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On Growth and Morphometrics of Leopard Tortoises, *Geochelone pardalis*, in Serengeti National Park, Tanzania, with Observations on Effects of Bushfires and Latitudinal Variation in Populations of Eastern Africa

Michael R.K. Lambert[1], Kenneth L.I. Campbell[1], and Jonathan D. Kabigumila[2]

[1]*Environmental Sciences Department, Natural Resources Institute (University of Greenwich), Central Avenue, Chatham Maritime, Chatham, Kent ME4 4TB, United Kingdom [Fax: 044-1634-880066/77; E-mail: Mike.Lambert@nri.org];*
[2]*Department of Zoology, University of Dar es Salaam, P.O. Box 35064, Dar es Salaam, Tanzania*

Abstract. – Leopard tortoises, *Geochelone pardalis*, in Serengeti National Park, Tanzania, associated with open woodland and regularly exposed to bushfires, were smaller than those in unburned areas of northeast Tanzania outside the park. Tortoises in unburned National Parks tended to be larger than those in unprotected areas. Tortoise size did not differ in cattle-grazed Masai steppe and village-settled agriculturally developed areas, possibly indicating that local people did not utilize tortoises. Serengeti tortoises bore burn-scarred carapacial scutes, and survivorship declined rapidly to zero by year 21, in contrast to those at Hargeisa, northwest Somalia, in which 50% still survived by year 25. Compared to those in northwest Somalia, and elsewhere in eastern and southern Africa, in which growth continued up to 24 yrs and greater maximum sizes were achieved, Serengeti tortoises attained a size at 12 yrs not reached until 13 and 18 yrs, respectively, by those of northwest Somalia and elsewhere. Size frequencies indicated that leopard tortoises at Hargeisa, northwest Somalia (9°30'N), tended to be larger than those in the eastern Cape Province, South Africa (32–34°S). These in turn exceeded those at latitudes of 2–4°S (northeast Tanzania) to 18°06'S (west Zimbabwe); tortoise sizes were very similar in the two latter areas. In Serengeti tortoises, the allometric relationship between carapace length (*y* in mm) and body weight (*x* in g) was $y = 1.17x^{0.35}$; weight range was 24 g – 9.9 kg. Females grew on average faster than males, achieving an asymptotic size at 12 yrs that was not reached by males until about 15 yrs, at which age the sexes were not significantly different. Assuming annual deposition of growth annuli, scute increments were greatest in both sexes during years 3-10, but there was considerable annual variation within and among individuals of the one population. Growth of the vertebral and pleural scutes in Serengeti tortoises was pyramidal (areolae on knolls). Mean annular growth did not correspond with seasonal rainfall over the range 341.1–812.3 mm. Mean Serengeti hatchling and asymptotic carapace lengths were calculated at 50 and 288 mm; the former was greater and the latter lower than corresponding values for northwest Somalia and elsewhere. Serengeti females above 210 mm plastron (240 mm calculated carapace) length became more rotund than males.

Key Words.– Reptilia; Testudines; Testudinidae; *Geochelone pardalis*; tortoise; morphometrics; growth; geographic variation; rainfall; cattle-grazed Masai steppe; village agriculture; bushfires; Serengeti National Park; Tanzania; Somalia; Zambia; Zimbabwe; South Africa

The leopard tortoise, *Geochelone pardalis* (Bell, 1828), has a range in eastern and southern Africa that stretches from southern Ethiopia, Djibouti, and northwest Somalia in the north to Cape Province, South Africa, in the south, with extensions west and northwest to Namibia and Angola (Iverson, 1992). It is the world's second largest mainland tortoise, but the size achieved varies greatly within the range. Large individuals have been recorded at northern and southern extremes (Lambert, 1995), and Wilson (1968), tabulating size-weight data in east Zambia, observed that dimensions of tortoises there were smaller than those from further south in Africa.

Recording the size of *G. pardalis* in the vicinity of Hargeisa (northwest Somalia), as well as in museum material from further south in Africa, Lambert (1995) suggested that tortoises may tend to be smaller between the Equator and Tropic of Capricorn (23°30'S). On the other hand, a dealer in Kenya, who had exported many hundreds of *G. pardalis*, reported that animals were smaller in areas of Tanzania, where tortoises had never been exploited, than just to the north in neighboring Kenya (P.C.H. Pritchard, *in litt.*). Lambert (1995) concluded that within the context of sustainable utilization, further data were required on ecological conditions normally influencing growth, size, and survivorship.

A large population of *G. pardalis* exists in Serengeti National Park, northeast Tanzania (latitude 2-3°S), which is exposed to bushfires at regular intervals. During the course of wildlife studies from 1986 to 1992, measurements were made of individual tortoises observed in the park. As a protected population, tortoises had not been utilized as food by local people, and there was no collection for the international live animal trade.

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MICHAEL R.K. LAMBERT[1], KENNETH L.I. CAMPBELL[1], AND JONATHAN D. KABIGUMILA[2]

[1]Environmental Sciences Department, Natural Resources Institute (University of Greenwich), Central Avenue, Chatham Maritime, Chatham, Kent ME4 4TB, United Kingdom [Fax: 044-1634-880066/77; E-mail: Mike.Lambert@nri.org];
[2]Department of Zoology, University of Dar es Salaam, P.O. Box 35064, Dar es Salaam, Tanzania

ABSTRACT. – Leopard tortoises, *Geochelone pardalis*, in Serengeti National Park, Tanzania, associated with open woodland and regularly exposed to bushfires, were smaller than those in unburned areas of northeast Tanzania outside the park. Tortoises in unburned National Parks tended to be larger than those in unprotected areas. Tortoise size did not differ in cattle-grazed Masai steppe and village-settled agriculturally developed areas, possibly indicating that local people did not utilize tortoises. Serengeti tortoises bore burn-scarred carapacial scutes, and survivorship declined rapidly to zero by year 21, in contrast to those at Hargeisa, northwest Somalia, in which 50% still survived by year 25. Compared to those in northwest Somalia, and elsewhere in eastern and southern Africa, in which growth continued up to 24 yrs and greater maximum sizes were achieved, Serengeti tortoises attained a size at 12 yrs not reached until 13 and 18 yrs, respectively, by those of northwest Somalia and elsewhere. Size frequencies indicated that leopard tortoises at Hargeisa, northwest Somalia (9°30'N), tended to be larger than those in the eastern Cape Province, South Africa (32–34°S). These in turn exceeded those at latitudes of 2–4°S (northeast Tanzania) to 18°06'S (west Zimbabwe); tortoise sizes were very similar in the two latter areas. In Serengeti tortoises, the allometric relationship between carapace length (y in mm) and body weight (x in g) was $y = 1.17x^{0.35}$; weight range was 24 g – 9.9 kg. Females grew on average faster than males, achieving an asymptotic size at 12 yrs that was not reached by males until about 15 yrs, at which age the sexes were not significantly different. Assuming annual deposition of growth annuli, scute increments were greatest in both sexes during years 3-10, but there was considerable annual variation within and among individuals of the one population. Growth of the vertebral and pleural scutes in Serengeti tortoises was pyramidal (areolae on knolls). Mean annular growth did not correspond with seasonal rainfall over the range 341.1–812.3 mm. Mean Serengeti hatchling and asymptotic carapace lengths were calculated at 50 and 288 mm: the former was greater and the latter lower than corresponding values for northwest Somalia and elsewhere. Serengeti females above 210 mm plastron (240 mm calculated carapace) length became more rotund than males.

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A large population of *G. pardalis* exists in Serengeti National Park, northeast Tanzania (latitude 2-3°S), which is exposed to bushfires at regular intervals. During the course of wildlife studies from 1986 to 1992, measurements were made of individual tortoises observed in the park. As a protected population, tortoises had not been utilized as food by local people, and there was no collection for the international live animal trade.

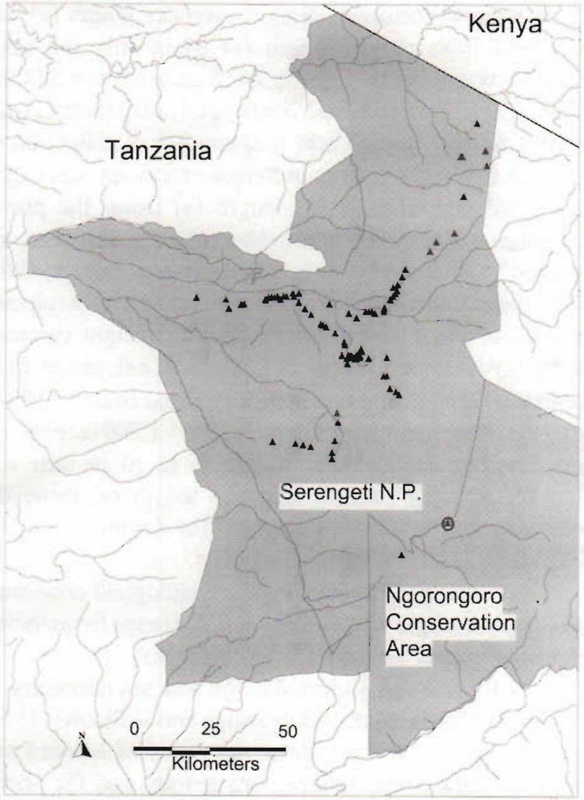

Figure 1. Serengeti National Park, Tanzania, showing open woodland locations where *Geochelone pardalis* were sighted and measured. Encircled point represents a tortoise found away from open woodland.

