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On Growth, Sexual Dimorphism, and the General Ecology of the African Spurred Tortoise, *Geochelone sulcata*, in Mali

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ABSTRACT. – ***Geochelone sulcata*** **(Cryptodira: Testudinidae) in Mali inhabits woodland savannah, grass-carpeted during June-October rains, but sparsely vegetated and livestock-trampled within six weeks of the start of the Sahelian dry season. Aestivation takes place. Refuge from insolation is sought during the middle of the day (>32°C air temp.). Mean annual rainfall in zones inhabited by the species was 140-1098 mm ranging bioclimatically from "desertic" to "warm tropical - dry season of long duration". In the face of continual removal of individuals by humans, populations in 1991 in parts of northern central Mali seemed not to have recovered from the 1969-84 drought. Neither the allometric relationship between carapace straight length (y) and body mass (x in g) of *Geochelone sulcata* in northern central Mali ($y = 12.64x^{0.36}$), nor isometric relationships between other characters, varied significantly from captive tortoises in Sudan. Carapace length and body mass had respective ranges in Malian females and males of 336-578 and 384-797 mm, and 6.1-47.0 and 11.8-93.0 kg. Nutrient intake was seasonal (annual grass, *Eleusine indica*, preferred) and carapacial growth annuli were deposited approximately annually. Third vertebral scute growth increments were greatest during years 8-20. Although normally full-grown after 24 years, large or slower growing individuals may deposit further annuli. Carapace outline became more elongate and gular scutes more developed in males than females; diameter of rear aperture in females was not correlated with body size. Trade-selected tortoises were bigger than those routinely found in other areas by villagers.**

The African spurred or Sahelian grooved tortoise *Geochelone sulcata* (Miller, 1779) is the largest of the world's continental tortoise species; in captivity it is known to reach a length of 830 mm and weight of 105.5 kg (Flower, 1925). Its range occupies a belt from Sénégal and Mauritania in the west to Eritrea and Ethiopia in the east (Loveridge and Williams, 1957; Iverson, 1992). Some information on the species in West Africa is given by Villiers (1958), but little is known generally (Broadley, 1989) and more is required in order to plan appropriate conservation measures.

The few published biological observations include those of Cloudsley-Thompson (1970), which considered size/growth relations among other aspects. Further investigations on size (dimensions and weight) of Sudanese specimens were carried out by Hirth and Abdel Latif (1981) and Mahmoud et al. (1986), but the analysis of results of the latter paper was critically reappraised by Meek and Avery (1988). Growth during the first year was also studied by Mahmoud and El Naiem (1988). Some observations on behavior were made by Grubb (1971a).

One purpose of this study was to determine whether the morphology of *G. sulcata* in Sahelian Africa varied geographically. The relationships between dimensions and weight in Mali were compared with those found in earlier studies in Sudan. Growth and sexual dimorphism were also investigated. General field observations made during 1991 in northern central Mali are also included here. These may provide a basis for further investigations of the ecological requirements of the species. A pilot program to conserve *G. sulcata* in sub-Saharan Africa is a specific project in the Action Plan of the IUCN Species Survival Commission Tortoise and Freshwater Turtle Specialist Group (Stubbs, 1989), and includes Mali with those countries in West Africa where initial status surveys should be concentrated. The work described in this paper supports the conservation program that has already been proposed by Devaux (1993) in an account of the species' natural history in Sénégal.

MATERIALS AND METHODS

Size-weight measurements and general ecological and locality information were obtained for *G. sulcata* in northern central Mali. Observations in September 1991 were made specifically on tortoises collected by local farmers from areas adjacent to cultivated land around the villages of Dilli (15°00'N, 7°40'W) and Mourdiah (14°28'N, 7°28'W) (Cercle de Nara). Animals measured during October and November 1991 had been deposited in large open-air enclosures in the Parc zoologique, Bamako. Most had been confiscated from a dealer who had been transporting them by road to Ghana in January 1991 for sale both as food and for shipment abroad. The overladen truck had overturned in the centre of Niono, and its live cargo of adult tortoises spilled onto the road. Regulations, although difficult to enforce, prohibit the collection of tortoises in Mali, and the event was brought to the attention of the Malian Government's Direction nationale des Eaux et Forêts, Bamako. The 65 animals seized were placed under jurisdiction of the Direction nationale des Eaux et Forêts in Bamako's Parc zoologique. They apparently originated from the region around Sokolo north to probably the Mauritanian border, in that a local inhabitant reported seeing tortoises stock-piled in three depots in late March 1990 2-3 km from the village of Farabougou (14°58'N, 6°08'W) (Cercle du Macina), 18 km N of Sokolo (a large irrigation village some 50 km NNW of Niono).

Measurements. — Weight was recorded using a sling and spring balance. It was the first parameter to be recorded since individuals sometimes urinated or defecated with prolonged handling. Animals of up to 50 kg were weighed to within 0.5 kg, and to within 1 kg above 50 kg with a Land-rover towing strap around the mid-region substituted for the sling. Greater accuracy was considered unnecessary since weight fluctuated daily according to food intake, bladder water and other factors.

Size characters selected were based on Lambert (1982) for *Testudo graeca* L., and followed Grubb (1971b) and Bourn and Coe (1978) for *Aldabrachelys elephantina* (Duméril and Bibron) - known until recently as *Geochelone (Aldabrachelys) gigantea* (Schweigger) (Pritchard, 1986). Dimensions were measured using a wooden cm/mm calibrated metre rule. Straight-line measurements to within approximately 1 cm accuracy (for curved surfaces, the distance between batons placed vertically at either end) included midline carapace length (the notch between the first marginal scutes to the supracaudal scute), midline plastron length (the gular notch to the anal groove), maximum carapace width (between the 5th marginal scutes approximately along the junction between the 2nd and 3rd vertebrals), and transverse width of the 3rd vertebral scute, the largest of the vertebrals. Widths of the growth annuli of this scute were also measured in each of three selected males and females, whose carapacial surfaces were relatively unabraded and still had distinct grooves with paler coloured keratinous material deposited at scute margins indicating continued growth. The 4th vertebral scute width, used previously by Lambert (1982), was smaller than the 3rd, and relatively smaller and rather more curved than in *T. graeca*, but was measured for comparison with the 3rd.

Anterior extension of the pair of gular scutes was measured perpendicularly from the gular-humeral suture at the plastral margin. In males, the gular scutes were particularly well developed and protruded forward as a two-pronged fork. The undamaged scute was measured when one of a pair was broken or abraded shorter than the other.

Sex Determination. — External characters usually differentiated males from female and immature tortoises (Villiers, 1958). Sexually indeterminate animals with carapace length over 300 mm and flared marginal scutes were deemed to be female; the smallest identifiable female recorded by Villiers (1958) was 308 mm. The most obvious character in males was the deeply concave hypo- and xiphiplastral bone region in addition to spur-like gular scutes, which could be highly developed. The supracaudal scute was also much more strongly convex in males than females. In full-grown males, the anal scutes could be strongly and widely recurved, and sometimes flared at the periphery (Fig. 1).

