Alao, O.S. 2015. Determinants of visitors' preference for wild animal species (A case study of Unilorin Zoo, Ilorin, Kwara State, Nigeria). Journal of Research in Forestry, Wildlife and Environment 7:124–135.

Ardjima, L., Hema, E.M., Konate, S., Sirima, D., Kabre, B.G., Petrozzi, F., Fa, J.E., and Luiselli, L. 2020. Unleashing the potential of local captive populations for conservation – the case study of the African spurred tortoise. Acta Oecologica 105:103581, 7 pp.

Arvy, C., Marissal, N., Dia, A.T., and Colas, F. 1997. Observations sur la répartition et les dimensions de *Geochelone sulcata* (Cryptodira, Testudinidae) en Mauritanie Occidentale. Bulletin de la Société Herpétologique de France 81:11–20.

Ballasina, D., Vandepitte, V., Mochi, E., and Fenwick, H. 2006. La nécessité de réintroduction de *Geochelone sulcata* nées en captivité: stratégies pour la gestion de groupes d'élevage en captivité. Chelonii 4:111.

Baur, M. 2003. Untersuchungen zur vergleichenden Morphologie des Gastrointestinaltraktes der Schildkröten. Frankfurt am Main: Edition Chimaira, 333 pp.

Biegler, A. 1966. A survey of recent longevity records for reptiles and amphibians in zoos. International Zoo Yearbook 6:487-493.

Boisson, D. and Capon, N. 1978. Vermehrung von *Testudo sulcata* Miller in Gefangenschaft. Die Aquarien- und Terrarien-Zeitschrift, Stuttgart 31(1):28–30.

Boulweydou, A. 2008. Caractérisation de l'habitat de la tortue sillonnée (*Geochelone sulcata*, Miller, 1979) dans le massif de Termit (Zinder-Niger). DEA Thesis, Université Abdou Moumouni de Niamey, Niger.

Bour, R. 2004. Un specimen gigantesque de *Centrochelys sulcata*. Manouria 7(24):43–44.

Bour, R. 2013. Le type de *Testudo sulcata* Miller, 1779. Chéloniens 31:14–27.

Branch, W.R. 2008. Tortoises, Terrapins and Turtles of Africa. Cape Town: Struik Publishers, 128 pp.

Broadley, D.G. 1989. *Geochelone sulcata*. In: Swingland, I.R. and Klemens, M.W. (Eds.). The Conservation Biology of Tortoises. Occasional Papers of the IUCN Species Survival Commission No. 5, pp. 47–48.

Buhlmann, K.A., Akre, T.S.B., Iverson, J.B., Karapatakis, D., Mittermeier, R.A., Georges, A., Rhodin, A.G.J., van Dijk, P.P., and Gibbons, J.W. 2009. A global analysis of tortoise and freshwater turtle distributions with identification of priority conservation areas. Chelonian Conservation and Biology 8:116–149.

Burney, D.A., Juvik, J.O., Burney, L.P., and Diagne, T. 2012. Can unwanted suburban tortoises rescue native Hawaiian plants? The Tortoise 1(1):104–115.

Cadi, A. 2004. Conservation of *Geochelone sulcata* (Miller, 1779) last populations in Ferlo Reserve (Senegal). Programm und Zusammenfassung der DGHT-Jahrestagung 2004:49–54.

Casimire-Etzioni, A.L., Wellehan, J.F., Embury, J.E., Terrell, S.P., and Raskin, R.E. 2004. Synovial fluid from an African spur-thighed tortoise (*Geochelone sulcata*). Veterinary Clinical Pathology 33:43–46.

Chirio, L. and Ineich, I. 2006. Biogeography of the reptiles of the Central African Republic. African Journal of Herpetology 55:23–59.

Chirio, L. and LeBreton, M. 2007. Atlas des Reptiles du Cameroun. Paris: Muséum National d'Histoire Naturelle, 686 pp.

Claro, F. 2003. Survey of fauna in Termit (Niger). http://www.catsg.org/cheetah/05_library/5_3_publications/C/Claro_2003_Survey_of_fauna_in_Niger.pdf, accessed 28 July 2020.

Cloudsley-Thompson, J.L. 1970. On the biology of the desert tortoise *Testudo sulcata* in Sudan. Journal of Zoology 160:17–33.