The objectives of the present study were to 1) test the hypothesis that tortoises in populations between the Equator and Tropic of Capricorn tended to be smaller than those north and south of these limits; 2) compare size/weight interrelationships in Serengeti tortoises, and 3) compare, in relation to the effects of bushfires and other ecological conditions, size composition, growth and survivorship (longevity) of Serengeti tortoises with those of populations elsewhere in eastern Africa.

MATERIALS AND METHODS

A total of 247 *G. pardalis* was recorded by KLIC within the confines of Serengeti National Park, Tanzania, between 3 November 1987 and 4 July 1991. Seven more were recorded in Serengeti by JDK, who also measured 430 more and weighed 387 of them elsewhere in northeast Tanzania (other national parks, cattle-grazed Masai steppe, inhabited areas with village agriculture, and animals of unknown provenance). Beside the populations of tortoises weighed during tsetse surveys in east Zambia (n = 310) by Wilson (1968), and measured and weighed in Hargeisa, northwest Somalia (n = 26) by Lambert (1995), size and weight data (n = 375 and 417, respectively) had been obtained from a population in Sengwa Wildlife Research Area, west Zimbabwe by I. Coulson (A. Hailey, *in litt.*). Such data were also included for tortoises sampled in the eastern Cape Province, South Africa (n = 109), by Burger and Branch (1994).

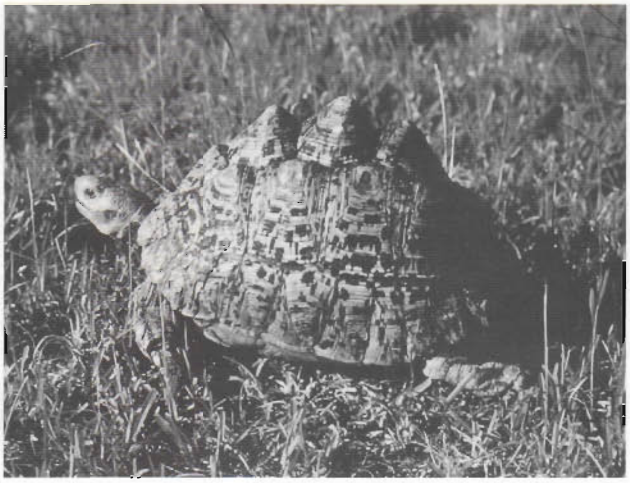

Figure 2. Adult leopard tortoise *Geochelone pardalis* in Serengeti National Park (Western Corridor) on grassland. Note pyramidal growth of vertebral and pleural scutes. Calculated carapace straight length 305 mm; 16 April 1989. Photograph by KLIC.

Distribution. — Localities in Serengeti National Park where tortoises were recorded, measured and weighed, were plotted on an outline map (Fig. 1). Tortoises were only observed after the onset of rains, and quantitative data were recorded incidental to other activities. Animals were found alongside roads and in the vicinity of buildings, or at the edges of tracks and adjacent short grass.

Rainfall and Temperature. — Monthly rainfall (mm), and monthly mean maximum (T) and minimum (t) daily temperatures (°C) were obtained from the Serengeti meteorological station at Seronera (2°26'S, 34°51'E; altitude 1554

Table 1. Rainfall (mm, showing annual total), and mean maximum T and minimum t daily temperatures (°C) during months of the year at Seronera meteorological station (altitude 1554 m), Serengeti National Park, Tanzania, 1987-91 (with averages). Figures in box represent the dry season (June – October, low level of activity/aestivation in *Geochelone pardalis*). * Annual rainfall range: 512.2–1167.8 mm.

Year		Annual Rainfall	J	F	M	A	M	J	J	A	S	O	N	D
1987		634.0	60.3	29.0	169.0	92.5	56.5	35.8	3.8	0.8	23.8	12.5	140.0	11.2
1988		941.6	231.0	14.7	98.5	280.0	14.4	23.0	14.4	72.6	31.5	63.7	19.6	78.7
1989		1051.9	145.0	119.0	163.0	126.0	131.0	13.8	11.0	25.2	104.0	3.8	57.4	153.0
1990		830.4	45.1	148.0	117.0	180.0	95.7	4.8	0.0	50.7	34.9	35.9	40.7	77.4
1991		675.5	98.6	33.1	138.0	132.0	68.8	90.0	0.0	3.7	10.8	69.9	4.1	26.6
Average (1961-93)		818.9*	89.5	83.8	102.4	128.5	81.2	34.0	15.5	25.7	40.7	42.2	79.3	86.3
Average Temperature (1981-90)	Max T°C		27.5	28.4	28.2	27.4	27.1	27.4	28.4	28.7	28.7	29.2	27.9	28.0
	Min t°C		15.9	15.6	16.6	16.2	15.0	13.5	13.2	14.0	14.8	16.0	16.2	16.0
	Difference		11.6	12.8	11.6	11.2	12.1	13.9	15.2	14.7	13.9	13.2	11.7	12.0

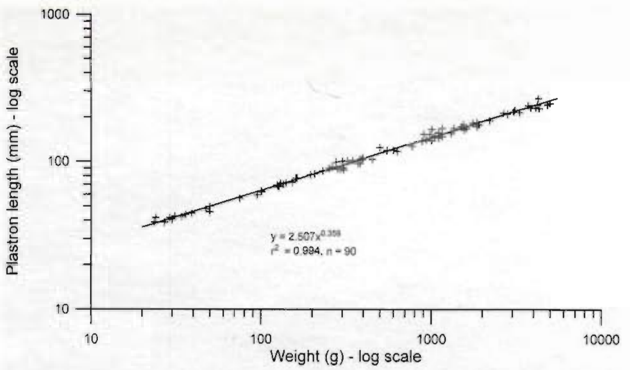

Figure 3. Allometric relationship between body weight under 5 kg (x) and plastron length (y) for *Geochelone pardalis* in Serengeti National Park, Tanzania.

m) during the years of the study (1987–91), together with average values for rainfall and temperature, respectively, covering the periods 1961–93 and 1981–90 (Table 1). Annual rainfall range was 634.0–1051.9 mm (1987–91), indicating marked annual fluctuation; monthly mean maximum and minimum daily air temperatures varied very little from year to year, and indeed there was little variation even between months, especially for maxima, with average values 27.1–29.2°C (minima, 13.2–16.6°C). Overall, the data indicated that the dry season, or period of lowest rainfall, was from June to October; the difference between T and t was higher than at other months of the year.

Monthly rainfall data (Table 1) indicated that the annual dual wet season pattern of short and long rains, described elsewhere in northern Tanzania by Norton-Griffiths et al. (1975), was on average weakly developed in the Seronera area of Serengeti National Park. Green vegetation therefore prevailed from November to June.

Measurements. — In Serengeti, tortoises up to 5.0 kg were weighed to the nearest g using an electronic balance. Whenever possible, tortoises were weighed as soon as found since defecation and urination usually results from prolonged handling of animals found in the field. Straight line measurements on tortoises were made with steel vernier calipers up to 17 cm, and larger individuals with a steel tape to approximately 5 mm accuracy, using flat surfaces when possible. The pleural, and especially the vertebral scutes, grew pyramidally to form humps, and areolae were elevated on knolls (Fig. 2). Measurements (in mm) included midline plastron length (gular notch to anal notch), plastron width (between plastral margins at the pectoral–abdominal suture), midline distance between gular notch and anal–femoral suture, and shell height. Weights of tortoises over 5 kg were calculated from the power regression between weight (x in g) and plastron length (y in mm) in measured animals (Fig. 3). Straight carapace length (x in mm) was calculated from plastron length (y) using the linear regression $y = 0.884x - 1.709$ derived from measurements for immature Hargeisa tortoises and animals elsewhere by Lambert (1995). Widths of the growth annuli, starting with the most recent, and areola of the right femoral scute were also measured (Fig. 4). Scute nomenclature is based on that of Ernst and Barbour (1989).

In Sengwa tortoises, straight carapace length (y) was calculated from curved length (x) when only the latter character was measured, using the regression $y = 2.000 + 0.747x$ ($r^2 = 0.994$; $n = 66$) derived by A. Hailey (*in litt.*) from a series of both parameters measured in a collection of specimens. Weight (x in g) in Sengwa tortoises was calculated from curved carapace length (y) using the power regression $y = 19.614x^{0.360}$ based on tortoises measured and weighed by Wilson (1968) in east Zambia (Lambert, 1995; Wilson only measured curved carapace length in 48 selected tortoises of the 310 that he weighed}. Straight carapace length (x) in eastern Cape tortoises was calculated from plastron length (y) measured by Burger and Branch (1994), using the isometric regression $y = 0.884x - 1.709$ (see above) from Lambert (1995), and weight (x in g) in turn was extrapolated from straight carapace length (y) using the regression $y = 14.822x^{0.350}$ calculated for Zambian tortoises by Lambert (1995).