Age Assessment. — Age of each tortoise was estimated. The deposition of keratinous material in the epidermal scutes provided a record of size increase with time. Growth depends on nutrient intake and follows the seasonal appearance of green vegetation with the onset of rains in June. It may be interrupted or curtailed if a mid-season rain failure results in a shortage of green vegetation. Soon after the start of the Sahelian dry season in October, the vegetation becomes increasingly dry, brown and sparse. Growth slows down as refuge is sought, and eventually ceases during the seven-month period of aestivation. The interruption in growth causes keratinous material to be deposited unevenly in the scutes. Concentric growth annuli are separated by deep grooves (sulci) (Fig. 2) that gave rise to the species' name. Approximately seventeen annuli are discernible on the 3rd vertebral scute in a photograph of *G. sulcata* exhibited during its eighteenth year by Flower (1928). Hatched from an egg laid by a tortoise brought from Sudan and maintained in the Giza Zoological Gardens (Egypt), the tortoise had

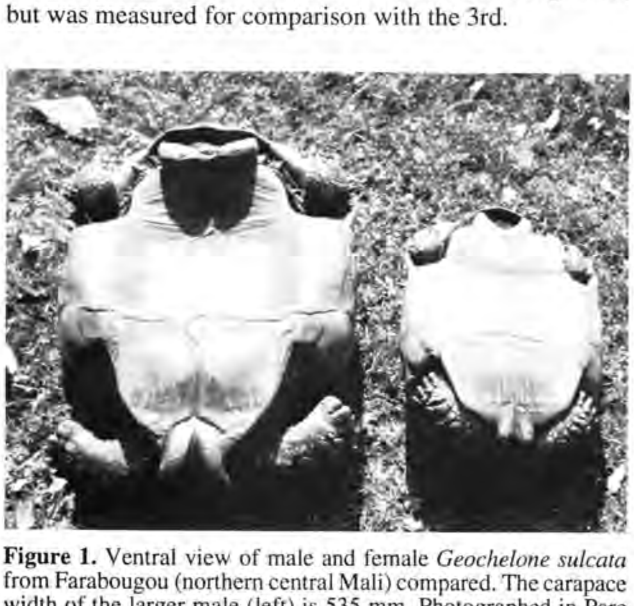

Figure 1. Ventral view of male and female *Geochelone sulcata* from Farabougou (northern central Mali) compared. The carapace width of the larger male (left) is 535 mm. Photographed in Parc zoologique, Bamako on 23 November 1991.

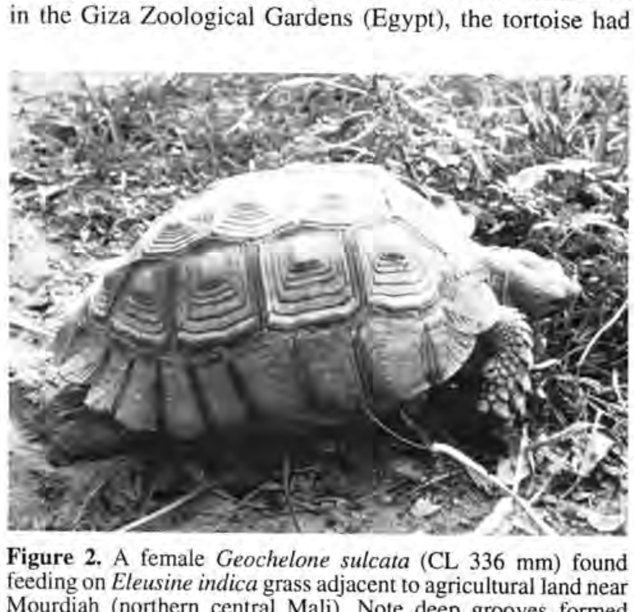

Figure 2. A female *Geochelone sulcata* (CL 336 mm) found feeding on *Eleusine indica* grass adjacent to agricultural land near Mourdiah (northern central Mali). Note deep grooves formed between annuli. Photographed on 22 September 1991.

presumably been exposed to seasonal climatic and rainfall changes in an outdoor enclosure. The use of growth annuli in chelonian age determination has been reviewed by Castanet (1988) and Zug (1991).

RESULTS

Size. — Ontogenetic shape changes occur with growth in *G. sulcata* as in other testudinids (e.g., Bourn and Coe, 1978; Lambert, 1982). Respective carapace length (x) ranges in immature (n = 9), female (n = 15), and male (n = 32) tortoises were 183-272 mm, 336-578 mm, and 384-797 mm. The relationship to plastron length (y) was isometric, differing graphically in males ($y = 73.905 + 0.758x$; r = 0.956; n = 32) from female and immature tortoises ($y = 2.643 + 0.907x$; r = 0.992; n = 24). The relationship to 3rd vertebral scute width (y) was likewise isometric, but there was no difference graphically between males and female and immature animals, and values were therefore pooled ($y = 0.317x - 1.207$; r = 0.982; n = 56). Hirth and Abdel Latif (1981) measured tortoises in Sudan, and found respective slopes and intercepts (when length and 3rd vertebral scute width are respectively y and x in cm) of 2.521 and 7.196, 2.368 and 14.184, and 3.571 and -6.051 for immature, female and male tortoises. My results yielded 3.185 and 0.043, 2.284 and 12.443, and 2.822 and 6.784 for Malian tortoises here.

For comparison with other characters in *G. sulcata*, and following Grubb (1971b), Hirth and Abdel Latif (1981) used 3rd vertebral scute width (x). It had respective ranges of 57-81 mm, 92-190 mm and 120-268 mm in Malian immature, female and male tortoises. The isometric relationship with 4th vertebral scute width (y) was $y = 0.796x + 1.399$ (r = 0.990; n = 56). With plastron length, using cm, Hirth and Abdel Latif (1981) obtained a slope and intercept for their Sudanese animals of 2.914 and 0.984 respectively (n = 30), which compared with 2.620 and 3.570 for the Malian animals examined in this paper (r = 0.986; n = 56).

Weight. — The respective weight ranges of immature, female and male *G. sulcata* recorded in Mali were 1.9-4.2 kg, 6.1-47.0 kg and 11.8-93.0 kg. As in other chelonians, *Testudo graeca*, *Testudo hermanni* Gmelin, *Emys orbicularis* (L.) and *Chrysemys scripta* (Schneider) (Meek, 1982), and as shown previously for *G. sulcata* (e.g., Cloudsley-Thompson, 1970), the relationship between length and body mass was strongly allometric. That between carapace length (y) and weight in grams (x) was $y = 12.643x^{0.363}$ (r = 0.987; n = 56). This was strikingly similar to Cloudsley-Thompson's (1970) data for Sudan ($y = 13.357x^{0.361}$; r = 0.999; n = 8). Extrapolating data from Fig. 1 of Mahmoud et al. (1986), the relationship for animals captive in Khartoum Zoo (Group B) was comparable ($y = 14.228x^{0.352}$; r = 0.846; n = 25), but that ($y = 39.257x^{0.253}$) for live tortoises on the grounds of the Sudan Natural History Museum (Group A) was somewhat different and less well correlated (r = 0.611; n = 20); the combined relationship was $y = 19.822x^{0.320}$ (r = 0.801; n = 45). The Zoo animals above 50 kg tended to be lighter for length ($y = 3.608x^{0.479}$; r = 0.967; n = 5) than those in Mali ($y = 21.808x^{0.312}$; r = 0.874; n = 6).

