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On Geographical Size Variation, Growth, and Sexual Dimorphism of the Leopard Tortoise, *Geochelone pardalis*, in Somaliland

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ABSTRACT. – *Geochelone pardalis* (Cryptodira: Testudinidae) in Somaliland (North-West Zone, Somalia) ($n = 26$) were larger than elsewhere in Africa. Carapace length ranges in mature males and females in Somaliland were respectively 578–650 and 518–654 mm – sexes were not significantly different – and elsewhere in Africa (museum material) 139.5–361 and 215–430 mm. The allometric relationship of carapace length (y in mm) to body weight (x in g) in Somaliland was $y = 10.49x^{0.40}$, which compared to $y = 14.82x^{0.35}$ in eastern Zambia. Body weight of mature males and females in Somaliland had ranges of 23.0–31.4 and 16.2–31.9 kg, and frequencies of heavy animals were greater than in eastern Zambia, where animals were utilized by local people as food. Assuming approximately annual deposition of growth annuli up to 24 years, scute increments in Somaliland were greatest during years 5–15; the rate was higher and variation greater than in animals elsewhere with more uniform growth. Carapacial outline was more elongate, and anal scutes more divergent in males than females. Diameter of posterior shell aperture showed an exponential increase relative to carapace length in females, especially large Somaliland tortoises, but a decrease in males elsewhere. The gular notch tended to protrude beyond the intermarginal notch in tortoises from elsewhere in Africa, but receded in those of Somaliland.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Geochelone pardalis*; tortoise; morphometrics; growth; sexual dimorphism; geographic variation; Somaliland; Somalia; Zambia

The leopard tortoise, *Geochelone pardalis* (Bell, 1828), is a large terrestrial chelonian (the world's second largest mainland species), widespread in xeric areas of eastern and southern Africa. Its range stretches from Djibouti, Somalia's North-West Zone (Republic of Somaliland), and southern Ethiopia in the north to Cape Province, South Africa, in the south, with extensions west and northwest to Namibia and Angola (Iverson, 1992). Much information on the species has been documented by Loveridge and Williams (1957). Overall knowledge of leopard tortoise biology has been reviewed more recently by Broadley (1989) and Ernst and Barbour (1989). Lanza and Sassi (1966) tabulated measurements of size characters for Somali specimens in Italian museums. Size-weight data from eastern Zambia were tabulated by Wilson (1968); he also reported that local people consumed the flesh of tortoises collected from near settlements. These eastern Zambian tortoises were of smaller mean dimensions than those from further south in Africa. Observers of growth in captivity include Archer (1948), Bally (1952), Wilson (1968), Poglayen-Neuwall (1983), and Rall (1988).

Geographical variation in size is known in several terrestrial chelonians. Smaller forms of the eastern Mediterranean spur-thighed tortoise, *Testudo terrestris* Forskål (David, 1994) (formerly *Testudo graeca*), occur in the southern part of its range (Flower, 1933), and the *Chelonoidis nigra* complex (David, 1994) of the Galapagos shows island-to-island variation in size (Pritchard, 1979). Males exceed females in size in South African *Chersina angulata*, and Van den Berg and Baard (1994) found that, while males showed no difference, females in the western Cape Province were significantly smaller than those of the eastern and northwestern parts of the range. Geographic sexual dimorphism has also been found by Pritchard and Trebbau (1984) in the freshwater turtle *Kinosternon scorpioides* complex, who recorded that males were larger than females in relatively xeric habitats in Venezuela, but the sexes were essentially identical in size in forested habitats of French Guiana.

Geochelone pardalis is not uncommon around Hargeisa in Somaliland. The objectives of this study were to investigate size composition and growth and to test whether *G. pardalis* at the northeastern limit of its range, like some in parts of South Africa at the southern limit (Boycott and Bourquin, 1988), were larger than those nearer the Equator. I also investigated whether sexual dimorphism is evident in shell characteristics alone. The interrelationships between different size dimensions and weight were compared with those recorded from earlier studies on the species and from further measurements of preserved specimens from elsewhere in the range. Size composition was also investigated in relation to utilization of this species for human consumption in parts of sub-Saharan Africa.

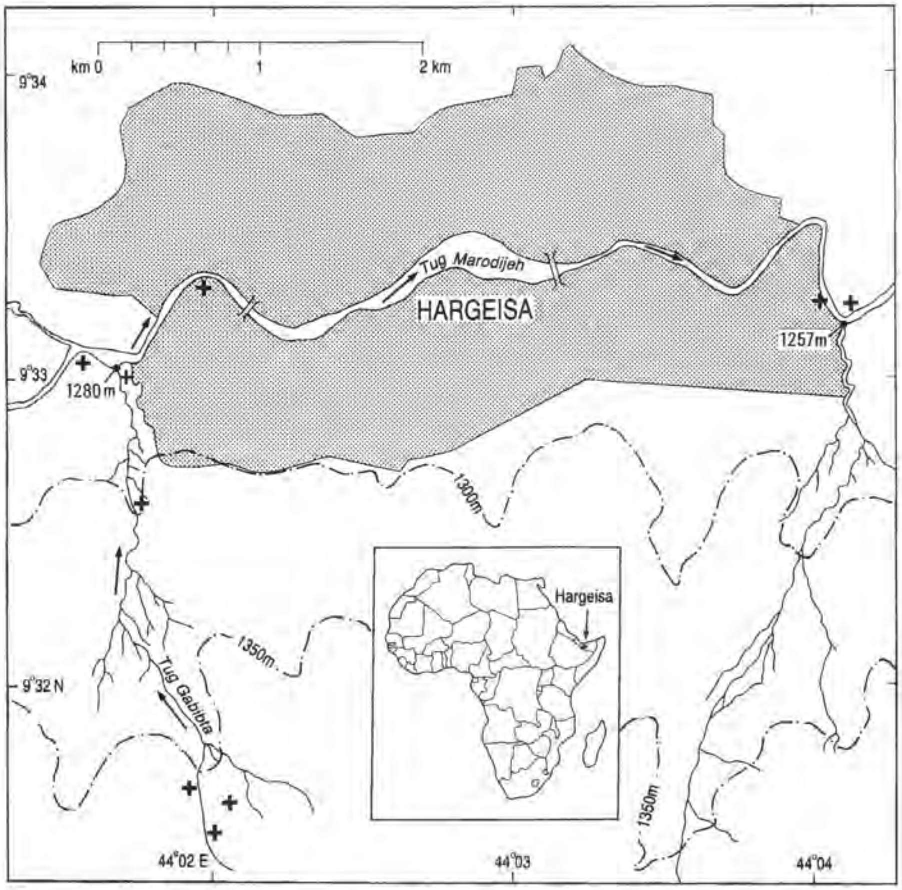

Figure 1. Map of the Hargeisa area, Somaliland, showing valleys and locations where *Geochelone pardalis* were recorded (+).