Since weight fluctuates with physiological condition, and carapace length was also required for range frequencies, calculated values were deemed to be useful since absolute accuracy for frequency classification was not necessary.

Sex Determination. — Loveridge and Williams (1957) had difficulty in distinguishing the sexes of leopard tortoises; in their view, relative tail length was the surest character (males longer). In addition, but less distinguish-

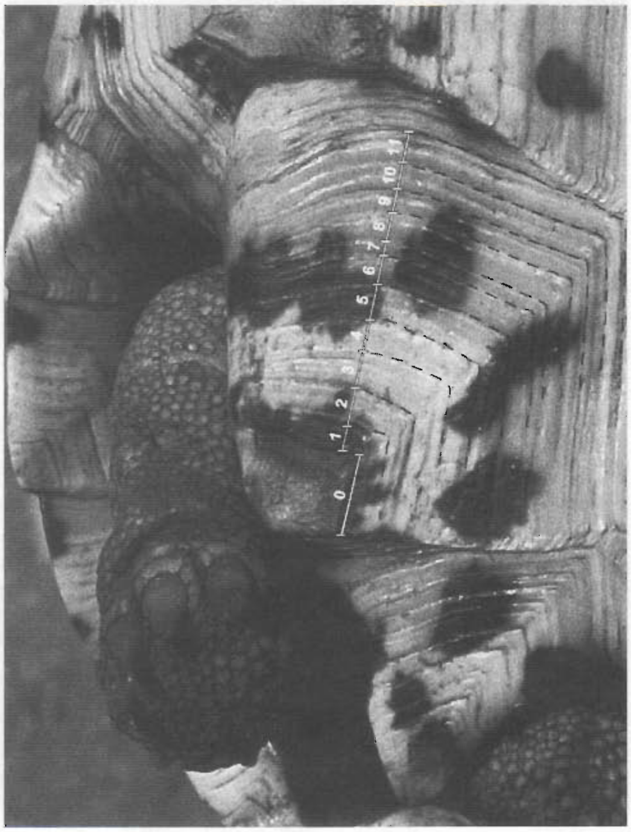

Figure 4. Annular measurements on right femoral scute of *Geochelone pardalis* (female) in Serengeti National Park, Tanzania. Note that dry-season grooves between annuli tend to be deeper than intermediate grooves. Femoral scute length 44 mm; 5 May 1990. Photograph by KLIC.

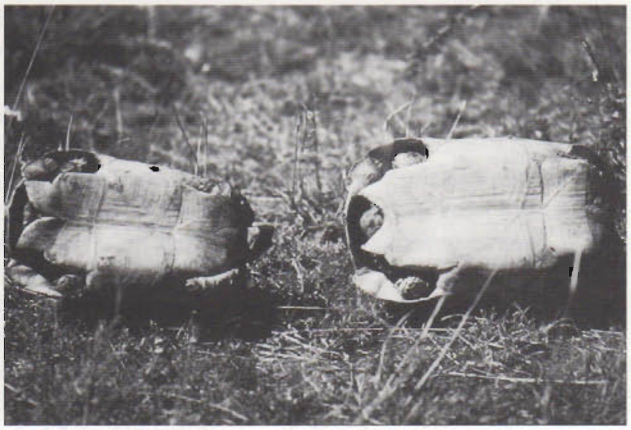

Figure 5. Ventral view of male (left) and female (right) *Geochelone pardalis* that had been observed copulating in Serengeti National Park. Note divergent anal scutes and V-shaped anal notch in male, and U-shaped anal notch and anal scutes directed to the rear in female. Male and female plastron lengths 155 and 190 mm, respectively. Tortoises are leaning laterally (towards photographer) due to knoll formation on the apex of the carapace from pyramidal growth of vertebral scutes; 28 November 1986. Photograph by KLIC.

ing, they noted in males that the posterior third of the plastron showed a slight concavity and the lower sides of the carapace were invariably almost vertical. Lambert (1995) observed that males were more elongate in dorsal outline than females. In combination with these secondary sexual characteristics, the main character used for Serengeti tortoises by KLIC was the angled (V-shaped) anal notch, with anal scute apices tending to diverge laterally as males

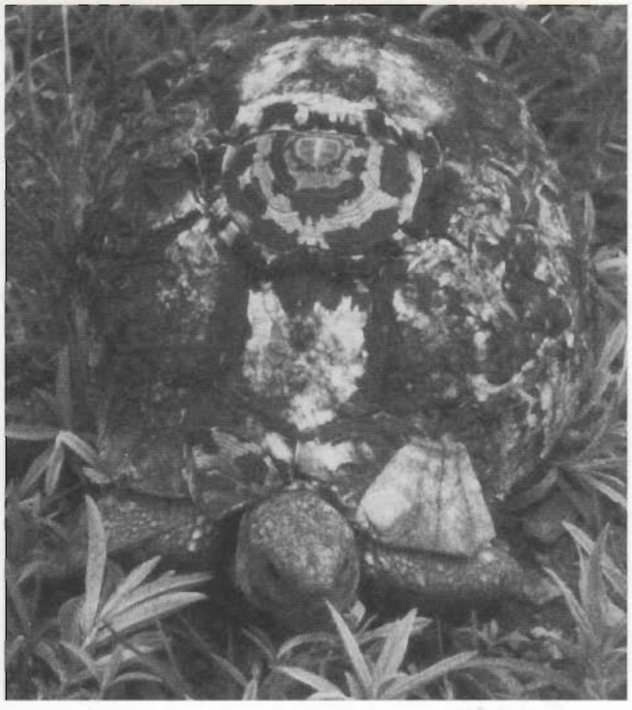

Figure 6. Anterior view of a male *Geochelone pardalis* damaged by bushfire in Serengeti National Park. Only part of the right first marginal, the whole 2nd vertebral, and anterior part of the 3rd vertebral scutes remain unburned. Plastron width 181 mm (calculated carapace straight length 278 mm); 4 January 1987. Photograph by KLIC.

increased in size, versus a recurved (U-shaped) notch in females with anal scute apices directed to the rear (Fig. 5).

Age Assessment. — Age of 163 Serengeti tortoises (66%) was estimated from the number of clearly defined growth annuli on the right femoral scute surface. Some judgement was necessary to differentiate intermediate mid-seasonal from annual wet season annuli, especially when recently deposited (Fig. 4). Interpretation of annual dry season grooves between wet season annuli was facilitated by running a finger nail along the grooves to the point where they angled with those running parallel to the midline suture. After two or three years, shallower mid-seasonal grooves tended to be abraded smooth rendering the deeper annual dry-season grooves between yearly annuli more easily visible. Since annular widths were measured by the same observer, interpretation error was a factor common to each. Error was estimated to be within 5 to 10%.

RESULTS

Distribution. — The distribution of tortoises found in Serengeti National Park in relation to river flood courses (Fig. 1) was associated with open woodland. One of two individuals in adjacent Ngorongoro Conservation Area was found on the plain.

Many Serengeti tortoises showed signs of having been in bushfires with most of the carapacial scutes burned or scarred (Fig. 6).

Size. — In Serengeti tortoises, the regression between midline plastron length (x in mm) and shell height (y in mm) was given by $y = 0.655x + 1.748$ ($r^2 = 0.970$; $n = 88$). Maximum plastron length recorded at Serengeti was 335 mm (maximum calculated carapace length 381 mm). Shell height was relatively greater in large, old individuals (plastron length above 250 mm) than smaller ones (Fig. 7A),

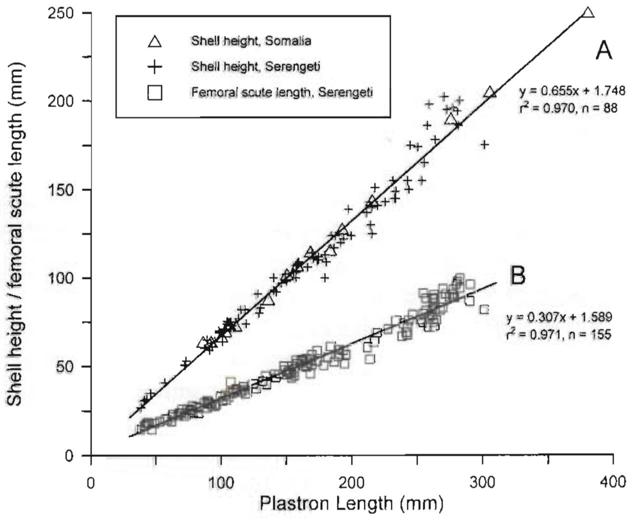

Figure 7. Relationships for *Geochelone pardalis* in Serengeti National Park, Tanzania, between plastron length (x) and (A) shell height (y) - data for Somalia from Lanza and Sassi (1966) shown for comparison - and (B) femoral scute length (y).