Hirth and Abdel Latif (1981) compared weight (in kg) with 3rd vertebral scute width (in cm) for their Sudanese *G. sulcata* ($\log_{10} \times \log_{10}$). The respective slope and intercept for this allometric relationship of 2.919 and -2.096 (n = 20) compared well with 2.655 and -1.778 for Malian tortoises here (r = 0.992; n = 56).

Size Structure. — Carapace lengths of *G. sulcata* found by villagers from 1988 to 1991 (and one in 1992) in the Cercle de Nara ranged from 218 to nearly 800 mm with the largest proportion of lengths estimated to be in the 300-399 mm range (Table 1). This was in contrast to the trade-collected tortoises from Farabougou in the Parc zoologique, Bamako, which were generally bigger with the greatest proportion in the 500-599 mm range (the immature tortoises weighed and measured had hatched from eggs laid in the Zoo). The difference in numbers making up proportions above and below 400 mm was significant ($chi^2 = 24.66$, $p<0.001$).

Growth. — Straight widths of 3rd vertebral scute annuli were a measurable record of external growth. Growth in Malian tortoises slowed down after the 20th annulus and could cease by the time approximately 24 had been deposited (Fig. 3). Further well defined annuli may be deposited by individuals growing more slowly (e.g. two Mourdiah tortoises) or achieving unusually large dimensions. Annuli ultimately became virtually uninterpretable and impossible to count as they narrowed with the slowing down of external

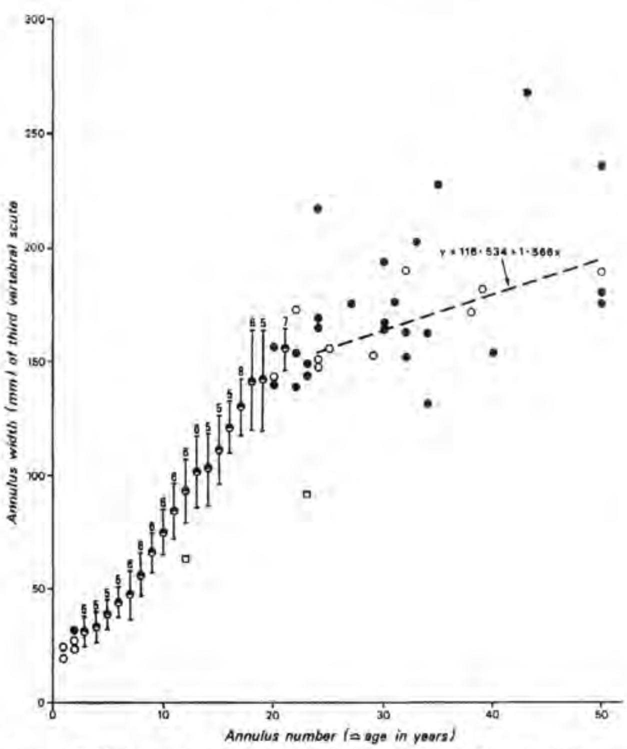

Figure 3. External growth in *Geochelone sulcata*. Standard deviations (bar lines) based on means from five or more values: Farabougou tortoises in Parc zoologique, Bamako (circles); tortoises at Mourdiah (squares); males (solid symbols), female and immature tortoises (open symbols), and pooled (split symbols). The regression is fitted for females with 24 or more annuli.

Table 1. Size composition (%) of *Geochelone sulcata* in northern central Mali.

Location	n	Carapace straight length (mm)						
		Below 200	200-299	300-399	400-499	500-599	600-699	700-799
Cercle de Nara	11	0	27.3	45.4	9.1	0	9.1	9.1
Cercle du Macina: Farabougou[1]	40	0	0	2.5	35.0	47.5	7.5	7.5

[1]Trade-collected; in Parc zoologique, Bamako

growth. Third vertebral widths with over 23 annuli formed were significantly correlated with annulus counts (r = 0.813; n = 8; p<0.01) in females (Fig. 3), but not in males. Mean widths in female (n = 8) and male (n = 20) *G. sulcata* with 24 or more discernible annuli were respectively 168 (S.D. ±18) and 185 (S.D. ±33) mm, corresponding to calculated carapace lengths of 533 and 587 mm.

As in *A. elephantina* (Bourn and Coe, 1978) and *T. graeca* (Lambert, 1982), annular growth increments varied and depended on nutrient intake with the availability of green vegetation corresponding to the year's rainfall. Growth was greatest during years 8-20 (Fig. 4a), but varied considerably in individuals (Fig. 4b).

Two individuals of 12 and 23 years found within the Mourdiah arrondissement had respective carapace lengths and weights of 218 and 352 mm and 2.0 and 6.1 kg. The values were lower than corresponding expected means of 388 and 504 mm and 15.1 and 26.1 kg for Farabougou animals in the Parc zoologique, Bamako. Third vertebral scute widths were similarly lower (Fig. 3).

Sexual Dimorphism. — Apart from the small difference between males and females, and immature tortoises reflected by slopes for the relationship between carapace and plastron length above, sexual dimorphism was more strongly marked by gular extension. The best-fitting relationship between gular extension and body size (carapace length) was isometric in males, but allometric in females (Fig. 5a).

Visually, the carapaces of males tended to become more elongate with growth, while those of females became more rotund. When represented graphically (Fig. 5b) and combining Sudanese data from Cloudsley-Thompson (1970), an allometric relationship between width (y) and length in millimeters (x) did indeed best-fit males (r = 0.924; n = 35), but an isometric one was the best fit for females (r = 0.939; n = 18). The slopes were not, however, significantly different from each other or for males from the isometric $y = 58.559 + 0.619x$ (r = 0.920; n = 35). An isometric relationship best-fitting immature tortoises ($y = 8.971 + 0.713x$; r = 0.993; n = 11) was close to that of Sudanese data extrapolated from Mahmoud et al. (1986), in which the best-fitting