MATERIALS AND METHODS

Size and weight measurements were conducted on 26 *G. pardalis* found between 15 March and 19 April 1993 in the vicinity of Hargeisa (9°33'N, 44°03'E), Somaliland (Fig. 1) [Gobol (Region of) Wogooyi Galbhed, North-West Zone, Somalia]. Most tortoises had taken refuge in vegetation during the latter part of the dry winter season and were inactive. Further specimens measured (n = 53) included those in the collections of the Natural History Museum, London, UK (BMNH), and the Senckenberg Museum, Frankfurt-am-Main, Germany (SMF). Localities and accession numbers of these specimens are given in the Appendix.

Loveridge and Williams (1957) recognized two subspecies. The nominate form reportedly occurs in southern Namibia and formerly in Cape Province, South Africa (type locality: "Promont. Bonae Spei" = Cape of Good Hope, Cape Province, South Africa), while *Geochelone pardalis babcocki* (Loveridge, 1935) (type locality: "the western slopes of Mount Debasien, Karamoja, Uganda at 5000 feet") occupies the entire balance of the range defined for the species. Greig and Burdett (1976) have suggested that subspecies may not be valid, a conclusion echoed by Boycott and Bourquin (1988), and subspecies have been discounted in this study.

Measurements. — Civil unrest prevailed in Hargeisa at the time of the study; mined zones limited mobility, and local gunmen could interfere with tortoise measuring in the field. When possible, weight was the first parameter to be recorded, since individuals sometimes defecated or urinated with prolonged handling. Seven tortoises were weighed using a sling and spring balance. Tortoises up to 5 kg were weighed to an accuracy of 0.05 kg and those up to 25 kg to 0.1 kg; those heavier than 25 kg could not be weighed.

Size characters selected were based on Lambert (1993) for *Geochelone sulcata* and followed Grubb (1971) and Bourn and Coe (1978) for *Dipsochelys elephantina* of Aldabra Atoll. Dimensions under 17 cm were measured with steel vernier calipers and those over 17 cm with a steel tape to within approximately 1 cm accuracy. Straight-line measurements (for curved surfaces, the distance between wooden dowels placed vertically at either end) included midline carapace length (intermarginal notch to supracaudal scute), maximum carapace width (between the 6th marginal scutes across the 3rd vertebral), midline plastron length (gular notch to anal notch), and transverse width of the 3rd vertebral scute, the largest of the vertebrals. The widths of the areolus and growth annuli of this last scute were also measured with vernier calipers in those animals whose carapacial surfaces were still relatively unabraded. In preserved specimens curved carapace length over peaks of the vertebral scutes was measured to facilitate comparison with measurements taken by Lanza and Sassi (1966) and Wilson (1968).

Figure 2. Ventral view of a male *Geochelone pardalis* in Somaliland. Midline plastron length 482 mm. Note divergent anal scutes and distinct plastral scute growth annuli. Photographed on alluvial soil of Tug Marodijeh after first day's rain, 16 April 1993, 2.5 km W. of Hargeisa.

Figure 3. Ventrolateral view of female *Geochelone pardalis* in Somaliland. Midline plastron length 525 mm. Note that loss of keratinous scutes on the plastral surface has exposed the underlying bone. Photographed on stony ground of the Tug Gabibta valley in late winter, 31 March 1993, 4 km S.W. of Hargeisa.

Since dimensions of the rear shell aperture are potentially sexually dimorphic, the longitudinal and transverse diameters were measured using vernier calipers. Distances were measured between the anal notch and edge of the supracaudal scute (rear aperture diameter) and between the apices of the anal scutes (anal notch width).

Sex Determination. — Loveridge and Williams (1957) had difficulty in distinguishing males from females, concluding that relative tail length was the only sure character – that of the male longer – and the posterior third of the plastron in males showing slight concavity. In addition, the lower sides of the carapace are invariably almost vertical in males, giving the impression from above of a more elongate shell outline than in females, while the anal notch can be curved rather than angular in females. A more reliable single character differentiating males was found to be lateral divergence of the anal scute apices (Fig. 2). They were directed

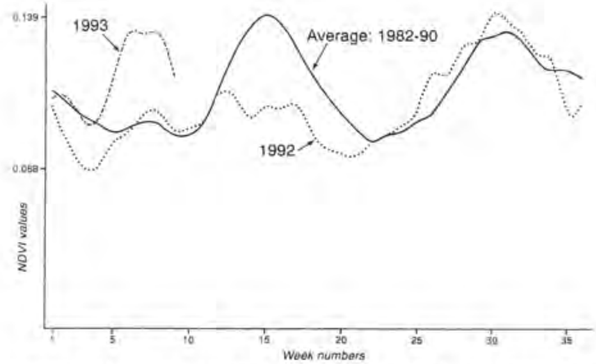

Figure 4. Normalized Difference Vegetation Index – NDVI (decadal absolute value) of photosynthetically active green leaf biomass from satellite imagery for Hargeisa over the first 36 weeks of 1992, and up to the end of February 1993, compared with the historical average, 1982–90 (P. Santacroce, *pers. comm.*).

laterally in males but tended to be orientated to the rear in female and immature or sexually undifferentiated animals (Fig. 3). In the case of Hargeisa tortoises, indeterminate animals with a carapace length of 518 mm or more and flared marginal scutes were deemed to be female (215 mm or more elsewhere in Africa).

Age Assessment. — Age of each tortoise was estimated from the number of growth annuli on the 3rd vertebral scute as outlined by Lambert (1993). Deposition of keratinous material in the epidermal scutes provides a record of size increase with time. Growth depends on the intake of nutrients, with active feeding upon green vegetation. Seasonal rains, giving rise to such vegetation in Hargeisa (Fig. 4) start at the end of March or in April (Hemming, 1966) and coincide with summer temperatures from May to September. Monthly rainfall at Hargeisa is bimodal (maxima in June and September) without separation by a summer dry period. Growth may be interrupted or curtailed if a mid-season rain failure results in a severe shortage of green vegetation. Vegetation becomes increasingly dry and sparse after the end of the rains in October, and, in association also with the lowering of temperature towards the end of this month, activity and growth slow down. Seasonal growth ceases by the time tortoises have sought refuge and become inactive, which in Hargeisa occurs from November (soon after the onset of the dry winter season) until late March. As in other tortoises (Castanet, 1988; Lambert, 1993) uneven deposition of keratinous material in the scutes is caused by interruptions in growth, and concentric growth annuli are separated by grooves. Many of the scutes of old adults, especially in rocky terrain, are abraded smooth, with underlying bone on the plastral surface exposed (Fig. 3). The use of growth annuli in chelonian age determination has been reviewed by Zug (1991), and problems of ageing based on annuli and climatic factors influencing their growth in North American tortoises have been discussed recently by Germano (1993, 1994).