Table 2. Size composition (%) of *Geochelone pardalis* in different populations and latitudes.

Location (latitude)	n	Carapace straight length (mm) < 200	200-299	300-399	400-499	500-599	600-699
Hargeisa, Somalia[1] (9°30'N)	26	3.8	23.1	15.4	3.8	15.4	7.7
Northeast Tanzania (2-4°S)	684	50.9	35.7	13.0	0.4	0	0
Sengwa, Zimbabwe[2] (18°06'S)	375	48.8	36.5	13.9	0.8	0	0
Eastern Cape Province, South Africa[3] (32-34°S)	109	35.8	18.3	24.8	20.2	0.9	0

References: [1]Lambert (1995); [2]from I. Coulson (A. Hailey, *in litt.*); [3]from Burger and Branch (1994)

because pyramidal growth of vertebral scutes elevated the areolae, that of the 2nd being the highest. The slope for the isometric relationship was therefore greater than that in eastern Cape tortoises (South Africa) measured by Burger and Branch (1994) in which the regression was given by $y = 0.575x + 6.130$ ($r^2 = 0.993$; $n = 23$). For tortoises measured in Somalia by Lanza and Sassi (1966), the regression was very similar to that for Serengeti animals: $y = 0.657x + 2.763$ ($r^2 = 0.997$; $n = 18$) (Fig. 7A). Maximum plastron length was 380 mm (maximum carapace length 432 mm). Maximum plastron length recorded in Hargeisa (northwest Somalia) tortoises by Lambert (1995) was 559 mm (maximum carapace length 654 mm).

The relationship between plastron length (x) and femoral scute length (y in mm), whose annular measurements were used to record growth, was determined (Fig. 7B), and found to be isometric: $y = 0.304x + 2.238$ ($r^2 = 0.962$; $n = 160$).

Weight. — The relationship between weight (x in g, up to 5000) and plastron length (y) was allometric ($\log_{10} \times \log_{10}$) (Fig. 3), and $y = 2.507x^{0.359}$ ($r^2 = 0.994$; $n = 90$) was used for calculations. The lightest tortoise weighed 24 g, and calculated body weight of the largest tortoise from plastron length (335 mm) was 9.95 kg. The regressions found by Kabigumila (1995) for females and males of northeast Tanzania outside Serengeti were respectively $y = 12.677x^{0.349}$ and $y = 15.668x^{0.327}$ (differences not significant), which were somewhat lower than for those inside the National Park. For straight carapace length (y), calculated from flat-surface measured plastron length (see above), the power regression with weight (x) was $y = 1.167x^{0.352}$. This was similar to that for east Zambian tortoises of $y = 14.822x^{0.350}$, but was lower than those of Hargeisa, northwest Somalia, at $y = 10.486x^{0.399}$ determined by Lambert (1995), and somewhat lower than those found by Kabigumila (1995) for females and males, respectively, of northeast Tanzania outside Serengeti of $y = 11.749x^{0.377}$ and $y = 14.090x^{0.358}$ (males again not significantly different from females).

Size Structure. — Carapace lengths of tortoises from the northernmost population at Hargeisa, northwest Somalia (Table 2), tended to be greater than those of animals in eastern Cape Province, South Africa ($\chi^2 = 57.4$, d.f. = 4, $p < 0.001$), although the occasional Cape individual may achieve comparable maximum size. The eastern Cape tortoises in turn were significantly larger than those in either Sengwa, west Zimbabwe ($\chi^2 = 77.4$, d.f. = 3, $p < 0.001$), or northeast Tanzania ($\chi^2 = 136.5$, d.f. = 3, $p < 0.001$), two populations between the Equator and Tropic of Capricorn whose carapace length frequencies were strikingly similar ($r^2 = 0.998$; $n = 5$). Sengwa tortoises (not exposed to bushfires) tended to be larger ($\chi^2 = 7.3$, d.f. = 2, $p < 0.05$) than those exposed to bushfires in Serengeti (Table 3), but they were significantly smaller than those in unburned areas of northeast Tanzania ($\chi^2 = 12.4$, d.f. = 3, $p < 0.01$; $n = 178$), especially those inside unburned national parks ($\chi^2 = 13.8$, d.f. = 3, $p < 0.005$; $n = 43$).

Size frequencies of tortoises in Tarangire and Lake Manyara National Parks were not significantly different (Table 3). Combined, size tended to be significantly larger than in unprotected areas ($\chi^2 = 5.3$, d.f. = 2, $p < 0.05$) and in Serengeti National Park ($\chi^2 = 30.0$, d.f. = 2, $p < 0.001$).

Size frequencies of tortoises in human-occupied and cattle-grazed unprotected areas were not significantly different. Combined, their sizes also tended to be significantly larger than those in Serengeti National Park ($\chi^2 = 17.7$, d.f. = 2, $p < 0.001$), but smaller than those in unburned protected areas.

Body weight is a less reliable indicator of size than carapace straight length, in that it fluctuates with physiological condition of the tortoises associated with activity and food availability at different times of the year. Furthermore, weight is only available from live or freshly dead tortoises. However, only weight frequencies were available for all tortoises in east Zambia (east of the Luangwa River) whose latitudinal range was between those of northeast Tanzania

Table 3. Carapace length frequency (%) of *Geochelone pardalis* in different populations and habitat conditions of northeast Tanzania. Frequencies of tortoises in Sengwa Wildlife Research Area, west Zimbabwe, not significantly different from those in northeast Tanzania, are included for direct comparison.

Provenance - conditions	n	Carapace Length (mm) Frequency (%) < 200	200-299	300-399	400-499
National Parks - protected areas - totals	297	54.5	31.0	14.1	0.3
Serengeti - frequent bushfires	254	60.3	28.7	11.0	0
Tarangire - few bushfires	20	20.0	40.0	35.0	5.0
Lake Manyara - no bushfires	23	21.7	47.8	30.5	0
Unburned National Parks - totals	43	20.9	44.2	32.6	2.3
Unprotected Areas - totals	135	37.0	44.4	18.6	0
Inhabited - village agriculture - good rainfall	93	36.6	43.0	20.4	0
Cattle-grazed - Masai steppe - poor rainfall	42	38.1	47.6	14.3	0
Sengwa Wildlife Research Area, west Zimbabwe - protected area[1]	375	48.8	36.5	13.9	0.8

[1]from I. Coulson (A. Hailey, *in litt.*)

Table 4. Weight composition (%) of *Geochelone pardalis* in different populations and latitudes. Body weight (kg) for unweighed tortoises was calculated from regressions with straight carapace length (Hargeisa, northwest Somalia), plastron length (Serengeti National Park, northeast Tanzania), straight carapace length calculated from plastron length (eastern Cape Province, South Africa) and curved carapace length (Sengwa, west Zimbabwe).

Location (latitude)	*n*	Body Weight (kg) frequency (%) <5	5-9	10-14	15-19	20-24	25-29	30-34	35-39
Hargeisa, Somalia[1] (9°30'N)	26	26.9	11.5	7.7	7.7	23.1	15.4	7.7	0
Northeast Tanzania (2-4°S)	641	88.1	11.4	0.5	0	0	0	0	0
East Zambia[2] (13-14°S)	310	44.2	49.0	6.8	0	0	0	0	0
Sengwa, west Zimbabwe[3] (18°06'S)	417	88.5	11.0	0.5	0	0	0	0	0
Eastern Cape Province, South Africa[4] (32-34°S)	109	53.2	15.6	20.2	10.1	0	0	0	0.9

References: [1]Lambert (1995); [2]from Wilson (1968); [3]after I. Coulson (A. Hailey, *in litt.*); [4]from Burger and Branch (1994)

and Sengwa in west Zimbabwe (Table 4). The east Zambian tortoises weighed by Wilson (1968) had already been shown to be smaller than those of Hargeisa, northwest Somalia, by Lambert (1995). Numbers indicated that they were also for the most part smaller than those of eastern Cape Province, South Africa ($\chi^2 = 40.1, p < 0.001$). East Zambian tortoises were also for the most part larger than those of populations in both northeast Tanzania ($\chi^2 = 35.8, p < 0.001$) and Sengwa, west Zimbabwe ($\chi^2 = 162.8, p < 0.001$), weight frequencies in these latter two being strikingly similar and therefore significantly correlated ($r^2 = 0.999$; $n = 4$). Small tortoises in east Zambia were, however, relatively poorly represented, the result probably of sampling bias (Wilson, 1968).

Table 5. Weight (kg) composition (%) of *Geochelone pardalis* in different populations and habitat conditions of northeast Tanzania. Frequencies of tortoises in Sengwa Wildlife Research Area, west Zimbabwe, are included for direct comparison since they were strikingly similar.