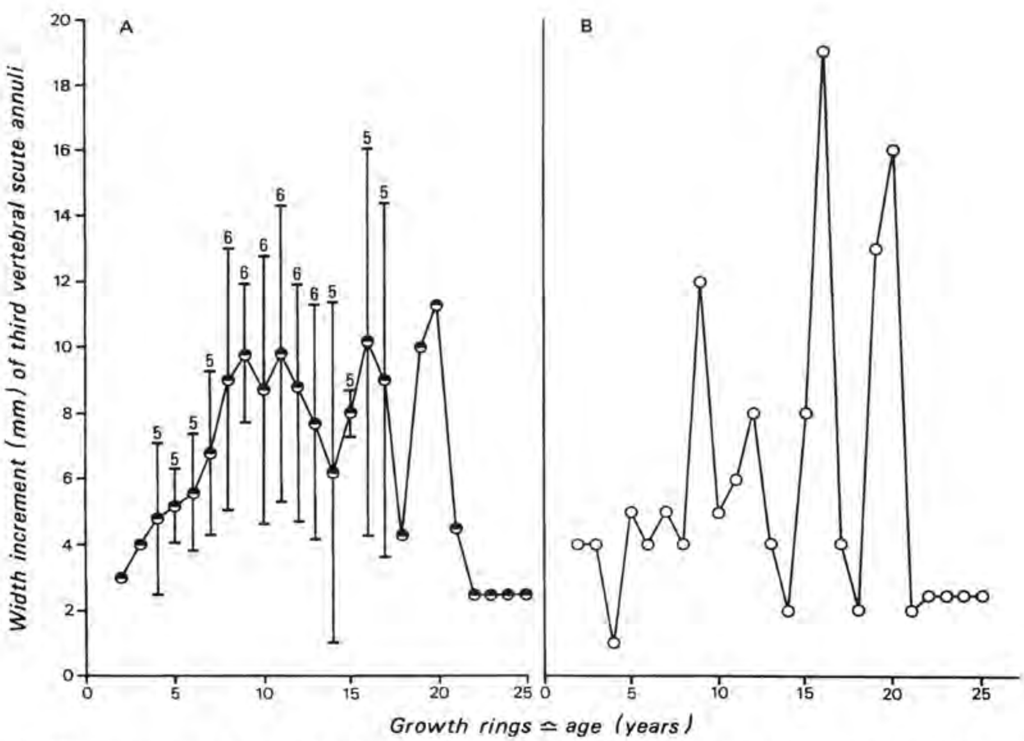

Figure 4. Mean width increment and standard deviation (bar lines) of 3rd vertebral scute annuli corresponding with age in *Geochelone*

Table 2. Bioclimatic data for *Geochelone sulcata* in Mali.

Locality (and co-ordinates)	Citation (if any)	Altitude (m)	Meteorological station and altitude (m)	Mean daily air temperature (°C) Minimum for coolest month	Mean daily air temperature (°C) Maximum for warmest month	Mean annual sunshine (h)	Mean annual rainfall (mm)
El Mraïti (19°13'N, 2°18'W)	Villiers, 1958	*c.* 250	Kidal (462)	12.2 (Jan.)	41.5 (June)	3530	140
Tombouctou (16°46'N, 3°01'W)	Papenfuss, 1969	*c.* 269	Tombouctou (269)	12.7 (Jan.)	42.9 (May)	3439	206
Dilli (15°00'N, 7°40'W)		256	Nara (265)	11.5 (Jan.)	41.3 (May)	3015	391
Mourdiah arrondissement[1]		269-314	Mourdiah (314)	12.2[2] (Jan.)	39.8[2] (May)	-	427
Sangha (14°28'N, 3°19'W)	Perolini, 1988	*c.* 575	Bandiagara (392)	13.9[3] (Jan.)	40.1[3] (May)	3024	469
Douentza (15°00'N, 2°57'W)	Papenfuss, 1969	*c.* 289	Douentza (620)	13.9[3] (Jan.)	40.1[3] (May)	3024	490
Farabougou (14°58'N, 6°08'W)		268	Sokolo (273)	12.2[2] (Jan.)	39.8[2] (May)	-	502
Bamako (12°39'N, 8°00'W)	Iverson, 1992[4]	480	Bamako-ville (331)	16.4 (Jan.)	38.9 (Apr.)	2869	1098

[1] Locality details: near Mourdiah village (14°28'N, 7°28'W); 24 km N of Mourdiah (14°41'N, 7°28'W) (N.D. Jago, *pers. comm.*); 3 km N of Girindingué (14°20'N, 7°40'W) (25 km SW of Mourdiah)
[2] For Niono (alt. 279 m) - nearest equivalent station (Direction National de la Metéorologie, Bamako)
[3] For Mopti (alt. 268 m) - nearest equivalent station (Meteorological Office, 1983)
[4] Based on a specimen in the Staatliches Museum für Tierkunde, Dresden

relationship ($r = 0.931$; $n = 45$) for both Groups combined (not differentiating between males and females) was also isometric ($y = 27.230 + 0.699x$) and not significantly different from the allometric $y = 850.699\log_{10}x - 1915.761$ ($r = 0.928$; $n = 45$). Villiers (1958) found that the ratios between carapace length and width (reciprocals of the slopes in the preceding isometric relationships) in immature, female and male *G. sulcata* (probably from Sénégal bordering the Atlantic Ocean) with respective lengths of 95, 308, and 677 mm were 1.26, 1.17, and 1.44. Again indicating that females were the least elongate, these compared with 1.39, 1.04, and 1.61 for Malian tortoises here in which the ratio for males was over 1.5 times that of females.

There was a sexual difference when the relationships between carapace and plastron length above were compared, but visually there was no obvious difference in the anterior relationship between the carapace and plastron (Fig. 1), notwithstanding dimorphism of the gular scutes. However, the distance between the anal groove and supracaudal scute representing rear aperture diameter (carapace length less midline plastron length) (y), as also used by Stubbs, Hailey, Pulford et al. (1984) in *T. hermanni*, was not correlated with carapace length (x) in females or immature tortoises, but was significantly so ($r = 0.722$; $n = 32$; $p<0.01$) in males ($y = 0.242x - 7.390$).

General Ecology. — The habitat of an immature tortoise found towards the end of the rainy season 3 km N of Girindingué (Mourdiah arrondissement) on 20 September 1991 consisted of lightly wooded savannah thickly carpeted with annual grasses and scattered herbaceous vegetation (Fig. 6). Main woody species present were combretaceous shrubs. This same area was very dry by 25 November after the rains had faltered in late September, with sparse annual vegetation intersected by the tracks of grazing animals (Fig. 7).

When allowed to roam freely in an area adjacent to agricultural land just outside the village, a previously captive female *G. sulcata* collected from near Mourdiah (Cercle de Nara) was observed to feed on the leaves of annual grass tufts *Eleusine indica* (Fig. 2). This is a grass commonly growing on heavy soils associated with water - a well overflow was within the vicinity.

Activity and Behavior. — *Geochelone sulcata* were found by villagers during the wet season from July to October (1988-1991) in the Cercle de Nara, northern central Mali. From the start of the dry season when cool in late October, they were sighted less frequently with reduced activity followed by aestivation during the time that the dry season becomes increasingly warm, and until it ends with the onset of rain in late June.

Observations were carried out in the Parc zoologique, Bamako, during the cool, dry season (30 and 31 October, 9 and 23 November 1991). With air temperature at sunrise (*ca.* 06.30 h LMT) 20-21°C., it rose with sunshine from 26 to 34.5°C. between 2 and 6 h later. The largest adult male sighted and measured in the late morning on 30 October was observed again the next morning some 80 m away at the opposite edge of the enclosure and on the other side of a small stream. The animal sought shade at 10.48 h with the air at 30.5°C. By around midday when air temperature exceeded 32°C., the greater proportion of tortoises had taken refuge from sunshine. With a decline in the sun's radiant heat by late afternon (air at approximately 31°C.), several adult tortoises became active between 15.45 and 16.00 h on 27 September near the end of the seasonal rains. At the start of the observation period one animal entered the small stream that flowed through a muddy area of the enclosure. The carapaces of some of the others on this and later occasions

Table 3. Mean monthly rainfall (mm) within the range of *Geochelone sulcata* in Mali (after Meteorological Office, 1983).