Cloudsley-Thompson, J.L. 1999. Daily and seasonal cycles, hibernation, aestivation and migration. In: Cloudsley-Thompson, J.L. The Diversity of Amphibians and Reptiles: An Introduction. Berlin: Springer, pp. 157–176.

Coulson, I.M. and Hailey, A. 2001. Low survival rate and high predation in the African hingeback tortoise *Kinixys spekii*. African Journal of Ecology 39:383–392.

Czernay, S. 1993. Spornschildkröten verteidigen ihren Nistplatz. DATZ, Stuttgart 46(10):648–649.

Czernay, S. and Praedicow, G. 1988. Haltung und Zucht der Spornschildkröte (*Testudo* [*Geochelone*] *sulcata*) im Thüringer Zoopark Erfurt. Der Zoologische Garten N.F. 58:281–305.

Del Prato, A. 1891. I reperti raccolti nella colonia Eritrea dal Capitano Vittorio Bottego. Bollettino della Societa Africana d'Italia, Sezione Fiorentina 7:19–77.

de Miranda, E.B. 2017. The plight of reptiles as ecological actors in the tropics. Frontiers in Ecology and Evolution 5(159), doi: 10.3389/fevo.2017.00159, 15 pp.

Devaux, B. 1993. *Geochelone sulcata* au Senegal. La Tortue 23:14–20.

Devaux, B. 1998. Les tortues au Senegal. La Tortue 44:16–20.

Devaux, B. 2000a. Mission au Soudan—à la recherche des tortues *Geochelone sulcata*. La Tortue 49:6–19.

Devaux, B. 2000b. La Tortue qui Pleure—The Crying Tortoise, *Geochelone sulcata* (Miller, 1779). Chelonii 1:1–87.

Devaux, B. 2004. *Centrochelys sulcata*. The tortoise that weeps. Reptilia (GB) 37:20–26.

Diagne, T. 1996. Etude et conservation de *Geochelone sulcata* au Senegal. In: Devaux, B. (Ed.). Proceedings – International Congress of Chelonian Conservation. Gonfaron, France: Editions SOPTOM, pp. 110–111.

Elliott, T.F., Bower, D.S., and Vernes, K. 2019. Reptilian mycophagy: a global review of mutually beneficial associations between reptiles and macrofungi. Mycosphere 10:776–797.

Garrigues, L. and Cadi, A. 2011. Re-introduction of African spurred tortoise in North Ferlo, Senegal. In: Soorae, P.S. (Ed.). Global re-introduction perspectives: 2011. More case studies from around the globe. Gland, Switzerland: IUCN/SSC Re-introduction Specialist Group and Abu Dhabi, UAE: Environment Agency, Abu Dhabi, pp. 94–97.

Gasperetti, J., Stimson, A.F., Miller, J.D., Ross, J.P., and Gasperetti, P.R. 1993. Turtles of Arabia. Fauna of Arabia 13:170–367.

Gray, J.E. 1831. Synopsis Reptilium; or Short Descriptions of the Species of Reptiles. Part I.—Cataphracta. Tortoises, Crocodiles, and Enaliosaurians. London: Treuttel, Wurz, and Co., 85 pp.

Gray, J.E. 1873. Hand-List of the Specimens of Shield Reptiles in the British Museum. London: British Museum, 124 pp.

Griaule, M. 1952. Les Dogons. In: Explorations outre-mer à travers l'Union française. Paris: Documentation Française, pp. 110–125.

Grubb, P. 1971. Comparative notes on the behavior of *Geochelone sulcata*. Herpetologica 27:328–333.

Hailey, A. and Coulson, I.M. 1996. Temperature and the tropical tortoise *Kinixys spekii*: constraints on activity level and body temperature. Journal of Zoology 240:523–536.

Hailey, A. and Lambert, M.R.K. 2002. Comparative growth patterns in Afrotropical giant tortoises (Reptilia Testudinae). Tropical Zoology 15:121–139.

Hailey, A., Wright, J., and Steer, E. 1988. Population ecology and conservation of tortoises: the effects of disturbance. Herpetological Journal 1(7):294–301.