RESULTS

Size. — Carapace length ranges of immature, male, and female tortoises from Somaliland (including a museum specimen from the Nogal Valley) were respectively 169–418 mm ($n = 13$), 578–650 mm ($n = 5$), and 518–654 mm ($n = 9$), and elsewhere in eastern, southern, and southern central Africa (museum material) 51–199 mm ($n = 27$), 139.5–361 mm ($n = 10$), and 215–430 mm ($n = 15$).

Mean lengths of males and females in which growth had ended (> 24 annuli) at Hargeisa, Somaliland, were respectively 613 (S.D. ± 38.6) and 590 (S.D. ± 44.3) mm ($n = 4$ and 9); the difference between sexes was not significant ($t = 0.83$, 11 d.f.).

Curved carapace length of *G. pardalis* from further south in Somalia ($n = 18$) was measured by Lanza and Sassi (1966) and was used by Wilson (1968) in eastern Zambia ($n = 48$). Curved carapace length (x) was therefore recorded in museum material from south of Hargeisa for comparison with these earlier measurements. The correlation with straight carapace length (y) in these specimens was highly significant (r = 0.995; n = 52), the regression being given by $y = 0.682x + 6.013$. Notwithstanding any individual measurement variation, this compared with $y = 0.663x + 7.361$ ($r = 0.999$; $n = 18$) for Lanza and Sassi's (1966) material. Combined, the data give $y = 0.677x + 6.255$ ($r = 0.996$; $n = 70$), and enabled straight carapace length to be estimated for Wilson's (1968) Zambian tortoises.

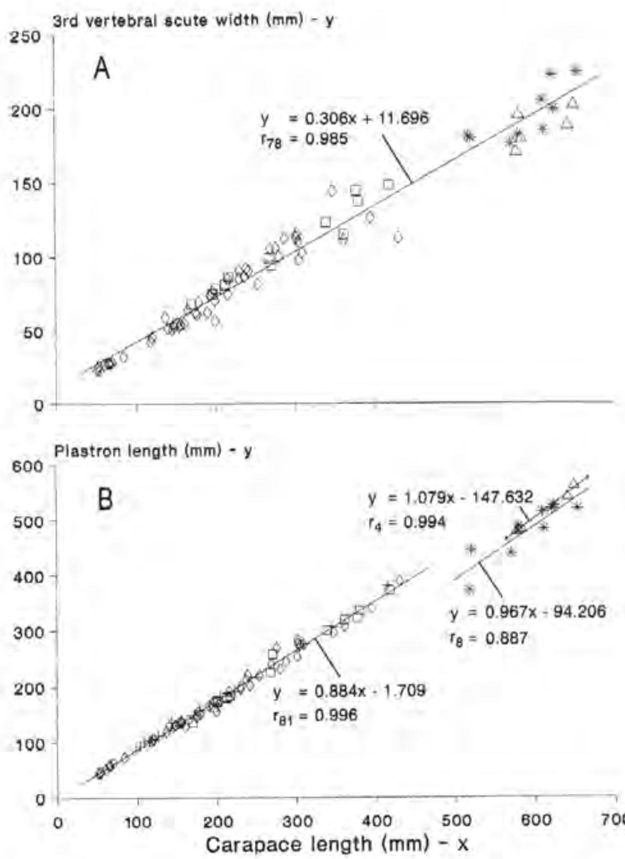

Figure 5. Relationships in *Geochelone pardalis* of carapace length (x) to (A) 3rd vertebral scute width (y) and (B) midline plastron length (y). Somaliland: immature tortoises (squares) and mature adults – males (triangles) and females (*), and elsewhere: immature and adult tortoises (diamonds). Unsexed tortoises in Somalia (Lanza and Sassi, 1966) are shown for comparison (+).

Table 1. Weight composition of *Geochelone pardalis* compared between eastern Zambia (Wilson, 1968) and the Hargeisa area, Somaliland. Weight was calculated from the power regression with carapace length for tortoises above 25 kg and others not weighed in the Hargeisa sample.

Location		Weight (kg)							
	n	<5	5-9	10-14	15-19	20-24	25-29	30-34	>35
Eastern Zambia	310	137	152	21	0	0	0	0	0
Somaliland	26	7	3	2	2	6	4	2	0

The isometric relationship ($r = 0.985$; $n = 79$) between 3rd vertebral scute width (y), whose annular widths were used to record growth, and carapace length (x) was $y = 0.306x + 11.696$ (Fig. 5A).

Areolar diameter (width of the third vertebral scute at year 0), measurable before annular deposition had started during the first year, was compared in tortoises of Somaliland ($n = 11$) and elsewhere ($n = 30$). Respective mean values were 25.4 (S.D. ± 1.88) and 21.1 (S.D. ± 1.94) mm [equivalent to calculated mean carapace lengths of 44.8 and 30.7 mm (see above)]. The difference was significant ($t = 6.3$, 39 d.f., $P < 0.001$); hatchling tortoises were thus larger in Somaliland than elsewhere.

The relationship of plastron length (y) to carapace length (x) in Lanza and Sassi's (1966) sexually undifferentiated Somali material was also isometric, and graphically did not differ from immature material from Somaliland nor from either mature or immature tortoises (plastron broken in one) from further south in Africa (Fig. 5B) [Wilson (1968) only measured maximum plastron length, and so his data are excluded]. Combined data for these animals fitted the isometric $y = 0.884x - 1.709$ ($r = 0.996$; $n = 82$); data combined separately for mature Hargeisa tortoises of both sexes fitted $y = 0.973x - 94.627$ ($r = 0.905$; $n = 14$).

Shell (y) and dome height (distance of the carapacial apex above the nuchal) (z) were also measured by Lanza and Sassi (1966); isometric relationships ($n = 18$) to carapace length (x) were respectively $y = 2.710 + 0.587x$ ($r = 0.997$) and $z = 8.557 + 0.240x$ ($r = 0.968$).

Weight. — As shown previously for *G. pardalis* in captivity by Rall (1988), and in other testudinid species (e.g., Lambert, 1982, 1993), weight increases exponentially. The strongly allometric relationship of weight (x in g) to carapace length (y) recorded in the tortoises at Hargeisa (Fig. 6) was $y = 10.486x^{0.399}$ ($r = 0.996$; $n = 7$). Thus, the calculated body weight of the largest unweighed tortoise (a female) from straight carapace length (654 mm) was 31.9 kg, and the largest male 31.4 kg (650 mm).