Meteorological station (and latitude)	Mean monthly rainfall, 1949-1970 J	F	M	A	M	J	J	A	S	O	N	D
Kidal (18°26'N.)	0	<1	1	1	6	12	38	53	26	3	<1	<1
Tombouctou (16°46'N.)	<1	<1	<1	1	4	20	54	93	31	3	<1	<1
Mopti (14°32'N.)	<1	<1	1	4	29	65	162	199	101	23	<1	1
Bamako-ville (12°38'N.)	1	<1	5	16	60	150	246	311	230	70	8	1

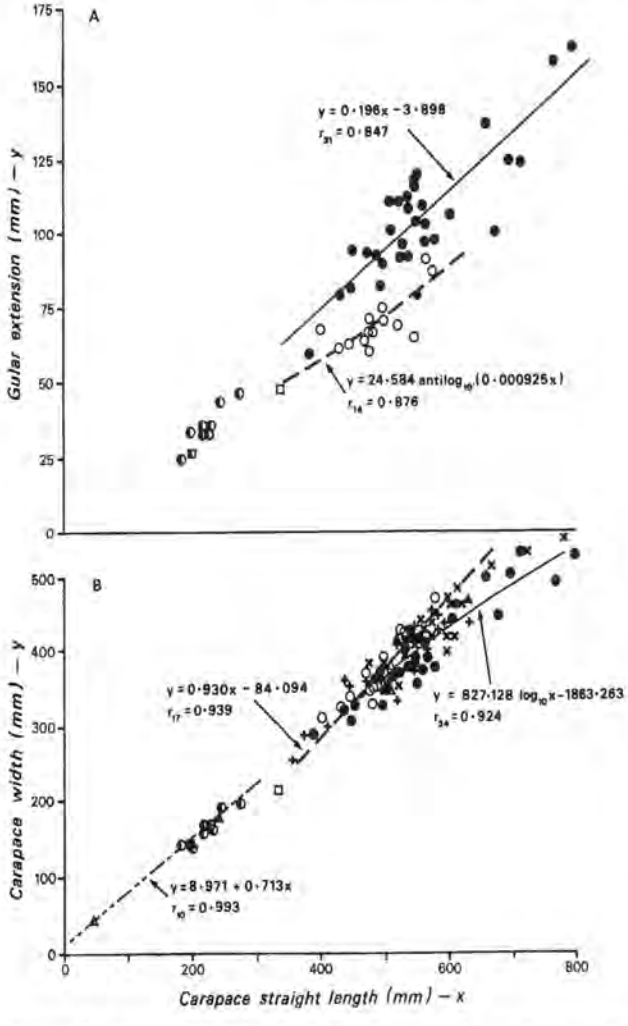

Figure 5. Sexual dimorphism in *Geochelone sulcata* showing the relationship of carapace length (x) with A. gular extension (y); B. carapace width (y). Solid, open and split symbols in respectively male, female, and sexually undifferentiated tortoises: circles, Farabougou tortoises, Parc zoologique, Bamako; squares, Cercle de Nara tortoises; triangles, Sudanese data in Cloudsley-Thompson (1970). The + and x respectively represent Groups A and B captive tortoises in Khartoum, extrapolated from data in Mahmoud et al. (1980), and are shown for comparison but excluded from calculations since not differentiated sexually.

were observed caked with dry mud.

Bamako's Parc zoologique is located on the outskirts of town and the enclosures containing tortoises (main enclosure photographed by Switak, 1972) have been built on natural sloping hillside facing SSW and therefore fully exposed to the sun. Refuges for the tortoises were provided by shallow recesses within rock formations, and tunnel access allowed entry to wider concavities up to *ca.* 3 m deep. A few individuals sought shelter away from rocks in shallow burrows in the soil.

Mean Rainfall, Sunshine, and Temperature. — *Geochelone sulcata* in Mali occurs in the Sahelo-Saharan, Sahelian, Sudanian and Sudano-Guinean zones of Africa's Sahelian region with respective mean annual rainfall ranges of 100-200, 200-500, 500-800, and 800-1000 mm (the Sahara Desert is defined by the 100 mm isohyet). In addition to localities in northern central Mali in this work, *G. sulcata* has been recorded elsewhere in the country by previous authors (Table 2). For these localities, mean rainfall and sunshine, and mean maximum and minimum daily temperatures for respectively the warmest and coolest months (based on 30 years) were obtained from synoptic stations included by the Meteorological Office (1983), or from data lodged at the Direction nationale de la Metéorologie, Bamako, and included with OMBeVi (1985). The distribution of *G. sulcata* in Mali did not appear to be limited by either temperature or sunshine. Depending largely on latitude, rainfall occurs predominantly between May and October (Table 3). El Mraïti at 19°13'N. (Villiers, 1958) is the northernmost known locality for *G. sulcata* in Mali. The species is unlikely to occur further south than Bamako. Within the range of rainfall, *G. sulcata* respectively occupies vegetationally "wadis/desert dunes with perennial vegetation", "Sahel *Acacia* woodland, grassland and deciduous bushland" and "undifferentiated woodland: Sudanian" - mapping units 71/70, 43, and 29a - *sensu* White (1983). The bioclimatic range with xerothermic index (the number of physiologically dry days in a year) *sensu* UNESCO-FAO (1963) is from desertic (xerothermic index: 300-350), through subdesertic (xerothermic index: 200-300), to barely warm tropical - dry season of long duration (xerothermic index: 150-200) at Bamako.

Effects of Human Pressure and Drought. — With an additional record in 1992, nine tortoises were known to have been collected over the years 1988-92 for purposes of consumption by villagers in the Mourdiah arrondissement. Warshall (1989) reported that small, easily transportable species were generally taken from within 10 km of the village, and therefore the area from which the animals had been removed approximated 300 km^2. At Farabougou, at least 65 animals had been amassed by a dealer in a period of over 10 months from within an estimated radius around the village of up to approximately 65 km (the maximum distance travelled by a donkey cart in a day) and amounting to an area of *ca.* 13,000 km^2. A local inhabitant (I. Coulibaly, *pers. comm.*) reported that *G. sulcata* used to be found frequently by farmers in the Cercle de Nara before 1985, but were now much more scarce following the sixteen drought years affecting northern central Mali. These are the only reports that provide even speculative information on the size and density of tortoise populations in the area.

Although annual rainfall normally fluctuates widely in the Sahelian region (Advisory Committee on the Sahel, 1983), the effects of drought or a period of general rainfall decrease first became noticeable in Mali during recent years in 1973. Mean rainfall in Mali's Sahelian region over 1969-1984 was only 9% (San) to 42% (Nioro du Sahel) of that recorded at fifteen synoptic meteorological stations in the 18-25 years prior to 1968 (OMBeVi, 1985). Thus, for the 23 years prior to 1991, sixteen drought years (1969-1984) were followed by seven post-drought years (1985-1991). The years of decreased rainfall brought pressure on domestic grazing animals. With subsistence hunting widespread in

Figure 6. Grassland savannah habitat of immature *Geochelone sulcata* during the season's penultimate rain (17 October 1991), 3 km N of Girindingué, Mourdiah arrondissement, Cercle de Nara, northern central Mali.

Figure 7. Grassland savannah habitat (25 November 1991) 6 weeks after the start of the dry season, heavily intersected by the tracks of grazing animals, 21 km WSW of Mourdiah, Cercle de Nara, northern central Mali.