Heimann, E. 1999. Haltung und Nachzucht der Spornschildkröte *Geochelone sulcata*. Rheinbach: Vortragszusammenfassung der DGHT-Jahrestagung 1999, p. 24.

Herz, M. 2014. Nachzucht der Spornschildkröte (*Geochelone sulcata* Miller, 1779) in der F3-Generation. Radiata 23(4):4–16.

Herz, M. 2018. La tortue sillonnée: *Centrochelys sulcata*. Paris: Animalia Editions.

Ineich, I., Ascani, M., Rabeil, T., Newby, J., and Chirio, L. 2014. Herpetofauna of the Termit Massif and neighbour areas in Tenere Desert, southeastern Niger, West Africa. Herpetological Notes 7:375–390.

Iverson, J.B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Richmond, IN: Privately printed, 363 pp.

Jost, U. and Jost, H. 2005. Bei den Spornschildkröten im Senegal. Testudo 14(3):10–30.

Keith, J.O. and Plowes, D.C.H. 1997. Considerations of wildlife resources and land use in Chad. Washington DC: Productive Sector Growth and Environment Division, Office of Sustainable Development, Bureau for Africa, U.S. Agency for International Development, 29 pp.

Klemens, M.W. and Thorbjarnarson, J.B. 1995. Reptiles as a food resource. Biodiversity and Conservation 4:281–298.

Kowalski, K., Szyndlar, Z., Młynarski, M., Bocheński, Z., and Rzebik-Kowalska, B. 1993. Remains of small vertebrates from Bir Tarfawi and their paleoecological significance. In: Wendorf, F., Schild, R., and Close, A.E. (Eds.). Egypt During the Last Interglacial. Boston: Springer, pp. 155–204.

Kuzmin, S.L. 2002. The Turtles of Russia and Other Ex-Soviet Republics (Former Soviet Union). Frankfurt am Main: Edition Chimaira, 159 pp.

Lambert, M.R.K. 1993. On growth, sexual dimorphism, and the general ecology of the African spurred tortoise, *Geochelone sulcata* in Mali. Chelonian Conservation and Biology 1:37–46.

Lambert, M.R.K. 1996a. On general biology and utilization of the African spurred tortoise, *Geochelone sulcata*, in Mali, West Africa. In: Devaux, B. (Ed.). Proceedings – International Congress of Chelonian Conservation. Gonfaron, France: Editions SOPTOM, pp. 112–114.

Lambert, M.R.K. 1996b. Biogeographical factors influencing the distribution of the African spurred tortoise *Geochelone sulcata* in the Sahel. Nature et Faune 12(4):10–12.

Lambert, M.R.K. 1999. On conservation of the Sahelian giant tortoise, *Geochelone sulcata*. In: Miaud, C. and Guyétant, R. (Eds.). Current Studies in Herpetology: Proceedings of the 9th Ordinary General Meeting of the Societas Europaea Herpetologica. Le Bourget du Lac, France, pp. 255–261.

Langtimm, C.C., Dodd, C.K., Jr., and Franz, R. 1996. Estimates of abundance of box turtles (*Terrapene carolina bauri*) on a Florida island. Herpetologica 52:496–504.

Largen, M.J. 1997. An annotated checklist of the amphibians and reptiles of Eritrea, with keys for their identification. Tropical Zoology 10:63–115.

Ligon, D.B., Bidwell, J.R., and Lovern, M.B. 2009. Incubation temperature effects on hatchling growth and metabolic rate in the African spurred tortoise, *Geochelone sulcata*. Canadian Journal of Zoology 87:64–72.

Livoreil, B. and van der Kuyl, A.C. 2005. Genetic analysis of mitochondrial DNA variation in eastern and western African spurred tortoises, *Geochelone sulcata*. Chelonian Conservation and Biology 4:951–954.

Lluch, P., Robin, S., and Lescure, J. 2004. Le crocodile du nil, *Crocodylus niloticus* Laurenti, 1768 dans le Tagant (Mauritanie). Bulletin de la Société Herpétologique de France 111/112:5–23.

Luiselli, L. 2003. Seasonal activity patterns and diet divergence of three sympatric Afrotropical tortoise species (genus *Kinixys*). Contributions to Zoology 72:211–220.