Provenance - conditions	*n*	Body Weight (kg) Frequency (%) <2	2-3	4-5	6-7	8-9	10-11
National Parks - protected areas							
Serengeti - bushfires	254	62.6	14.6	18.1	3.9	0.8	0
Tarangire and Lake Manyara - no bushfires	24	25.0	41.7	16.7	0	4.2	12.4
Unprotected Areas - totals	127	41.7	35.5	7.9	10.2	4.7	0
Inhabited - village agriculture - good rainfall	88	39.8	34.1	7.9	12.5	5.7	0
Cattle-grazed - Masai steppe - poor rainfall	39	46.1	38.5	7.7	5.1	2.6	0
Sengwa Wildlife Research Area, west Zimbabwe - protected area[1]	417	54.9	26.9	5.0	4.6	0.7	0.5

[1]from I. Coulson (A. Hailey, *in litt.*)

Table 6. Age composition (%) of *Geochelone pardalis* compared between Hargeisa area, northwest Somalia, and Serengeti, northeast Tanzania. Mean annual frequency up to 19 yrs = 2.4% for Hargeisa and 5.2% for Serengeti.

Location (latitude)	*n*	Growth annuli (approx. age in years) < 5	5-9	10-14	15-19	20+
Hargeisa (9°30'N)[1]	26	0	7.7	30.8	7.7	53.8
Serengeti (2-3°S)	180	45.6	28.3	22.2	3.3	0.6

[1]From Lambert (1995)

Weight and carapace length of Serengeti tortoises exposed to bushfires tended to be lower than those in nearby unburned national parks (Table 5) when numbers above and below 2 kg were compared ($\chi^2 = 1.3, p < 0.001$) (in unweighed tortoises, weight was calculated from the regression with plastron length). Tortoises in the unburned park areas were not significantly heavier than those in unprotected areas outside national parks, nor was there any significant difference between frequencies of tortoises above and below 2 kg in inhabited agricultural and cattle-grazed Masai steppe areas.

Serengeti tortoises also tended to be smaller than those in Sengwa Wildlife Research Area, west Zimbabwe ($\chi^2 = 4.3, p < 0.05$), which in turn tended to be smaller than those in unburned areas both inside ($\chi^2 = 6.8, p < 0.01$) and outside ($\chi^2 = 6.3, p < 0.025$) national parks of northeast Tanzania.

Age Structure. — Tortoises in the Serengeti population were, on average, much younger than those in Hargeisa (Table 6) aged by Lambert (1995), and the numbers of tortoises above and below 10 yrs of age were significantly different ($\chi^2 = 41.2, p < 0.001$). Only one (< 1%) of the age-estimated Serengeti tortoises had achieved 20 yrs.

Survivorship. — Age determination of Serengeti tortoises enabled survivorship of males and females to be compared (Fig. 8). There was little difference between the sexes.

Survivorship of all Serengeti tortoises was compared with that of Hargeisa animals (Fig. 9) aged by Lambert (1995). The Hargeisa sample was small, based mostly on large individuals (none less than 9 yrs old) sighted in the field during the latter part of the dry season (when smaller ones

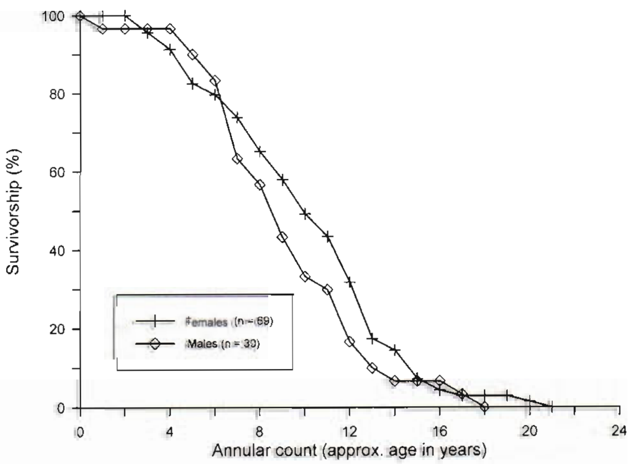

Figure 8. Survivorship curves (%) comparing male and female *Geochelone pardalis* in Serengeti National Park.

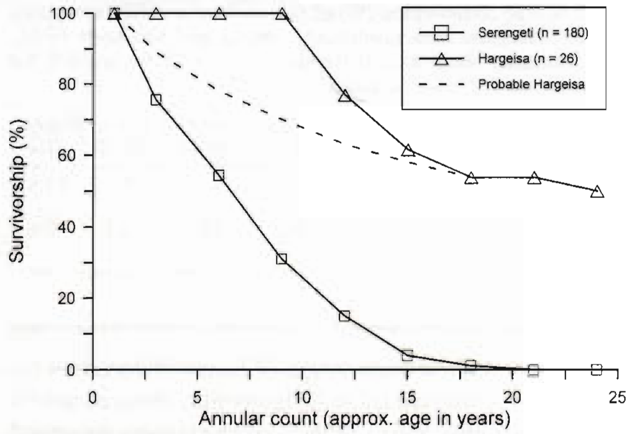

Figure 9. Survivorship curves (%) comparing *Geochelone pardalis* in Serengeti National Park and Hargeisa, northwest Somalia (probable curve indicated).

were probably hiding), but compared to Serengeti tortoises, survivorship was high.

Growth. — Mean increments of femoral scute annuli indicated that on average females grew faster than males (Fig. 10A), with most rapid linear growth in both sexes during years 3-10. Growth increased from year 1 and declined after year 11, especially in females (Fig. 10B). Even though tortoises were from within the same general population in Serengeti National Park, annual increments varied greatly within and among individual tortoises. Mean increments of the sexes at each annular count were not significantly different.

Cumulative annular anterior length of the right femoral scute was used as a measurable record of external growth. Growth was faster in females than males and appeared to have ceased by the time the 12th, approximately yearly, annulus had been deposited (Fig. 10B). In males, growth ceased by about the 15th annulus. Tortoises of both sexes had therefore apparently reached maximum sizes by then. Mean femoral scute lengths of the sexes at each annular count were not significantly different.

Right femoral scute length reached in asymptotic tortoises after the last complete (penultimate) annulus had been deposited was compared in the sexes. Mean femoral scute length from year 12 ($n = 12$) and 15 ($n = 2$) in respectively females and males (Fig. 10B) was 84.01 (S.D. 8.33) and 71.10 (S.D. 5.37) mm. The sample of asymptotic male tortoises was small, but the difference between means was not significant ($t = 0.42$, d.f. = 12). As in full-grown tortoises of Hargeisa, northwest Somalia (Lambert, 1995), the size achieved by full-grown females and males therefore appeared to be similar, despite the slower growth rate of the latter.

The number of animals bearing further annuli after year 11 also declined (Fig. 10), and taking into account the relatively rapid decrease in survivorship to zero by year 21 (Fig. 9), this additionally suggested that relatively few tortoises were surviving to reach greater ages.

Plastron length was a character measured in both Serengeti tortoises and in those from northwest Somalia and elsewhere in eastern and southern Africa by Lambert (1995).

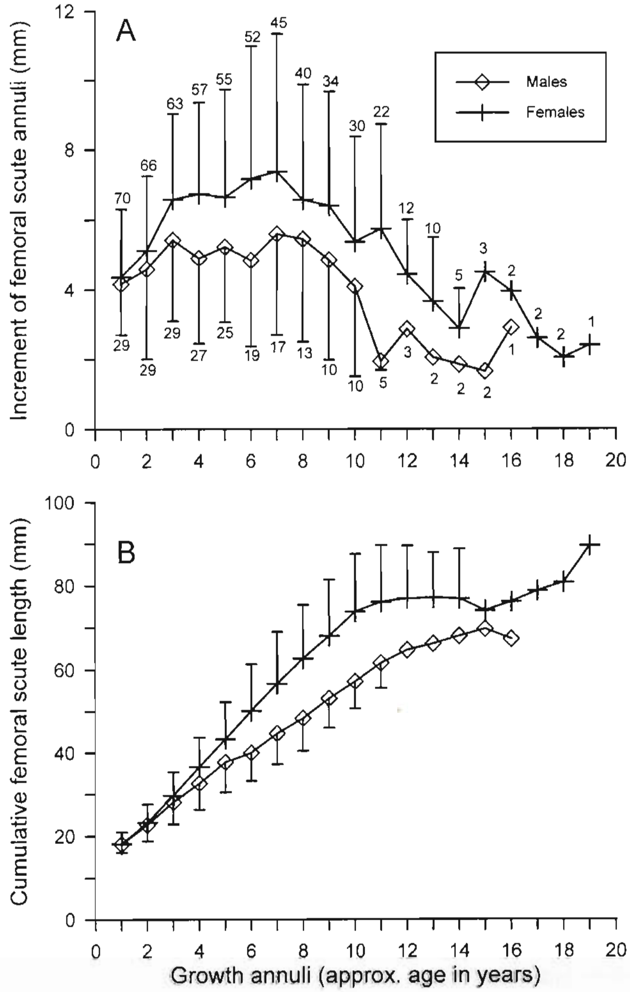

Figure 10. Annular growth of right femoral scute corresponding with age in *Geochelone pardalis* of Serengeti National Park, Tanzania. The last mid-seasonal (incomplete) annulus is excluded. None of the annular means for the sexes were significantly different. **(A)** Growth increments — means and standard deviations (bar lines) based on five or more values (indicated); **(B)** Cumulative incremental external growth (bar line values and symbols as in A).