The allometric relationship of weight (x: range 113 g – 11.1 kg) to curved carapace length (y) in tortoises measured by Wilson (1968) in eastern Zambia ($n = 48$) was given by $y = 19.614x^{0.360}$ ($r = 0.995$), and to straight carapace length (y) calculated from curved carapace length (see above) by $y = 14.822x^{0.350}$.

Size Structure. — Tortoises of the Hargeisa area tended to be heavier (using calculated weights at a given size for

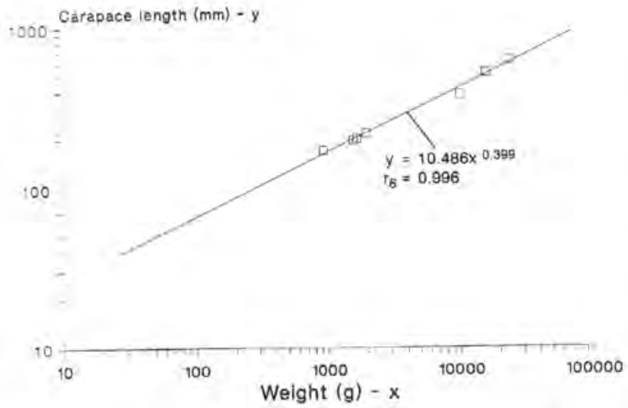

Figure 6. Allometric relationship between carapace length (y) and body weight (x) of *Geochelone pardalis* measured in Somaliland.

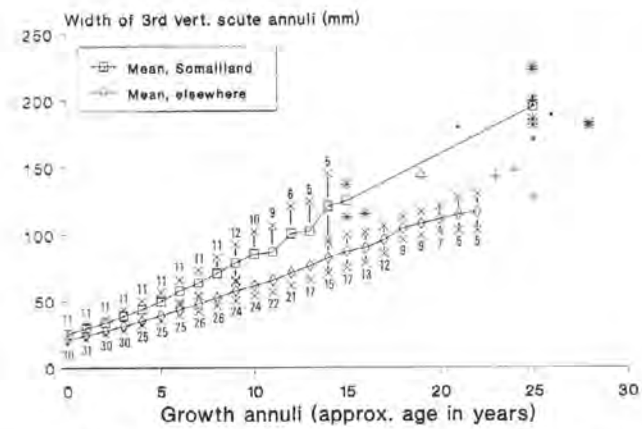

Figure 7. External growth from width of 3rd vertebral scute annuli in *Geochelone pardalis*. Standard deviations (bar lines) are based on means from five or more values (indicated): individual Hargeisa females (*) and males (solid squares); individual females from elsewhere in Africa (+), exceptionally large captive female, Sudan (triangle).

those unweighed) than those recorded by Wilson (1968) in eastern Zambia (Table 1); the difference in numbers of specimens above and below 10 kg was significant ($\chi^2 = 76.4$; $P < 0.001$). Tortoises 3–4 km southwest of Hargeisa in the Tug Gabibta valley, a tributary above Hargeisa's main valley (Tug Marodijeh), tended to be larger than those in the valley below (Table 2), with a significant difference between numbers of individuals above and below 400 mm ($\chi^2 = 10.1$; $P < 0.005$).

Age Structure. — Twenty-six tortoises found in the Hargeisa area were aged from 3rd vertebral scute annuli. Carapacial surfaces of full-grown animals in the heavily grazed, dry, stony habitat of the Gabibta valley had been abraded smooth, and few showed freshly deposited keratinous annuli at the scute edges. Gabibta valley tortoises tended to be older (Table 3) than those in the lower Marodijeh valley, with numbers of specimens above and below 15 years of age significantly different ($\chi^2 = 8.0$; $P < 0.005$).

Growth. — Straight widths of 3rd vertebral scute annuli are a measurable record of external growth. Growth appeared to have ceased by the time 24 annuli had been deposited (Fig. 7). Annuli that still remained unabraded ultimately became virtually uninterpretable and impossible to count as they narrowed with the slowing of external growth. Full-grown tortoises with at least 24 annuli could therefore be several years or even decades older. For annuli numbers 6, 7, 9, and 14, standard deviations of means do not overlap visually. The smallest difference was between the means of areolar diameter, but this, and the differences between widths of yearly annuli deposited subsequently, were significant (see above). Tortoises of Somaliland were thus significantly larger than elsewhere.

Annular growth increments varied and depended on the active intake of nutrients, which was influenced by temperature and the availability of green vegetation corresponding to rainfall intensity over the species' range. Assuming that annuli were deposited yearly during seasonal growth, increments were greatest during years 5–15 in Hargeisa tortoises (Fig. 8A), whereas increments in animals further south were more uniform with only relatively small variations from year 5 until full size after year 24.

Yearly increments varied greatly within and between individuals (Fig. 8B) of different geographical zones, where seasonal rainfall and temperature regimes were dissimilar (Table 4).

Mating Activity. — Courtship was observed in the Gabibta valley between a male and female of respectively 642 and 610 mm carapace length (calculated weights of 29.9 and 26.3 kg) during the late morning (1100 h) of 21 March 1993 at an air temperature of 29.5°C.

Sexual Dimorphism. — Males tended to be more elongate and, indeed, had slightly narrower carapaces than females (Fig. 9). No significant dimorphism was noted in plastral length (Fig. 5B).

Sexual dimorphism was more strongly marked by the isometric relationship between carapace length and anal

Table 2. Size composition of *Geochelone pardalis* in the Hargeisa area, Somaliland.

Location		Carapace straight length (mm)						
	n	<200	200+	300+	400+	500+	600+	>700
Tug Gabibta[1]	13	0	0	1	1	5	6	0
Tug Marodijeh[2]	13	2	7	3	0	2	1	0
Totals	26	2	7	4	1	7	7	0

[1] tributary valley above main valley, 3–4 km S.W. of Hargeisa town center
[2] main valley of Hargeisa

Table 3. Age composition of *Geochelone pardalis* in the Hargeisa area, Somaliland.