Luiselli, L., Akani, G.C., Eniang, E.A., Di Vittorio, M., Petrozzi, F., Hema, E.M., Segniagbeto, G.H., Dendi, D., Diagne, T., Chirio, L., and Fa, J.E. In press. Age-stratified interview campaigns suggest ongoing decline of a threatened tortoise species in the West African Sahel. Biodiversity (in press).

Mallon, D.P., Hoffmann, M., and McGowan, P.J.K. 2015. An IUCN situation analysis of terrestrial and freshwater fauna in West and Central Africa. Occasional Papers of the IUCN Species Survival Commission, No. 54, 162 pp.

Massana, J.S. and Martínez-Silvestre, A. 2016. La tortue sillonnée, *Centrochelys sulcata*: problèmes de gestion en Catalogne. Chéloniens 40:31–33.

Merchán, M., Coll, M., and Fournier, R. 2005. Macromorfometría de juveniles de *Geochelone sulcata* (Testudines : Testudinidae) en Costa Rica. Revista de Biología Tropical 53:213–225.

Mill, E. 2005. Spornschildkröten (*Geochelone sulcata*)—einige Anmerkungen zur Haltung, Zucht und Situation im Tschad. Radiata 14(3):13–25.

Miller, J.F. 1779. *Testudo sulcata*, pl. 26. In: Miller, J.F. 1776–1784. Icones Animalium et Plantarum. (Various subjects of Natural History, Wherein are Delineated Birds, Animals and Many Curious Plants). London, 10 pp., 60 pls.

Miller, J.F. and Shaw, G. 1796. Cimelia Physica. Figures of Rare or Curious Quadrupeds, Birds, &c. Together with Several of the Most Elegant Plants, with Descriptions. London: Benjamin and John White and John Sewell, 106 pp., 60 pls.

Moore, J.E. 1997. Potential threats to tortoise populations in Parc National de "W," Niger, West Africa. In: Van Abbema, J. (Ed.). Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference. N.Y. Turtle and Tortoise Society, pp. 28–30.

Nickel, H. 2006. *Geochelone sulcata*: la tortuga Africana de espolones en Mauritania. Reptilia 61:64–68.

Nickel, G. and Selah, M. 2002. Spornschildkröten in Mauretanien. Reptilia (Münster) 36:32–37.

Ogbonna, P.C., Nzegbule, E.C., and Okorie, P.E. 2015. Environmental impact assessment of coal mining at Enugu, Nigeria. Impact Assessment and Project Appraisal 33:73–79.

Olaniyi, O.E., Esan, D.B., Odewumi, O.S., Oladeji, S.O., and Oyeleke, O.O. 2016. Ecotourism Resources Mapping of T.A. Afolayan Wildlife Park in Ondo State, Nigeria. Proceedings of NTBA/NSCB Joint Biodiversity Conference, Unilorin, pp. 21–31.

Padial, J.M. 2006. Commented distributional list of the reptiles of Mauritania (West Africa). Graellsia 62:159–178.

Perolini, M. 1988. *Geochelone sulcata*—chez les Dogons. La Tortue 8:9–10.

Petrozzi, F., Luiselli, L., Akani, G.C., and Eniang, E.A. 2015. Supplementary distribution data of *Centrochelys sulcata* (Miller, 1779), in northern Nigeria (West Africa). Herpetozoa 28:92–94.

Petrozzi, F., Hema, E.M., Luiselli, L., and Guenda, W. 2016a. A survey of the potential distribution of the threatened tortoise *Centrochelys sulcata* populations in Burkina Faso (West Africa). Tropical Ecology 57:709–716.

Petrozzi, F., Eniang, E.A., Akani, G.C., Amadi, N., Hema, E.M., Diagne, T., Segniagbeto, G.H., Chirio, L., Amori, G., and Luiselli, L. 2016b. Exploring the main threats to the threatened African spurred tortoise *Centrochelys sulcata* in the West African Sahel. Oryx 52:544–551.

Petrozzi, F., Hema, E.M., Sirima, D., Douamba, B., Segniagbeto, G.H., Diagne, T., Amadi, N., Amori, G., Akani, G.C., Eniang, E.A., Chirio, L., and Luiselli, L. 2017. Habitat determinants of the threatened Sahel tortoise *Centrochelys sulcata* at two spatial scales. Herpetological Conservation and Biology 12:402–409.