The relationship with femoral scute length in Serengeti tortoises (Fig. 7B) was isometric. The similarly isometric relationship of 3rd vertebral scute width (y) with plastron length (x) for animals in northwest Somalia and elsewhere measured by Lambert (1995) was $y = 0.356x + 13.956$ ($r^2 = 0.847$; $n = 78$). Mean plastron length (x) was thus calculated as a character common to all three populations, and used for direct comparison to demonstrate that growth was at a greater rate, and asymptotic size reached earlier, in Serengeti tortoises (sexes combined) than in animals elsewhere (Fig. 11).

The asymptotic mean size of Serengeti tortoises, reached at 12 yrs (248 mm plastron length), was not reached until 13 yrs in northwest Somalia or 18 yrs by tortoises elsewhere in eastern and southern Africa. Maximum mean carapace length, calculated from plastron length, using the regression equation above, was thus 288 mm in Serengeti tortoises, while means of measured values were 597 and 414 mm in tortoises of northwest Somalia and elsewhere, respectively (Lambert, 1995). Mean hatchling plastron length in Serengeti tortoises

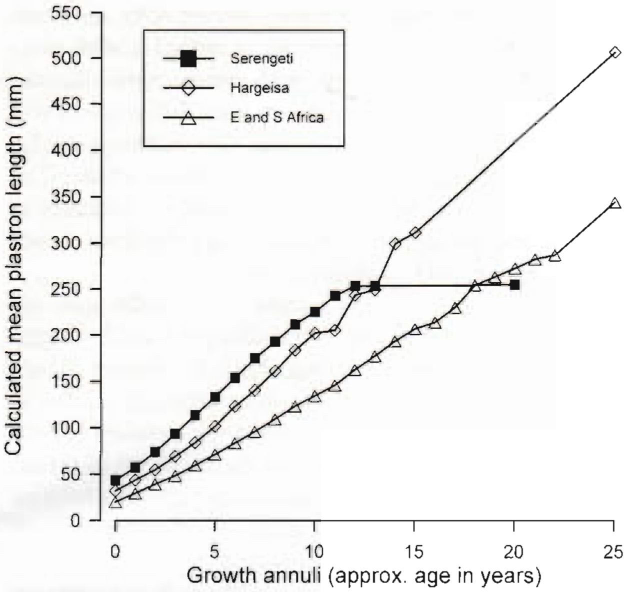

Figure 11. Calculated mean plastron length and age in *Geochelone pardalis*. Growth rates for Serengeti, Hargeisa (northwest Somalia), and elsewhere in eastern and southern Africa are compared. Mean plastron length calculated from femoral scute length (Serengeti) or 3rd vertebral scute width (northwest Somalia and elsewhere). Maximum mean (asymptotic) carapace length, calculated from plastron length, was, respectively, 288, 575, and 392 mm in Serengeti, northwest Somalia, and elsewhere; mean hatchling carapace lengths were, respectively, 50, 38, and 25 mm.

was similarly calculated at 44 mm, which was within the standard deviation of mean measured plastron length at year 0 ($n = 6$) of 45.5 ± 3.2 mm. The equivalent carapace length of 50 mm was in contrast to that of 45 and 31 mm, calculated from mean areolar width of the 3rd vertebral scute, in tortoises from northwest Somalia and elsewhere in eastern and southern Africa, respectively (Lambert, 1995). Although not tested statistically, since mean calculated plastron lengths were derived from different shell characters, this implied that mean size of Serengeti hatchlings was greater than in the others, despite the smaller adult size.

Growth increments of femoral scute annuli in individuals varied from year to year. Annual increments of tortoises within a 5 km radius of the meteorological station at Seronera ($n = 68$) were plotted graphically against wet season rainfall (November – June) for the years 1971–89 (Fig. 12). Mean yearly increment was not significantly correlated with rainfall over the range 341.1–812.3 mm, implying that over this range, sufficient green vegetation was available as food.

Sexual Dimorphism. — Females with plastron length over 210 mm (calculated carapace length 240 mm) were more rotund than males (Fig. 13A); males were therefore were more elongate. Since rear aperture shape and dimensions were sexually dimorphic in adults (Lambert, 1995), sexual differentiation of midline anal scute length was investigated in Serengeti tortoises. The relationship with plastron length was weak (Fig. 13B), and regression slopes for the sexes not significantly different.

Sexual Size Composition. — Plastron length frequencies indicated that female tortoises tended to be larger than males ($\chi^2 = 42.7$, d.f. = 4, $p < 0.001$) in the Serengeti National Park population (Table 7). Males and females peaked in the 150–199 and 250–299 mm ranges, respectively.

Sex Ratio. — A total of 163 tortoises was sexed in Serengeti National Park. The male:female ratio was 1:1.91.

DISCUSSION

Although the largest individual *G. pardalis* have been recorded at latitudes 32–34°S in South Africa's eastern Cape Province (Branch et al., 1990), size and weight frequencies indicated that tortoises near Hargeisa, northwest Somalia (9°30'N), tended to be of the greatest average size. Frequencies also demonstrated that eastern Cape tortoises in turn tended to be larger than those further north in west Zimbabwe (18°06'S), east Zambia (13–14°S) and northeast Tanzania (2–4°S). Thus, as proposed by Lambert (1995), *G. pardalis* in mid-range populations between the Equator and Tropic of Capricorn (23°30'S) did indeed tend to be smaller than those at northern and southern extremes. Likewise, in South America, as already discussed by Lambert (1995), *Chelonoidis carbonaria* tended to be smaller at the southern end of its range (Pritchard and Trebbau, 1984), and *C. chilensis* in Argentina smaller towards the Equator at the northern end of its range (Ernst and Barbour, 1989).

The reason for latitudinal size variation is probably climatic, with increased insolation associated with higher temperatures towards the Equator tending to favor smaller animals. Smaller animals are likely to be more mobile than larger ones, and can therefore move more promptly into shaded areas for purposes of thermoregulation, and can also find deep shade under bushes and inside clumps of vegetation that may not be able to accomodate large tortoises as readily. Small tortoises are therefore more able to avoid overheating than large ones. Furthermore, in the case of *G. pardalis*, the climate north of the Kenyan Highlands, which straddle the Equator, is more xeric than in the south. However, Archer (1948) reported considerable size variation of

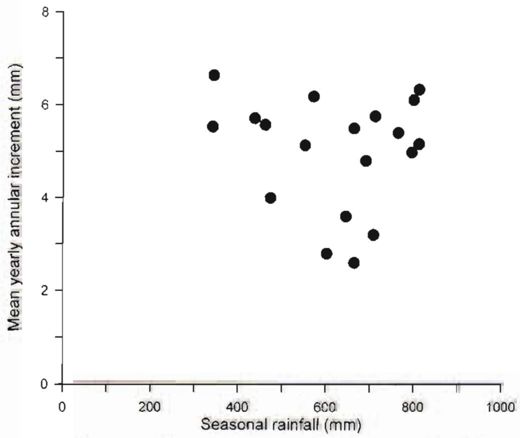

Figure 12. Mean yearly annular growth increments (after year 1) of right femoral scute in *Geochelone pardalis* and seasonal rainfall. Tortoises ($n = 68$) from within 5 km of Seronera meteorological station, Serengeti National Park, Tanzania. Standard deviations (range 1.4–3.9 mm), based on five or more individuals, are excluded for purposes of visual clarity.

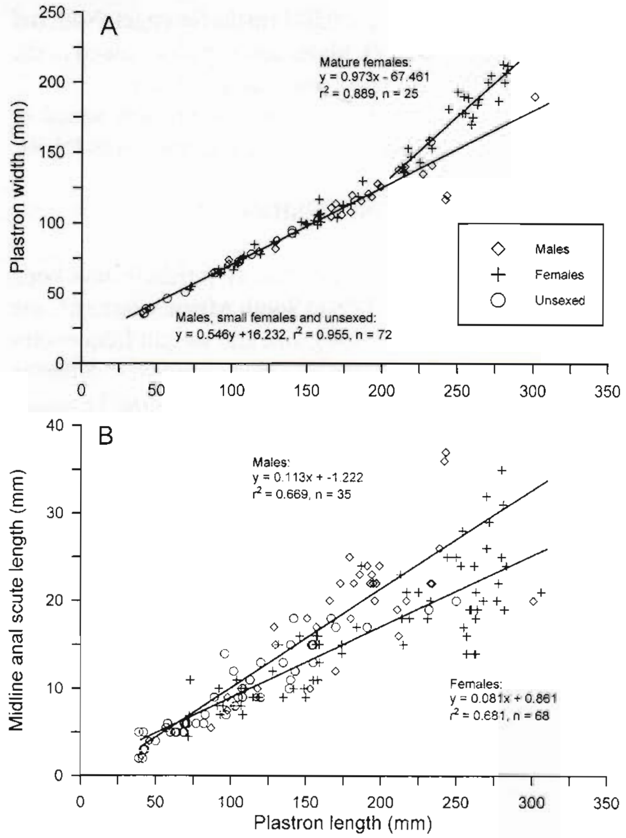

Figure 13. Relationships for *Geochelone pardalis* in Serengeti National Park, Tanzania, between plastron length (x) and **(A)** plastron width (y) and **(B)** midline anal scute length (y), weakly differentiating males and females (symbols as in A).