Location		Growth annuli (approx. age in years)				
	n	<5	5-9	10-14	15-19	>20
Tug Gabibta[1]	13	0	0	1	1	11
Tug Marodijeh[2]	13	0	2	7	1	3
Totals	26	0	2	8	2	14

[1] tributary valley above main valley, 3–4 km S.W. of Hargeisa town center
[2] main valley of Hargeisa

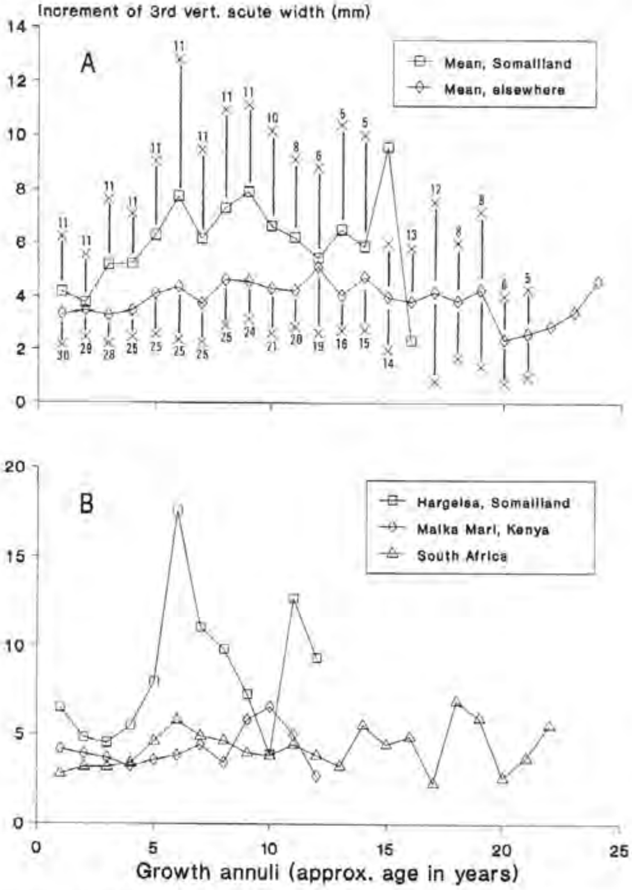

Figure 8. Width increment of 3rd vertebral scute annuli corresponding with age in *Geochelone pardalis*. (A) Mean width increment and standard deviations (bar lines) based on five or more values (indicated) in Hargeisa tortoises are compared with those elsewhere in the African range; (B) increment variation of individual tortoises from Hargeisa and elsewhere in Africa.

notch width, which also varied geographically (Fig. 10A). While the correlation in Hargeisa males was significant, that in females was not (Fig. 10A(i)); the correlation was significant, however, for females elsewhere (Fig. 10A(ii)), and notch width tended to decrease exponentially.

Carapace length minus midline plastron length was used for rear aperture diameter in *G. sulcata* by Lambert (1993), following Stubbs et al. (1984) for Mediterranean *Testudo hermanni*, and it was found to be significantly correlated with measured aperture diameter of *G. pardalis* in the present study ($r = 0.882$; $n = 78$).

The relationship of carapace length (x) to rear aperture diameter (y) was compared. Data for Hargeisa tortoises showed no significant sexual dimorphism as diameter increased exponentially (Fig. 10B(i)) but did for animals elsewhere (Fig. 10B(ii)), with diameter in males tending to decrease exponentially.

The relationship between gular notch and intermarginal notch indicated geographic variation but not sexual dimorphism. Plastron length plus aperture diameter exceeded carapace length in 64.7% of tortoises with complete plastra ($n = 51$) from elsewhere in Africa and 7.4% in those of Somaliland ($n = 27$); the gular notch thus tended to protrude beyond the intermarginal notch in the former and receded in the latter ($\chi^2 = 25.8$; $P < 0.001$). The gular notch protruded in 70% of males ($n = 10$) and 63.4% of female and juveniles ($n = 41$) from elsewhere in Africa, and receded in 100% of males ($n = 5$) and 90% of female and juveniles ($n = 22$) in Hargeisa; differences between each pair set were not significant. The receding gular notch in Hargeisa tortoises was also not significantly related to terrain; it receded in 84.6% of those found on alluvial soil in the Marodijeh valley ($n = 13$) and 100% in those of the abrading rocky Gabibta valley habitat ($n = 13$).

Color Pattern. — Dark pigmentation on unabraded carapacial surfaces of tortoises at Hargeisa was confined to small spots laterally and posteriorly, and these specimens appear similar to the adult depicted in Pritchard (1979: 266) from Djibouti (P.C.H. Pritchard, *pers. comm.*). Background color, sometimes tinged lateritic red, and dark patterning of tortoises from elsewhere in the range, was variable.

DISCUSSION

Ontogenetic shape changes occur with growth in testudinids (e.g., Bourn and Coe, 1978; Lambert, 1993). Size, weight, and rate of growth of *Geochelone pardalis* in Somaliland at the northeast end of the range tend to be greater than in tortoises from further south in Africa. Museum specimens from South Africa suggest that larger sizes could also be achieved there than further north. Measured mid-range animals from between the Equator and Tropic of Capricorn varied little in size.

Geographical size comparisons in tortoises are based on measurements of hatchlings before growth, of adults at the end of growth, and in tortoises of similar age as estimated from the number of growth annuli. Size comparisons at sexual maturity can also be made. The diameter of the areolus and the width of third vertebral scute annuli in animals of the same age indicated that the tortoises of Somaliland were larger than those elsewhere. It is not known whether or not the few large tortoises in museum collections from elsewhere had stopped further growth, although growth lines were becoming closely packed in certain large individuals. In relation to size at sexual maturity, successful mating in captivity was reported in Zimbabwe by Bennefield (1982) between a wild-collected male and female (which laid eggs) of respective carapace lengths and weights of 280.5 and 341.0 mm, and 5.0 and 6.5 kg. These dimensions are substantially less than 642 and 610 mm (calculated weights of 29.9 and 26.3 kg) of the pair observed during courtship at Hargeisa.

Broadley (1989) indicates that the length and weight of the largest male ever recorded, which was in South Africa's eastern Cape Province's Addo Elephant National Park, were 656 mm and 43 kg (Branch and Braack, 1987). However, the weight was an estimate, for subsequently Branch et al. (1990) noted that before death in 1976 an accurate weight of the specimen had not been obtained; they give the length as 655 mm. The largest female recorded by them, which was

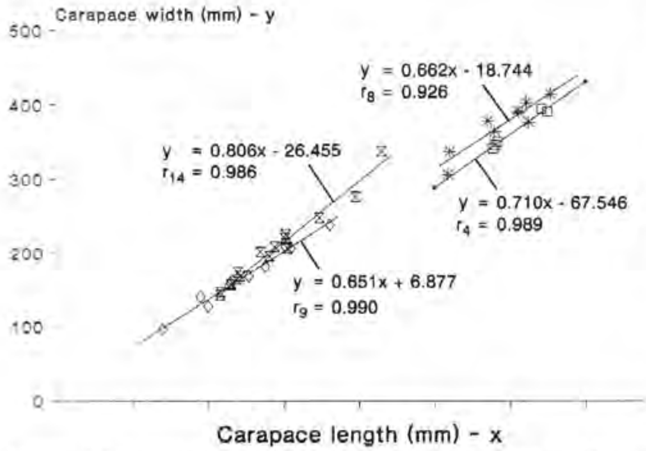

Figure 9. Relationship between carapace length (x) and width (y) showing sexual dimorphism in adult *Geochelone pardalis*. Males (squares) and females (∗) in Somaliland are compared to those elsewhere in Africa: males (diamonds) and females (⊠).