Mali, and firearms readily available (although ammunition is limited in rural areas), the local human population resorted to wild animals to make up a protein shortfall, taking small animals from within 10 km of the village rather than big unmanageable game species from further afield (Warshall, 1989). The current low density of *G. sulcata* has thus probably been brought about at least partly by human pressure in combination with drought. Tortoise populations have apparently not yet recovered despite the rains' return. Unenforced regulations on trade collection (as evidenced by the Farabougou depots) and the perennial harvesting for food by local people have also probably contributed to the species' continued general decline in northern central Mali. Potential meat production per unit area for exploitation on a sustainable basis requires further evaluation as part of the Action Plan of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group (Stubbs, 1989).

DISCUSSION

Size dimensions and weight of Malian *G. sulcata* differed very little from those of Sudanese tortoises. The tendency for large animals above 50 kg weight in Sudan measured by Mahmoud et al. (1986) to be lighter for size than smaller ones was probably due to differences in conditions of captivity, notwithstanding any individual variation in making measurements. The general similarity therefore suggests that the species shows little geographical variation, at least between Sudan and Mali, and probably also to Sénégal at the western edge of the range. The dimensions of tortoises further east in the highlands (>2000 m) of Ethiopia and on the Red Sea coast of Eritrea have not been recorded.

Several growth studies have been carried out on wild tortoise populations in the tropics; the most comprehensive probably being those on *A. elephantina* of Aldabra Atoll by Gaymer (1968), Grubb (1971b) and Bourn and Coe (1978). Although larger specimens (1700 mm, 230 kg) have been recorded in captivity (Swingland, 1989), the largest male of this giant species recorded by Grubb (1971b) had a carapace length of 1060 mm and corresponding weight of 130 kg. It therefore exceeded the known full-grown size dimensions of a male *G. sulcata*. A hatchling *G. sulcata* in Sudan had at emergence a carapace length of 45 mm and weighed 27.6 g (Cloudsley-Thompson, 1970), and a "typical" hatchling in captivity in the USA was similar (45 mm and 25 g) with the largest hatchling 60.3 mm and 35.2 g (Stearns, 1989). The mass tends therefore to be less than means of 60 g and 48 g recorded in *A. elephantina* hatchlings from respectively the heaviest and lightest 50 eggs on Malabar (Aldabra Atoll) by Swingland and Coe (1978). An adult male *G. sulcata* achieving 830 mm and 105.5 kg (Flower, 1925) therefore increases its length by 18 times and its weight by 3822 times. These increases are apparently even greater than those of 8 to 14 fold and 1750 to 3300 fold respectively achieved by *A. elephantina* (Grubb, 1971b). The Aldabran species benefits from a somewhat higher rainfall (>1000 mm) than the Sahelian species, and together with maritime humidity, a generally greater availability of green vegetation.

The biggest Malian male recorded here was 797 mm long and weighed 93 kg (respectively reflecting 18 and 3370 fold increases on Cloudsley-Thompson's (1970) hatchling); the larger dimensions recorded by Flower (1925) probably resulted from a high captive growth rate. In *A. elephantina*, growth in captivity at the Aldabra research station was also observed by Swingland (*pers. comm.*) to be faster than in at least the dense south-east Grand Terre (Cinq Case) population (Bourn and Coe, 1978). Furthermore, the sizes reached by the low density eastern Malabar population were greater than those of exposed, overgrazed Grand Terre (Grubb, 1971b). Thus, growth rate and size in both of these large tropical species of tortoise, one continental and the other insular, are strongly influenced by ecological conditions.

The observation that the *G. sulcata* in the Parc zoologique, Bamako, were larger than those gathered by farmers in the Cercle de Nara suggests either that the latter tended to be smaller (possibly the result of local harvesting over the years) than elsewhere in northern central Mali, or that animals obtained and selected by trade tended to be of medium or above average size. Size selection of trade-collected tortoises was also reported by Lambert (1981a) for *T. graeca* exported from Morocco.

The relationship between growth rate and weather conditions (especially rainfall), manifest in the scute annuli in *G. sulcata*, has also been observed in *T. graeca* in the Mediterranean region (Lambert, 1982). Clear, deep grooves are formed both in aestivating *G. sulcata* in the Sahel and in dormant *Testudo graeca ibera* Pallas in the severe winter of the eastern Mediterranean, whereas they are less distinct in *Testudo graeca graeca* in the milder winter of more oceanic NW Africa.

An apparent relationship between annulus formation and season, as in *G. sulcata*, also exists in the Aldabran *A. elephantina* (Grubb, 1971b; Bourn and Coe, 1978), although the relatively small Cinq Cases tortoises on Grand Terre have no annuli visible at all (probably due to shallow groove formation and abrasion). The annuli are formed also in response to variation in the seasonal quality and quantity of green vegetation on this Indian Ocean atoll, and the number discernible in *A. elephantina* (Bourn and Coe, 1978) indicate that animals could be full-grown by around 24 years, as in *G. sulcata*. However, the number was not related to age in the desert tortoise *Gopherus agassizii* (Cooper) of southwestern USA (Woodbury and Hardy, 1948), probably because of non-seasonal rainfall.

Two tortoises from the Mourdiah arrondissement were smaller than comparably aged Farabougou animals in the Parc zoologique, Bamako. The latter came from the vicinity of an irrigation area, which may have offered access to green vegetation for a greater proportion of the year. The increased nutrient intake probably allowed a higher rate of growth.

The significance of sexual size dimorphism in chelonians has been reviewed by Berry and Shine (1980). In terrestrial species, males generally exceed females in size when there is male combat and forcible insemination of females. This is observed in the population of *A. elephantina* on Aldabra Atoll (Frazier, 1968; Grubb, 1971b). The level of density on Aldabra seemingly results in competition among males, while the females are probably continually harrassed by mature, libidinous males that come into contact with them. This is likely to result in successful copulation only being achieved by forceful, invariably large males. The natural densities of *G. sulcata* probably never reach the level of that on Aldabra, but the males must indulge in combat, as observed among captive animals in the USA (Stearns, 1989), for like *Gopherus agassizii*, and such species as *Chersina angulata* (Schweigger) and *Geochelone yniphora* (Vaillant) (e.g., Honegger, 1981), they are accordingly armed with well developed gular scutes.

The anal scutes in full-grown male *G. sulcata* could be strongly and widely recurved, and sometimes flared at the periphery, as in *Gopherus agassizii*. The thickening and general strengthening was probably associated with the use of the xiphiplastral region to ram, and flared anal scutes to lift, the rear of the carapace of females, which were either reluctant to mate or required stimulation if the rear of their carapaces were to be raised and ingress of the male's tail and penis allowed towards the cloacal aperture. Comparable behavior has also been observed by Stubbs (*pers. comm.*) in a smaller, Mediterranean species, *Testudo hermanni*, even to the extent of infection around the cloacal region resulting from damage caused by continual stabbing from the horny scale on the tip of the tail of libidinous males.

The non-correlation of the gape of the rear aperture in females with size is probably explained by the need to be just big enough to allow the egress of eggs, but not any bigger to become vulnerable to attack. Such an adaptation, even in big animals, would not impede large clutches of similarly sized eggs from being laid, and yet would have a selective advantage in affording maximum protection. On the other hand, copulation of females with relatively narrow apertures is possibly more difficult for big males to achieve than small ones, and rear aperture gape may also be related to size assortative mating as considered by Swingland and Stubbs (1985) in *Testudo hermanni*.