Petrozzi, F., Hema, E.M, Sirima, D., Douamba, B., Segniagbeto, G.H., Diagne, T., Amadi, N., Amori, G., Akani, G.C., Eniang, E.A., Chirio, L., and Luiselli, L. 2018. Distance-generated field density estimates for the threatened Sahel tortoise *Centrochelys sulcata*. Russian Journal of Herpetology 25:83–87.

Petrozzi, F., Hema, E.M., Segniagbeto, G.H., Amadi, N., Akani, G.C., Burke, R.L., Chirio, L., and Luiselli, L. 2019. Correlates of African Spurred Tortoise, *Centrochelys sulcata*, occurrence in the West African Sahel. Chelonian Conservation and Biology 18:19–23.

Petrozzi, F., Hema, E.M., Sirima, D., Segniagbeto, G.H., Akani, G.C., Eniang, E.A., Dendi, D., Fa, J.E., and Luiselli, L. 2020. 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. Acta Oecologica 105:103572.

Pouvreau, J.-P. 1989. *Geochelone sulcata*—n° 3, estivation—braconnage. La Tortue 11:1–20.

Rhodin, A.G.J., Stanford, C.B., van Dijk, P.P., Eisemberg, C., Luiselli, L., Mittermeier, R.A., Hudson, R., Horne, B.D., Goode, E.V., Kuchling, G., Walde, A., Baard, E.H.W., Berry, K.H., Bertolero, A., Blanck, T.E.G., Bour, R., Buhlmann, K.A., Cayot, L.J., Collett, S., Currylow, A., Das, I., Diagne, T., Ennen, J.R., Forero-Medina, G., Frankel, M.G., Fritz, U., García, G., Gibbons, J.W., Gibbons, P.M., Shiping, G., Guntoro, J., Hofmeyr, M.D., Iverson, J.B., Kiester, A.R., Lau, M., Lawson, D.P., Lovich, J.E., Moll, E.O., Páez, V.P., Palomo-Ramos, R., Platt, K., Platt, S.G., Pritchard, P.C.H., Quinn, H.R., Rahman, S.C., Randrianjafizanaka, S.T., Schaffer, J., Selman, W., Shaffer, H.B., Sharma, D.S.K., Haitao, S., Singh, S., Spencer, R., Stannard, K., Sutcliffe, S., Thomson, S., and Vogt, R.C. 2018. Global conservation status of turtles and tortoises (Order Testudines). Chelonian Conservation and Biology 17(2):135–161.

Ritz, J., Griebeler, E.M., Huber, R., and Clauss, M. 2010. Body size development of captive and free-ranging African spurred tortoises (*Geochelone sulcata*): high plasticity in reptilian growth rates. Herpetological Journal 20:213–216.

Scherman, P.J. and Riveros, F. 1989. Tropical grasses. Rome: FAO Plant Production and Protection Series, No. 23.

Schneider, J.G. 1784. Sammlung vermischter Abhandlungen zur Aufklärung der Zoologie und der Handlungsgeschichte. IV. Beiträge zu der Naturgeschichte der Schildkröten. Berlin: J.F. Unger, pp. 304–317.

Scortecci, G. 1928. Rettili dell'Eritrea esistenti nelle collezioni del Museo Civico di Milano. Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale, Milano 67:290–339.

Segniagbeto, G.H., Bour, R., Ohler, A., Dubois, A., Roedel, M-O., Trape, J-F., Fretey, J., Petrozzi, F., Aïdam, A., and Luiselli, L. 2014. Turtles and tortoises of Togo: historical data, distribution, ecology and conservation. Chelonian Conservation and Biology 13:152–165.

Shi, Q., Wang, J., Liu, J., Jiang, H., and Nie, L. 2017. The complete mitochondrial genome of *Geochelone sulcata*. Mitochondrial DNA, Part B 2:463–464.

Siddig, A.A.H. 2014. Biodiversity of Sudan: between the harsh conditions, political instability and civil wars. Biodiversity Journal 5:545–555.