G. pardalis in populations even within South Africa, and a dealer who had collected tortoises in Kenya for export reported that adult size of tortoises in unexploited populations just to the south in Tanzania were smaller than those found in neighboring Kenya (P.C.H. Pritchard, *in litt.*, in Lambert, 1995). Lambert (1995) implied that ecological factors influencing size were likely to be complex. They were not just based on temperature and seasonal rainfall pattern alone, nor did they simply reflect levels of utilization from harvesting as food by local people (Wilson, 1968) or collection for the international live animal trade.

The size achieved by tortoises varies not only with ecological conditions, but also between species. In Africa, tortoises in the northern half of the continent range from the size of *Testudo kleinmanni*, which, with average adult length of 100 mm (200 g weight), is among the world's smallest tortoises (Stubbs, 1989), to that of *Geochelone sulcata*, the world's largest mainland species, achieving a length of 830 mm and over 100 kg in weight (Broadley, 1989). The two species live in the "sahel" fringing, respectively, the north and south of the Sahara Desert (mean annual rainfall 100–400 mm and 100–1000 mm), with similar xeric climatic conditions. The reasons for the very great difference in size between these two species is unclear. *Geochelone pardalis*, although a large mainland species, is somewhat smaller than *G. sulcata*. However, the large *G. pardalis* tortoises at Hargeisa and the largest ones in the Cape Province, South Africa, approached *G. sulcata* in size.

Fully-grown male and female *G. pardalis* were recorded to be similar in size in both Hargeisa and Serengeti populations, suggesting that courtship preliminaries did not involve combat between males with an advantage conferred on larger males. On the other hand, larger tortoises of both sexes would be more immune from the attentions of predators, and so size in leopard tortoises was perhaps a balance between the needs for thermoregulation and immunity from predation.

Tortoise size corresponds generally with age, and size frequencies in a population reflect selective ecological pressures to which tortoises may be subjected for the duration of their lives. The effects of these pressures are probably different in hatchlings and large adults. Tortoises in general are peculiarly unable to move away rapidly from an unfavorable area, although they may emigrate, or, depending on size, migrate seasonally over relatively small distances of some tens or hundreds of meters during a period of several days. *Geochelone pardalis* maintains a relatively small home range (Weatherby, 1995). With such site fidelity, tortoises must have the capacity to withstand climatic variation and resist other factors, or perish. The rigid shell of land tortoises enables adults to withstand predation from a variety of raptors and carnivores.

The effects of removing tortoises from a population episodically or at regular intervals, especially when of a particular age or over a specific size range, will be reflected by altered size frequencies of the animals remaining, although individual tortoises will continue to grow over a period of years. Moreover, assuming high primary production and other favorable ecological conditions allowing unimpeded growth, large tortoises of great age will only be present in significant numbers in populations that have for a long time remained relatively undisturbed from wildlife and human predation, and bushfires or other natural catastrophes.

Size frequencies of *G. pardalis* in Sengwa Wildlife Research Area (west Zimbabwe) and in northeast Tanzania generally were very similar. Sengwa tortoises tended to larger than tortoises in the population of Serengeti National Park regularly exposed to bushfires and probably jackal and hyena predation, but smaller than those in unburned areas of northeast Tanzania, especially in pristine, or only occasionally burned national parks elsewhere. These latter tortoises in turn tended to be larger than in unprotected areas that were also unburned. Thus, the pressure of regular bushfires on the tortoise population in Serengeti may have resulted in animals that were smaller than outside the park: even smaller

Table 7. Size frequency (%) compared in male and female *Geochelone pardalis* (median ranges in bold type) from Serengeti National Park, northeast Tanzania.

		Plastron Length (mm) Frequency (%)						
Sex	n	<50	50-99	100-149	150-199	200-249	250-299	300-349
Males	56	0	8.9	10.7	**57.2**	21.4	0	1.8
Females	107	0	9.3	16.8	15.0	15.0	**41.1**	2.8

than those in unprotected inhabited agricultural and cattle-grazed Masai steppe areas.

The similarity of size frequencies of tortoises in inhabited and largely uninhabited cattle-grazed areas of northeast Tanzania also suggested that tortoises were not utilized by local people as indicated by P.C.H. Pritchard (*in litt.*).

As a result of many tortoises succumbing to regular bushfires, tortoises in the Serengeti population were very much younger than those of Hargeisa, Somalia, many of which were old (25 or more yrs) with carapacial surfaces abraded smooth and growth annuli uncountable (Lambert, 1995). Survivorship of Serengeti tortoises was also very much lower than in Hargeisa, with a steady rate of mortality with age. The Hargeisa tortoises included full-grown old animals that were of large size. Most interestingly, however, the Serengeti tortoises were sexually mature when still quite small. It is worth considering how this phenomenon might have developed.

Growth increased from year 1 in Serengeti tortoises and declined after year 13. This differed somewhat from leopard tortoise growth elsewhere south of the Equator (Lambert, 1995) in which mean growth was relatively uniform from year 5 to full-size after year 24. Growth was also at a greater rate and smaller adult size was reached earlier in Serengeti tortoises than in those elsewhere in eastern and southern Africa and at Hargeisa, Somalia. Rapid growth and early maturity in Serengeti tortoises may be an evolutionary adaptation as a response over the millenia to perennial external pressure such as bushfires and predation. Serengeti hatchlings were also apparently larger than those elsewhere. This was additionally a possible reflection of a higher level of primary production in areas that also supported dense populations of herbivorous game animals inside the park, as compared to more xeric habitats with little green vegetation supporting *G. pardalis* in other parts of eastern Africa. The latter are also often subject to more intense grazing pressure from pastoralists' herds than inside national parks. In order to remain viable, the Serengeti tortoise population has probably had to adapt to a shorter life expectancy in response to the impact of regular bushfires.

Assuming that scute annuli are deposited annually, Serengeti female and male tortoises were full-grown by 12 and 15 yrs, respectively. Green vegetation prevailed from November to June, although there may have been some relatively small year-to-year variations in NDVI (Normalized Difference Vegetation Index) values, corresponding to rainfall fluctuations during these months. Trophic levels during the season of rains (Sinclair, 1975) were unlikely to descend to levels affecting the feeding requirements of tortoises, especially with the animals' ability to locate areas of herbaceous green vegetation available at least somewhere in the area of the park that they inhabit during this period. Therefore, in *G. pardalis* of Serengeti National Park, annual growth annuli, separated by deep dry season grooves, were unlikely to be interrupted by intermediate grooves from a growth slow-down due to shortage of green vegetation during the months of the year with higher-than-average-rainfall. Any intermediate grooves were more likely to be due to interrupted growth from some other physiological reason. Elsewhere in northern Tanzania, the short and long rainy seasons may be more distinct, with a definite dry season in between, and this might interrupt annular growth, with intermediate grooves forming in *G. pardalis* as a result. This has been suggested to be the case in another species, the pancake tortoise *Malacochersus tornieri* (Moll and Klemens, 1996), which frequents rather drier habitats of Tanzania than around Seronera in Serengeti National Park.

Mean growth increments were not found to be correlated with the same season's rainfall. This suggests that growth in *G. pardalis* in Serengeti National Park was independent of the level of primary production varying with intensity of the year's rains. *Geochelone pardalis* in west Zimbabwe is completely herbivorous (Hailey and Coulson, 1995), and despite variations in rainfall, the availability of green vegetation as food must exceed the basic feeding requirements of tortoises, even in years of low rainfall. Growth at this time was therefore probably influenced by other factors.

Fast growth is assisted by inhabiting an area of high primary production. Females grow even faster than males, and it is presumably important that they reach reproductive size and bear eggs as early as possible in an area exposed to bushfires. Females are also the more important sex in terms of reproduction and propagation of the species than males, especially since a single male may have the capacity to copulate with more than one female — an especially libidinous male may even fertilize a large number of females in the area. Selection for rapid growth may therefore be less intense in males than females. Chelonian sex ratios are also known to be influenced by incubation temperature, and the male:female sex ratio indicated that there were nearly twice as many females as males. There was also little evidence of combat between males for females. On the other hand, energy spent by males searching out females for reproductive purposes may result in less time spent feeding, and the associated lower level of nutrient intake may affect growth rate. In functional terms, however, ecological pressures are likely to have less dire consequences on population size if growth in females is less affected than in males, and females are therefore able to increase in size and reach maturity sooner.