still alive in 1990 on a game farm in Bedford District of the eastern Cape, had a carapace length of 705 mm (total length, 750 mm) and a weight of 48.64 kg. This exceeds the size of the largest female at Hargeisa in this study (654 mm, ca. 31.9 kg). The unusually big Addo Elephant National Park male exceeded by only 5 mm the 650 mm (measured to the nearest cm) of the largest male at Hargeisa, whose calculated weight was 31.4 kg, and thus lower than that estimated for the National Park male. This may be due to the reduced weights of inactive tortoises recorded in March1993 at the end of Hargeisa's winter. The tortoises had probably ingested little or no green food during the cool weather of the previous 4–5 months, although NDVI (Normalized Difference Vegetation Index) values indicate that green vegetation was present during February 1993. Gans (1965) also recorded "numbers of specimens near 70 cm in length" (equivalent to about 38 kg) in Somalia 40 km N. of Mogadishu, and P.C.H. Pritchard (*in litt.*) reports a specimen weighing 31.3 kg (equivalent to about 649 mm) in Djibouti, west of Hargeisa.

Van Zyl (1966) discussed the weight of *G. pardalis* in South Africa's Transvaal (range 5.5–9.5 kg) and considered that adult body weight may vary geographically. Wilson (1968) also found that his eastern Zambian tortoises, which had been exploited as food by the local people, were much lighter than those of Cape Province, and noted that the latter were much larger than those from other parts of Africa. Although those of the Graaff-Reinet area were the biggest (one acheiving 47.6 kg – sex not recorded), Archer (1968) reported considerable size variation even within South Africa. A dealer in Kenya who had exported many hundreds of *G. pardalis* had also noted that adult sizes in areas of Tanzania where tortoises have never been exploited are smaller than in neighboring Kenya to the north (P.C.H. Pritchard, *in litt.*).

The large size of Cape Province and Hargeisa tortoises, and those observed by P.C.H. Pritchard (*in litt.*) and Gans (1965) in northeast Africa, suggests that the sizes achieved by *G. pardalis* in mid-range, between the Equator and

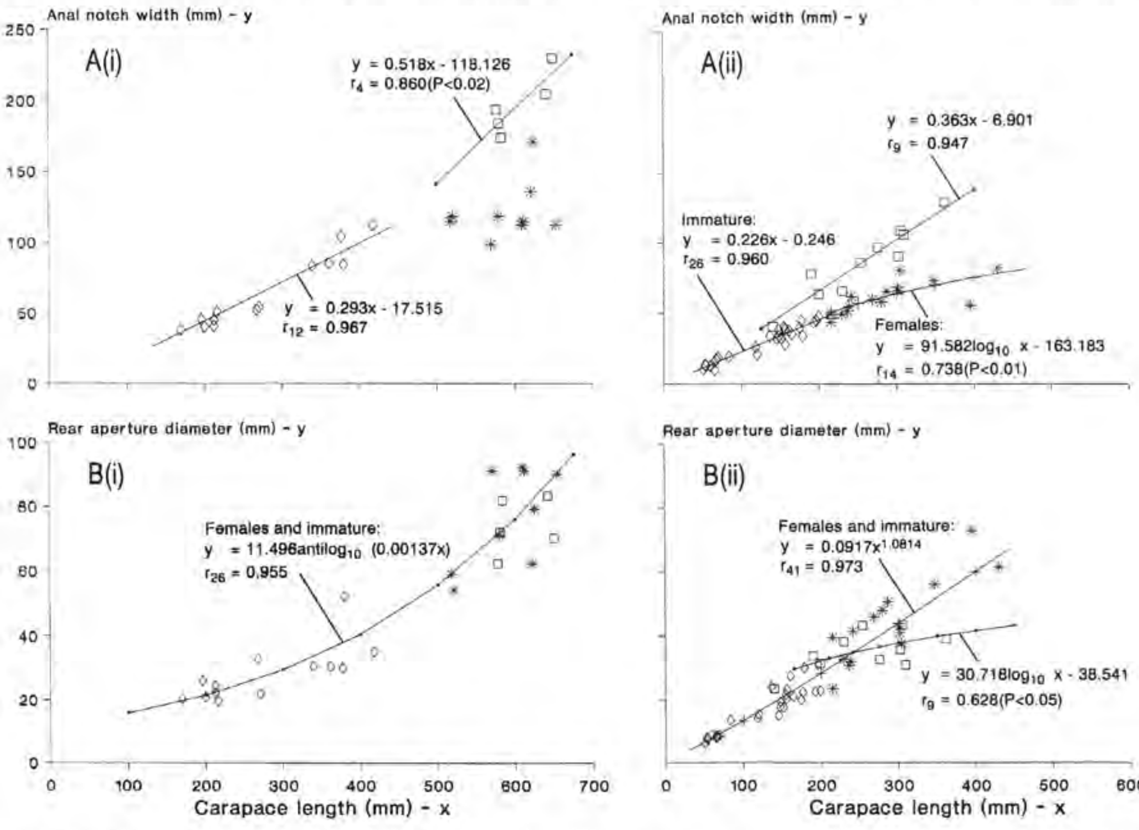

Figure 10. Sexual dimorphism and geographical variation in *Geochelone pardalis*. Relationships of carapace length (x) to (A) anal notch width (y) and (B) rear aperture diameter (y) are compared in: (i) Somaliland tortoises, and (ii) elsewhere in the African range. Mature males (squares) and females (∗), and indeterminate tortoises (diamonds).

Table 4. Mean rainfall (mm – showing annual total), and mean minimum *t* and maximum *T* daily temperatures (°C) during months of the year at selected stations (Meteorological Office, 1983) within the geographical range of *Geochelone pardalis* in eastern and southern Africa. Factors influencing periods of growth and activity are indicated: active food intake (figures in bold type) and hibern-/aestivation (in italics).