The savannah habitats selected by *G. sulcata* in the Sahelian zones of Africa optimally provide both shade from sunshine during the hottest hours of the day and also green vegetation as food, including such annual grasses as *Eleusine indica* during the rains. But in most areas of the Sahel the tortoises must compete with herbivorous game and the stock animals of local people which graze and trample the scant dry-season vegetation. Competition of this kind must constrain the rate of growth and population densities achieved by tortoises in areas such as the Mourdiah arrondissement.

The rapid 80 meter displacement by a large male observed in Bamako's Parc zoologique may suggest that in natural conditions large distances can be traversed in the search for females in low density populations, or for food in areas of sparse or patchy green vegetation.

During the warmest hours of the day, and even during the early part of the cool, dry season, adult *G. sulcata* seek shade. Shade was similarly sought during the middle of the day by *A. elephantina* on Aldabra Atoll (e.g. Gaymer, 1968), and this is probably true of all tortoises in hot, sunny places, including such non-tropical species as *T. graeca* (e.g. Lambert, 1981b). While *T. graeca* hibernates during the cold, wet winter in Africa north of the Sahara Desert, especially at altitudes above 1000 m (Lambert, 1983), *G. sulcata* in subSaharan Africa on the other hand aestivates during the very dry, initially cool but increasingly hot, time of year. *Geochelone pardalis babcocki* (Loveridge), which in southern Ethiopia is sympatric with *G. sulcata*, but ranges much further south in eastern and southern Africa (Iverson, 1992), becomes similarly inactive during the cool, dry winter months in Zimbabwe (Broadley, *pers. comm.*), especially at higher altitudes (> 1200 m), and in the South African highveld. *Aldabrachelys elephantina* on Aldabra Atoll does not appear to experience such a period of inactivity (e.g., Gaymer, 1968).

Cool, damp burrows are probably required by *G. sulcata* for aestivation during the dry season, as they are by the desert tortoise *Gopherus agassizii* in southwestern USA (Woodbury and Hardy, 1948), with whose behavior there are similarities. Hatchlings probably seek the disused burrows of small mammals away from rocky outcrops in their natural habitats where the soil is light and sandy. The tortoises possibly enlarge rather than vacate these burrows as they grow. Alternatively, new burrows are excavated, since adult animals in captivity have been observed to dig into muddy soil during rain (Grubb, 1971a), using their forelimbs in rapid jerks (Devaux, 1993) [burrow-digging behavior, apparently instinctual, was recorded by Pouvreau (1989) in Sénégal, and was also reported among captive tortoises in the USA (Stearns, 1989)]. The burrows are sloping, with a vertical depth of 70-80 cm, and 3.65 m long (Villiers, 1958) [a length of 5 m has been recorded by Pouvreau (1989)]. The need to excavate burrows [often made at the base of a tree with a mound of displaced sand at the entrance (Pouvreau, 1989; Devaux, 1993)], which during a tortoise's lifetime is required to accommodate its ever increasing size, may need to be considered in any conservation exercise involving translocation, especially of large animals. Burrow-use and digging have also been taken into account in conservation of *Gopherus polyphemus* (Daudin) in southeastern USA (e.g., Hansen, 1963; Douglass, 1978; McRae et al., 1981; Diemer, 1986).

Geochelone sulcata is confined to Africa's Sahelian region, but may have surprisingly wide environmental tolerances. The range in Mali is not apparently influenced by temperature and sunshine, and the species' few precise locality records have been in zones of between 140-1098 mm mean annual rainfall. The impact of Sahelian drought conditions on the status of natural populations is unknown. Further information on the distribution and habitat requirements in Sahelian countries is required in order to elucidate the factors restricting the species' range. Information on both population status and limiting factors are important in drawing up conservation plans of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group (Stubbs, 1989). The program proposed for the species in Sénégal is coupled with research in bioclimatically similar Mali, Niger, Chad, Sudan and elsewhere (Devaux, 1993).

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Résumé

Geochelone sulcata (Cryptodira: Testudinidae) habite au Mali les zones de savane arborée, couvertes d'herbe pendant la saison des pluies, de juin à octobre; après le début de la saison sèche, la végétation, piétinée par le bétail, devient en moins de six semaines très clairsemée. Lorsque la température de l'air dépasse 32°C les tortues cherchent un refuge pour se protéger du soleil de midi; elles estivent durant la saison sèche. L'espèce habite la zone soudano-sahélienne, où les précipitations annuelles sont comprises entre 140 et 1098 mm et dont le bioclimat est évalué comme variant de "désertique" à "tropical chaud et sec accentué". En raison du prélèvement continuel de tortues, les populations du Mali nord-central n'ont sans doute pas encore, en 1991, recouvré leurs effectifs décimés par la longue période de sécheresse qui a sévi de 1969 à 1984. Ni l'expression allométrique entre la longueur en ligne droite de la dossière (y) et la masse (x en g) de *Geochelone sulcata* du Mali nord-central ($y = 12{,}64x^{0{,}36}$, ni les expressions isométriques entre les autres caractéristiques, ont varié significativementes à celles obtenues à partir de tortues du Soudan captives. La longueur de la dossière de femelles et de mâles du Mali est respectivement de 336-578 et de 384-797 mm, leur masse étant de 6,1-47,0 et de 11,8-93,0 kg. L'alimentation était saissonnière (la graminée annuelle, *Eleusine indica*, est spécialement prisée des tortues) et les anneaux de croissance des écailles de la carapace se déposent à peu près régulièrement chaque année. La largeur de ces anneaux (mesurée sur la 3^e^ vertébrale) est variable; c'est entre la 8^e^ et la 20^e^ année qu'elle est la plus importante. Les dimensions maximales d'un individu peuvent être atteintes vers l'âge de 24 ans, mais les plus grandes tortues et celles dont la croissance est lente peuvent encore acquérir de nouveaux anneaux à cet âge. Les mâles développent des gulaires saillantes et fourchues, le contour de leur dossière est proportionnellement plus allongé que celui des femelles. L'ouverture postérieure de la carapace de ces dernières (entre dossière et plastron) n'augmente pas lors de la croissance. Les tortues recueillies dans un but commercial sont en moyenne plus grandes que celles rencontrées communément par les indigènes dans un autre secteur.

LITERATURE CITED

Advisory Committee on the Sahel. 1983. Environmental change in the West African Sahel [contributed to by E. Bernus, K. Butzer, R. Fishwick, S. Nicholson, and W. Roder]. Washington: National Academy Press for the Board on Science and Technology for International Development, 92 pp.

Berry, J.F. and R. Shine. 1980. Sexual size dimorphism and sexual selection in turtles (Order Testudines). Oecologia 44:185-191.

Bourn, D. and M. Coe. 1978. The size, structure and distribution of the giant tortoise population of Aldabra. Phil. Trans. R. Soc. Lond. (B) 282:139-175.

Broadley, D.G. 1989. *Geochelone sulcata*. *In*: Swingland, I.R. and M. Klemens (Eds.). The Conservation Biology of Tortoises. Occasional Papers of the IUCN Species Survival Commission 5:47-48.