The surface of the carapace was uneven in Serengeti tortoises, and pyramidal growth of vertebral and pleural scutes elevated the areolae on knolls. The humps so formed have also been recorded among captive tortoises (Jackson et al., 1976; Lambert, 1986) in which growth rate was very much higher than in wild animals. Such humped carapaces of fast growing North American and Mediterranean tortoises in captive conditions are not seen in the wild, and final dimensions of captive Mediterranean tortoises appeared to be stunted (Lambert et al., 1988), with X-rays revealing abnormal bone thickening. The humped growth of Serengeti tortoises may have been the result of an inadequate calcium supply — the tortoises, possibly in their search for calcium, were observed by KLIC to ingest dry bones of dead herbivores — or an incorrect calcium:phosphorus ratio required for normal bone formation (M. Peaker, *in litt.*). It was more likely, however, to be coupled with a rich diet from high primary production and the opportunity, on occasions perhaps, for tortoises to scavenge at mammalian carcasses or ingest the protein-rich feces of Serengeti carnivores. It was certainly not due to lack of sunshine, as has also been proposed for animals in captivity, especially home-bred Mediterranean tortoises in northern Europe (Lambert et al., 1988). Interestingly, pyramidal growth of the carapacial and pleural scutes and elevated areolae develop naturally with age in the Indian starred tortoise *Geochelone elegans*, and in the South African tent tortoise *Psammobates tentorius* and geometric tortoise *P. geometricus* (Ernst and Barbour, 1989; Bonin et al., 1996).

It is also possible that dorsal knoll formation confers an advantage on tortoises in Serengeti National Park, with selection for tortoises with pyramidally-grown apical scutes. Serengeti tortoises inhabit flat, lightly wooded grassy plains. Should they inadvertently become overturned, perhaps after being kicked by migratory herds of hooved herbivores, knolls formed on the dorsal apices of vertebral scutes would cause a change in a tortoise's center of gravity. An inverted tortoise would tend therefore to list towards one side (see Fig. 5). On the hard smooth surface of a flat grassy plain, a lateral list would facilitate the tortoise in its efforts to right itself before becoming overheated during the warmest hours of the day from tropical sunshine beating down on the heat-sensitive plastral surface (Lambert, 1981).

The carapacial outline of Serengeti male tortoises grew more elongate than females, as recorded in *G. pardalis* of comparable size elsewhere south of the Equator in eastern and southern Africa (Lambert, 1995). The more rotund form of females is probably associated with the space needed to contain voluminous egg clutches. Plastron length in *G. pardalis* was not found to be sexually dimorphic by Lambert (1995), but rear aperture diameter in animals of eastern and southern Africa south of the Equator was. Midline anal scute length in Serengeti tortoises was, however, only weakly dimorphic compared to both rear aperture diameter and anal notch width measured in animals elsewhere (Lambert, 1995).

The relationship between shell height and length indicated that *G. pardalis* in populations of South Africa's eastern Cape Province were more domed than in Serengeti, northeast Tanzania, or Somalia. Ecological factors causing this difference were unclear, and may be based on subspecific variation. The distribution of *Geochelone pardalis pardalis* (Bell, 1828) is given as west Cape Province and south Namibia, as distinct from *Geochelone pardalis babcocki* Loveridge, 1935, in the remainder of the species' range (Loveridge and Williams, 1957; Iverson, 1992). *Geochelone pardalis* with higher domes than in those from Serengeti and Somalia, however, were recorded only from eastern Cape Province, South Africa, which is outside the range given for *G. p. pardalis*. Nevertheless, carapacial doming may vary, not only between individuals and populations for ecological reasons, but also geographically.

Observations in this work indicated that size frequency of *G. pardalis* in populations of eastern and southern Africa responded to ecological pressures. Serengeti hatchlings especially tended to be larger and dimensions of full-grown adults smaller than in populations elsewhere, even those also within the limits of the Equator and Tropic of Capricorn. Within the context of wildlife exploitation further investigations on population density, reproduction, recruitment, and demographic parameters are required on the effects and levels of utilization that wild tortoise populations can sustain.

Acknowledgments

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LITERATURE CITED

ARCHER, W.H. 1948. The mountain tortoise (*Geochelone pardalis*). Afr. Wildlife 2(2):75-78.

BELL, T. 1828. Descriptions of three new species of land tortoises. Zool. Journ. 3:419-421.

BONIN, F., DEVAUX, B., AND DUPRÉ, A. 1996. Toutes les tortues du monde. Les encyclopédies du naturaliste. Lausanne, Switzerland: Delachaux et Niestlé, 254 pp.

BRANCH, W.R., BAARD, E., AND DE VILLIERS, A. 1990. Some exceptionally large southern African chelonians. J. Herpet. Assoc. Afr. 37:53-54.

BROADLEY, D.G. 1989. *Geochelone sulcata*. Spurred tortoise (English). Abu gatta, abu gefne (Arabic). In: Swingland, I.R., and Klemens, M.W. (Eds). The Conservation Biology of Tortoises. Occasional papers of the IUCN Species Survival Commission 5:47-48.

BURGER, M., AND BRANCH, W.R. 1994. Tortoise mortality caused by electrified fences in the Thomas Baines Nature Reserve. S.-Afr. Tydskr. Natuurnav. 24:32-37.

ERNST, C.H., AND BARBOUR, R.W. 1989. Turtles of the World. Washington, DC: Smithsonian Institution Press, 313 pp.

HAILEY, A., AND COULSON, I.M. 1995. Habitat association of the tortoises *Geochelone pardalis* and *Kinixys spekii* in the Sengwa Wildlife

Research Area, Zimbabwe. Herpet. J. 5(4):305-309.

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

JACKSON, C.G., TROTTER, J.A., TROTTER, T.H., AND TROTTER, M.W. 1976. Accelerated growth rates and early maturity in *Gopherus agassizi*. Herpetologica 32: 139-145.

KABIGUMILA, J. 1995. Conservation biology of the tropical leopard tortoise (*Geochelone pardalis babcocki* Loveridge) in Tanzania. In: Devaux, B. (Ed.). Proceedings - International Congress of Chelonian Conservation. Gonfaron, France: Editions SOPTOM, pp. 123-126.

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

LAMBERT, M.R.K. 1986. On growth of captive-bred Mediterranean *Testudo* in N. Europe. In: Rocek, Z. (Ed.). Studies in herpetology. Prague, Czech Republic: Charles University for Societas Europaea Herpetologica, pp. 309-314.

LAMBERT, M.R.K. 1995. On geographical size variation, growth, and sexual dimorphism of the leopard tortoise, *Geochelone pardalis*, in Somaliland. Chelonian Conservation and Biology 1(4):269-278.

LAMBERT, M.R.K., COLLINS, P.W.P., AND EVANS, P.A. 1988. Report on growth and survivorship of home-bred Mediterranean tortoises (*Testudo*) in southern England. Testudo - British Chelonia Group 2(6):31-56.

LANZA, B., AND SASSI, A. 1966. Le testuggini terrestri e d'acqua dolce della Somalia (Reptilia Testudines). Monit. Zool. Ital. Suppl. 74:257-272.

LOVERIDGE, A., AND WILLIAMS, E.E. 1957. Revision of the African tortoises and turtles of the suborder Cryptodira. Bull. Mus. Comp. Zool. 15(6):163-557.

MOLL, D., AND KLEMENS, M.W. (1996).Ecological characteristics of the pancake tortoise, *Malacochersus tornieri*, in Tanzania. Chelonian Conservation and Biology 2(1):26-35.

NORTON-GRIFFITHS, M., HERLOCKER, D., AND PENNYCUICK, L. 1975. The patterns of rainfall in the Serengeti ecosystem, Tanzania. E. Afr. Wildl. J. 13:249-271.

PRITCHARD, P.C.H., AND TREBBAU, P. 1984. Turtles of Venezuela. Society for the Study of Amphibians and Reptiles, 403 pp.

SINCLAIR, A.R.E. 1975. The resource limitation of trophic levels in tropical grassland ecosystems. J. Anim. Ecol. 44:497-520.

STUBBS, D. 1989. *Testudo kleinmanni*. Egyptian tortoise. In: Swingland, I.R., and Klemens, M.W. (Eds). The Conservation Biology of Tortoises. Occasional papers of the IUCN Species Survival Commission 5:39-40.

WEATHERBY, C. 1995. The South African mountain tortoise (*Geochelone pardalis*): home range, movement patterns, and site fidelity. In: Devaux, B. (Ed.). Proceedings - International Congress of Chelonian Conservation. Gonfaron, France: Editions SOPTOM, pp. 118-120.

WILSON, V.J. 1968. The leopard tortoise, *Testudo pardalis babcocki*, in eastern Zambia. Arnoldia (Rhodesia) 3:1-1.

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