		Altitude	Years of	Annual		Months of the Year											
Latitude	Station	(m)	Records	Rainfall	Factor	J	F	M	A	M	J	J	A	S	O	N	D
09°29'N	Hargeisa, Somaliland	1326	1944-60	412	*rainfall*	*2*	*2*	*36*	**53**	**49**	**61**	**38**	**81**	**61**	*20*	*8*	*1*
					min. t	*11.2*	*12.0*	14.6	16.1	17.2	17.0	16.7	16.7	16.8	14.7	*12.6*	*11.6*
					max. T	*24.5*	*26.4*	28.9	**29.5**	**30.6**	**30.9**	**29.5**	**29.4**	**30.1**	28.3	*25.5*	*24.0*
03°32'N	Moyale, Kenya	1107	1942-70	734	*rainfall*	16	17	**60**	**200**	**125**	*16*	*16*	*20*	*19*	**111**	**93**	**41**
					min. t	**18.3**	**19.1**	**19.0**	**18.5**	17.6	*16.3*	*15.7*	*15.8*	*16.4*	17.2	17.5	**17.7**
					max. T	**30.1**	**31.3**	**30.2**	**27.1**	25.0	*24.3*	*23.8*	*24.3*	*26.0*	26.2	27.0	**28.5**
02°02'N	Mogadishu, Somalia*	17	1941-58	371	*rainfall*	*1*	*<1*	*6*	**57**	**54**	**82**	**56**	**32**	**17**	**16**	**42**	*8*
					min. t	22.9	23.3	25.6	26.6	25.8	24.3	23.5	23.4	24.0	24.8	24.8	23.8
					max. T	29.4	29.5	30.7	32.1	31.4	29.4	28.4	28.3	29.2	30.1	30.2	29.8
00°16'S	Nakuru, Kenya	1863	1941-70	908	*rainfall*	22	25	62	143	116	83	99	113	78	63	68	36
					min. t	7.9	8.3	9.4	11.0	10.9	*9.4*	*9.7*	*9.5*	*8.4*	8.5	9.3	8.6
					max. T	**27.9**	**28.9**	**28.5**	**26.3**	25.3	*24.8*	*24.1*	*24.3*	*25.3*	25.9	25.1	**26.2**
16°31'S	Kariba, Zimbabwe	604	1948-70	690	*rainfall*	**162**	**176**	**77**	**27**	*5*	*3*	*0*	*1*	*1*	*12*	**70**	**156**
					min. t	21.9	21.0	20.7	19.2	*15.3*	*12.8*	*12.8*	15.6	20.2	24.2	23.8	21.9
					max. T	**30.8**	**30.7**	**31.3**	**31.3**	29.0	*26.7*	*26.6*	29.3	33.2	35.7	**33.7**	**31.0**
33°59'S	Port Elizabeth, Cape Province, South Africa*	60	1941-70	626	*rainfall*	39	34	45	51	63	64	46	66	70	57	52	39
					min. t	**16.8**	**17.1**	**16.2**	13.2	*10.5*	*8.1*	*7.7*	*8.7*	*10.5*	*12.4*	14.0	**15.6**
					max. T	**25.1**	**25.1**	**24.5**	22.5	*21.4*	*20.0*	*19.4*	*19.5*	*19.8*	*20.6*	22.3	**23.9**

*Stations by the Indian Ocean

Tropic of Capricorn (23°30'S), are less. In South America, a continent also spanning the Equator, *Chelonoidis carbonaria* is smaller towards the Equator at the southern extreme of its range (Pritchard and Trebbau, 1984), while in *Chelonoidis chilensis* of Argentina, a larger form is found in the south, and a smaller form ranges towards the Equator in the north.

Archer (1968) reported that in South Africa's Graaff-Reinet area *G. pardalis* at 6000 feet (1829 m) were larger (and more distinctly marked) than those at 4000 feet (1219 m). Hargeisa tortoises were found at an altitudinal range of 1257–1346 m, but size is unlikely to be influenced over an elevation range of less than 100 m. Moreover, Gans (1965) also recorded large tortoises on Somalia's coastal plain, and there was no obvious difference between montane and lowland animals of comparable ages in museums from localities further south in the range.

Warm wet summers following inactivity induced by cool winters, particularly at Hargeisa (Hemming, 1966), may elevate levels of activity and stimulate a high intake of green vegetation, giving rise to a rapid rate of growth. One might speculate, therefore, that the relatively greater size of tortoises in Somaliland than elsewhere is due to climatic differences. Except in Zimbabwe, the climate further south is less seasonally defined (Table 4), and rains may give rise to green vegetation in association with lower temperatures, or, notwithstanding temperature, rainfall may be strongly bimodal or less intensely seasonal. In South Africa's Cape Province, monthly rainfall is more uniform than towards the north, but the clearly defined drop in temperature during winter months probably reduces tortoises' activity, and it may cause them to hibernate, as they do in the highveld, especially at higher altitudes (> 1200 m) in Zimbabwe (D.G. Broadley, *pers. comm.*).

Broadley (1989) considered that males in South Africa appear to reach a slightly larger size than females, while data further north suggested that males are considerably smaller than females. Boycott and Bourquin (1988) considered that both sexes in natural conditions attained much the same size; full grown males and females do not differ in size at Hargeisa, Somaliland.

Few tortoises ever exceeded 15 lb (6.8 kg) in an area of human settlement in eastern Zambia (Wilson, 1968), and they were much smaller than *G. pardalis* at Hargeisa, where, although not apparently considered *harram* (forbidden) as food, they were not eaten by the predominantly Moslem local population. This may not be due to religious reasons, as proposed by Broadley (1989), for further west in Sahelian Africa, the flesh of *G. sulcata* is eaten as a delicacy by local Moslem people in northern central Mali (Lambert, 1993). The reasons may be cultural. Mali was formerly occupied by France, whose soldiers in Algeria north of the Sahara Desert were reported by Rozet (1833) to ingest the flesh of *Testudo graeca*. Indeed, until 1979, when halted on health grounds (Lescure, 1980), Mediterranean tortoises were seen on sale in Paris fishmongers (Fretey, 1979). The custom may therefore have been introduced to Mali by the French. The Somali people, with possibly more conservative palates than Bantu people further south, may not have developed this culinary tradition, nor was one developed during British suzerainty. Not suffering from human predation, therefore, large tortoises included in the Hargeisa population have remained alive. Perhaps, likewise, large tortoises have survived in South Africa's Cape Province where consumption of tortoise flesh has been infrequently reported (Boycott and Bourquin, 1988).

The size and age of tortoises varied in different populations of Hargeisa. Those found 3–4 km southwest of the town in the Gabibta valley (1295–1346 m) were predominantly large, compared to those at the town's periphery in the Marodijeh valley (1257–1280 m). Most were full-grown (> 24 years in age), and few showed freshly deposited keratinous annuli at the scute edges. The animals were inactive towards the end of the dry winter, and few young, immature tortoises were found. The total absence of immature animals in the Gabibta valley may suggest either that tortoises made up a relict population in which recruitment through breeding is at a low or negligible level or that larger tortoises tended to migrate away from the Marodijeh valley. Certainly, younger animals, suggesting at least some recruitment, were found among rough ground vegetation and in woodland habitat supported by the alluvial soil in the lower valley; however, no small tortoises with fewer than nine growth annuli were detected.