Stanford, C.B., Iverson, J.B., Rhodin, A.G.J., van Dijk, P.P., Mittermeier, R.A., Kuchling, G., Berry, K.H., Bertolero, A., Blanck, T.E.G., Bjorndal, K.A., Buhlmann, K.A., Burke, R., Congdon, J., Diagne, T., Edwards, T., Eisemberg, C., Ennen, J., Forero-Medina, G., Frankel, M., Fritz, U., Gallego-García, N., Georges, A., Gibbons, J.W., Gong, S., Goode, E.V., Shi, H.T., Hoang, H., Hofmeyr, M.D., Horne, B.D., Hudson, R., Juvik, J., Koval, P., Kiester, R., Le, M., Lindeman, P., Lovich, J.E., Luiselli, L., McCormack, T., Meyer, G., Páez, V.P., Platt, K., Platt, S.G., Pritchard, P.C.H., Quinn, H., Roosenburg, W., Seminoff, J., Shaffer, H.B., Spencer, R., Van Dyke, J.U., Vogt, R.G., and Walde, A.D. 2020. Turtles and tortoises are in trouble. Current Biology 30:R721–R735.

Stauffer, K.E. 2003. Captive care of the African spurred tortoise, *Geochelone sulcata*. Journal of Herpetological Medicine and Surgery 13(4):38–44.

Stearns, B.C. 1989. The captive status of the African spurred tortoise *Geochelone sulcata*: recent developments. International Zoo Yearbook 28:87–98.

TEWG [Turtle Extinctions Working Group: Rhodin, A.G.J., Thomson, S., Georgalis, G., Karl, H.-V., Danilov, I.G., Takahashi, A., de la Fuente, M.S., Bourque, J.R., Delfino, M., Bour, R., Iverson, J.B., Shaffer, H.B., and van Dijk, P.P.]. 2015. Turtles and tortoises of the world during the rise and global spread of humanity: first checklist and review of extinct Pleistocene and Holocene chelonians. In: Rhodin, A.G.J., Pritchard, P.C.H., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Iverson, J.B., and Mittermeier, R.A. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 5(8):000e.1–66.

Trape, J.-F., Trape, S., and Chirio, L. 2012. Lézards, crocodiles et tortues d'Afrique occidentale et du Sahara. Marseille: IRD éditions, 503 pp.

TTWG [Turtle Taxonomy Working Group: Rhodin, A.G.J., Iverson, J.B., Bour, R. Fritz, U., Georges, A., Shaffer, H.B., and van Dijk, P.P.]. 2017. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (8th Ed.). In: Rhodin, A.G.J., Iverson, J.B., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Pritchard, P.C.H., and Mittermeier, R.A. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 7:1–292.

Vetter, H. 2005. Leopard- and African Spurred Tortoise *Stigmochelys pardalis* and *Centrochelys sulcata*. Frankfurt-am-Main: Edition Chimaira, 189 pp.

Villiers, A. 1958. Tortues et crocodiles de l'Afrique noire Française. Institut Francais d'Afrique Noire, Initiations Africaines 15:1–354.

Vincke, X., Hornick, J.L., Njikam, N.I., and Leroy, P. 2005. Gestion de la faune sauvage au Sénégal: comparaison du Parc national du Niokolo Koba et de la Réserve privée de Bandia. Annales de Médecine Vétérinaire 149:232–237.

Walls, K. 1997. Landschildkröten. Ruhmannsfelden: Bede-Verlag.

Warshall, P. 1989. Mali: Biological Diversity Assessment. Washington DC: U.S. Agency for International Development, Natural Resources Management Support, Project no. 648-0467.

Wiesner, C.S. and Iben, C. 2003. Influence of environmental humidity and dietary protein on pyramidal growth of carapaces in African spurred tortoises (*Geochelone sulcata*). Journal of Animal Physiology and Animal Nutrition 87:66–74.

Wilson, R. and Wilson, R. 1997. The Care and Breeding of the African Spurred Tortoise *Geochelone sulcata*. London: Carapace Press, 36 pp.

Zwartepoorte, H. 2006. Husbandry and breeding of the African spurred tortoise, *Geochelone sulcata* (Miller, 1779) linked to reintroduction plans. In: Artner, H., Farkas, B., and Loehr, V. (Eds.). Turtles: Proceedings: International Turtle and Tortoise Symposium Vienna 2002. Frankfurt: Edition Chimaira, pp. 374–381.

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