Castanet, J. 1988. Les méthodes d'estimation de l'âge chez les chéloniens. Mesogée - Bulletin du Muséum d'Histoire Naturelle de Marseille 48:21-28.

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

Devaux, B. 1993. *Geochelone sulcata* au Sénégal. La Tortue, le journal de la SOPTOM et du Village des Tortues 23:14-20.

Diemer, J.E. 1986. The ecology and management of the gopher tortoise in the southeastern United States. Herpetologica 42:125-133.

Douglass, J.F. 1978. Refugia of juvenile gopher tortoises *Gopherus polyphemus* (Reptilia, Testudines, Testudinidae). J. Herpetol. 12:413-415.

Flower, S.S. 1925. Contributions to our knowledge of the duration of life in vertebrate animals. III - Reptiles. Proc. zool. Soc. Lond. 1925:911-981.

Flower, S.S. 1928. Exhibition of a living specimen of the great African tortoise (*Testudo sulcata*). Proc. Zool. Soc. Lond. 1928:654.

Frazier, J. 1973. Behavioral and ecological observations on giant tortoises on Aldabra Atoll. Ph.D. Thesis, University of Oxford, 733 pp.

Gaymer, R. 1968. The Indian Ocean giant tortoise *Testudo gigantea* on Aldabra. J. Zool., Lond. 154:341-363.

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

Grubb, P. 1971b. The growth, ecology and population structure of giant tortoises on Aldabra. Phil. Trans. R. Soc. Lond. (B) 260:327-372.

Hansen, K.L. 1963. The burrow of the gopher tortoise. J. Fla. Acad. Sci. 26:353-360.

Hirth, H.F. and E.M. Abdel Latif. 1981. Morphometrics of the spurred tortoise, *Geochelone sulcata*, in the Sudan. J. Herpetol. 15:120-121.

Honegger, R. 1982. Testudinata. *In*: CITES Identification Manual Committee, Identification Manual. Vol. 3 - Reptilia, Amphibia and Pisces. Gland, Switzerland: CITES Secretariat, unpaginated.

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

Lambert, M.R.K. 1981a. The Mediterranean spur-thighed tortoise, *Testudo graeca*, in the wild and in trade. *In*: Coborn, J. (Ed.). Proceedings, European Herpetological Symposium, Cotswold Wild Life Park, Oxford, 1980. Burford, UK: Cotswold Wild Life Park, pp. 17-23.

Lambert, M.R.K. 1981b. Temperature, activity and field sighting in the Mediterranean spur-thighed or common garden tortoise, *Testudo graeca* L. Biol. Conserv. 21:39-54.

Lambert, M.R.K. 1982. Studies on the growth, structure and abundance of the Mediterranean spur-thighed tortoise, *Testudo graeca*, in field populations. J. Zool., Lond. 196:165-189.

Lambert, M.R.K. 1983. Some factors influencing the Moroccan distribution of the western Mediterranean spur-thighed tortoise, *Testudo graeca graeca* L., and those precluding its survival in N.W. Europe. Zool. J. Linn. Soc. 79:149-178.

Loveridge, A. and E.E. Williams. 1957. Revision of the African tortoises and turtles of the suborder Cryptodira. Bull. Mus. Comp. Zool. Harv. 115:163-541.

Mahmoud, Z.N. and D.A. El Naiem. 1988. Studies on the growth of the desert tortoise (*Testudo sulcata*) in Sudan: changes in morphometrics and body weight from hatching to one year (0+). Herpetol. J. 1:280-284.

Mahmoud, Z.N., D.A. El Naiem, and D.M. Hamad. 1986. Weight and measurement data on the grooved tortoise *Testudo sulcata* (Miller) in captivity. Herpetol. J. 1:107-110.

McRae, W.A., J.L. Landers, and J.A. Garner. 1981. Movement patterns and home range of the gopher tortoise *Gopherus polyphemus*. Am. Midl. Nat. 106:165-179.

Meek, R. 1982. Allometry in chelonians. Brit. J. Herpet. 6:198-199.

Meek, R. and R.A. Avery. 1988. Allometry in *Testudo sulcata*: a reappraisal. Herpetol. J. 1:246-247.

Meteorological Office. 1983. Tables of temperature, relative humidity, precipitation and sunshine for the world. Part 4. Africa, the Atlantic Ocean south of 35°N and the Indian Ocean. London: Her Majesty's Stationery Office, 229 pp.

OMBeVi - Office Malien du Bétail et de la Viande. 1985. Impact actuel de la sécheresse au Mali. Bamako: OMBeVi, Ministère Chargé des Ressources Naturelles et de l'Elevage, Projet Sectoriel de l'Elevage USAID No. 688-0218, Document No. 123, 95 pp.

Papenfuss, T.J. 1969. Preliminary analysis of the reptiles of arid central West Africa. Wasmann J. Biol. 27:249-325.

Perolini, M. 1988. *Geochelone sulcata* - chez les Dogons. La Tortue, le journal de la SOPTOM 8:9-10.

Pouvreau, J.-P. 1989. *Geochelone sulcata* - n°3, estivation - braconnage. La Tortue, le journal de la SOPTOM et du Village des Tortues 11:1-4, 20.

Pritchard, P.C.H. 1986. A reinterpretation of *Testudo gigantea* Schweigger, 1812. J. Herpetol. 20:522-534.

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

Stubbs, D. (Ed.) 1989. Tortoises and freshwater turtles. An action plan for their conservation. Gland, Switzerland: IUCN Species Survival Commission Tortoise and Freshwater Turtle Specialist Group, 47 pp.

Stubbs, D., A. Hailey, E. Pulford, and W. Tyler. 1984. Population ecology of European tortoises: review of field techniques. Amphibia-Reptilia 5:57-68.

Swingland, I.R. 1989. *Geochelone gigantea*. *In*: Swingland, I.R. and M. Klemens (Eds.). The Conservation Biology of Tortoises. Occasional Papers of the IUCN Species Survival Commission 5:105-110.

Swingland, I.R. and M.J. Coe. 1978. The natural regulation of giant tortoise populations on Aldabra Atoll. Reproduction. J. Zool., Lond. 186:285-309.

Swingland, I.R. and D. Stubbs. 1985. The ecology of a Mediterranean tortoise (*Testudo hermanni*): reproduction. J. Zool., Lond. 205:595-610.

Switak, K.H. 1972. Tortoise keeping at its best. Int. Turtle Tortoise Soc. J. 6(4):20-25, 39.

UNESCO-FAO. 1963. Bioclimatic map of the Mediterranean zone [prepared by L. Emberger, H. Gaussen, M. Kassas and A. de Philippis]. Paris: UNESCO-FAO Arid Zone Research 21, 1 p.

Villiers, A. 1958. Tortues et crocodiles de l'Afrique noire française. Init. Afr. 15:1-354.

Warshall, P. 1989. Mali: biological diversity assessment. Washington: US Agency for International Development, Natural Resources Management Support Project [no. 698-0467], 95 pp.

White, F. 1983. The vegetation of Africa. Paris: UNESCO, 356 pp.

Woodbury, A.M. and R. Hardy. 1948. Studies of the desert tortoise, *Gopherus agassizii*. Ecol. Monogr. 18:145-200.

Zug, G.R. 1991. Age determination in turtles. Herpetological Circular 20:1-28.