Sexual size dimorphism varies in tortoises (Berry and Shine, 1980) and is normally associated with combat when males are larger than females. Male *G. pardalis* do not exceed females in size at Hargeisa. However, in another somewhat larger sub-Saharan species, *G. sulcata*, which appears to be sympatric with *G. pardalis* in southern Ethiopia (Iverson, 1992), the males are larger, have more elongate shells in horizontal outline, and bear more strongly developed gular scutes than females. In females there is no correlation between rear aperture diameter and size (Lambert, 1993). As in *G. sulcata*, carapacial outline in adult male *G. pardalis* becomes more elongate, but the anal scutes become increasingly divergent, and rear aperture diameter decreases exponentially – in females, rear aperture diameter increases exponentially. Some of these secondary sexual characteristics are presumably involved with courtship and may facilitate intromission in relation to the mechanical limitations imposed by a rigid skeletal exterior. There was, however, no evidence that the exponential increase of aperture diameter in female *G. pardalis* was related to size-assortative, or dissortative, mating as discussed by Swingland and Stubbs (1985) in the smaller Mediterranean *Testudo hermanni*.

The sparse shell pigmentation of tortoises at Hargeisa is similar to the Djibouti animal depicted by Pritchard (1979). Patterning on museum *G. pardalis* from elsewhere in the range was variable and is unlikely to provide a basis for taxonomic differentiation.

The range of *G. sulcata* forms an east-west band across Sahelian Africa, while *G. pardalis* has an extensive north-south range spanning the Equator in xeric parts of the eastern half of Africa (Iverson, 1992). Evidence suggests that there is little geographical size variation in the former species (Lambert, 1993), while in this work considerable variation was found in *G. pardalis*. The difference might be explained by the obvious difference in climate (see Table 4), with high or consistent rainfall at respectively the northern and southern range extremes coinciding with the warmer months of the year. Such conditions from April to September in the north and December to March in the south of the range give rise to copious green vegetation and fast growth. Wet summers and dry winters west of Somaliland are also experienced across Africa's Sahelian zone by *G. sulcata* (Lambert, 1993), which grows to be the largest of the world's mainland tortoise species. In South America, north-south variants of *Chelonoidis chilensis* in the Southern Hemisphere exhibit the same cline in size (Ernst and Barbour, 1989) as *G. pardalis*.

Further investigations, within the context of sustainable utilization of *G. pardalis*, are required on the interaction between the effects of collection for local human consumption and trade, and climatic variation on body size and population density. The factors and ecological conditions in sub-Saharan Africa normally influencing growth, size, and survivorship need greater understanding.

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APPENDIX

Localities from north to south, with museum accession numbers where valid, for preserved material of *Geochelone pardalis* measured: **Somaliland**: Nogal Valley (ca. 7°21'N, 47°27'E), BMNH 1931.7.20.411; **Somalia**: unspecified localities, SMF 34191 (Zoo Leipzig), 34353, 34443; **Ethiopia**: SW Lake Abaya (ca. 6°04'N, 37°25'E), BMNH 1969.299, 1969.303; NW Lake Chamo (ca. 6°01'N, 37°23'E), BMNH 1969.298; NE Lake Chamo (ca. 5°35'N, 37°28'E), BMNH 1969.302; **Sudan**: Bahr-el-Jebel (Upper Nile), BMNH 1932.7.22.1-2; **Kenya**: Murri (= Malka Mari) (4°14'N, 40°49'E), BMNH 1952.1.9.12-13; Ndogo, S. of Lake Baringo (ca. 0°31'N, 36°06'E), BMNH 1893.11.21.1; unspecified locality (coll. J. Leakey, 1970); **Uganda**: Mt. Elgon (1°08'N, 34°33'E), BMNH 1934.10.23.1; **Tanzania**: Western Kilimanjaro-steppe (ca. 3°00'S, 37°00'E) (coll. C.G. Schillings, 1.ix.1896), SMF 7755; "East Central Africa", probably Tanzania: unspec. locality (coll. Capt. J. Speke), BMNH 1863.8.11.9; **Zimbabwe**: Mt. Darwin (16°52'S, 31°37'E), BMNH 1902.7.24.1; Matusadona Nat. Park (16°47'S, 28°33'E) (coll. M.R.K. Lambert, 31.vii.1990); **Angola**: Moçâmedes (15°10'S, 12°09'E), BMNH 1984.1275; Cubal (13°02'S, 14°19'E) (coll. W. Schack, 1936), SMF 22278; **Botswana**: Mahalapye (23°04'S, 26°50'E), BMNH 1910.5.27.16; **Namibia**: Waterberg (20°31'S, 17°14'E), BMNH 1937.12.3.170-171, and Waterberg Plateau (20°25'S, 17°15'E), 1937.12.3.172-174; Omatjene, nr. Otjiwarongo (20°24'S, 16°31'E) (coll. R. Mertens, 25.x.1952), SMF 46245; Ogosogomingo (?=Okozongoro; 21°08'S, 16°04'E) (coll. R. Mertens, 28.x.1952), SMF 46246; Windhoek (22°28'S, 16°39'E) (coll. G. Mertens, 1934), SMF 22305-6; 8 km S. of Otjiwarongo (20°28'S, 16°52'E) (coll. A.F. Triebner, 21.ii.1955), SMF 52800; Sukses, S. of Waterberg (21°02'S, 16°52'E) (coll. H. Finkeldey, 27.ii.1963), SMF 59430; 16 km W. of Fransfontein, Kaokoveld (20°13'S, 14°59'E) (coll. W. Trieb, 5.viii.1956), SMF 66268; unspec. localities, SMF 7751-2 (coll. H. Schinz, 1889), 7753 (Zoo Frankfurt, 1910), 7756-61 (1911), 7762 (coll. A.

Schenck, 1891); **South Africa**: Port Elizabeth (Algoa Bay) (33°50'S, 25°50'E), BMNH 1863.7.3.1; unspec. localities, BMNH 1838.6.9.123, 1846.2.13.18, 1851.7.9.12, 1854.5.4.2, 1862.6.27.1 (two); unspecified country, probably Namibia: SMF 7754 (old collection, 1845), 29984 (E. Kühnscherf estate, 1939); probably Kenya: SMF 70621 (from animal trade, 19.x.1981, D. Boxheimer).

Further locality records for *G. pardalis* in the Gobol (Region of) Wogooyi Galbhed, Somaliland: Arabsiyo (9°41'N, 43°46'E), 37 km W.N.W. of Hargeisa, many observed during rains from April to June 1992 feeding and causing damage to lettuce crops (Mohammed Warsame Farah, *pers. comm.*); Tog Wajale (9°37'N, 43°19'E), 83 km W. of Hargeisa, common (Gibbs, 1988).

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