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## Population Structure and Density of Leopard Tortoises (*Geochelone pardalis*) on Farmland in the Nama-Karoo

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**ABSTRACT.**—The Leopard Tortoise (*Geochelone pardalis*) is the largest of the southern African species and has a wide distribution encompassing a variety of habitats. There is a paucity of ecological information about Leopard Tortoises in these habitats. The goal of this study was to determine the population density, biomass, sex and age distributions, and morphometrics of Leopard Tortoises on farmland in the semi-arid Nama-Karoo. Because previous studies have found that body size distributions vary between mesic and xeric habitats, we expected that these Leopard Tortoises would show an increased body size compared to those from more mesic areas. In addition, we expected lower densities of Leopard Tortoises compared to more mesic areas. In total, 92 tortoises were caught with a male to female sex ratio of 1:1.3 that was not significantly

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different from unity. Adult females were significantly larger than males with respect to all morphometric measurements. Leopard Tortoises (excluding juveniles) were larger than those from more mesic areas. A population estimate of  $57.6 \pm 4.0$  tortoises in a 5500 ha area was obtained using a mark-recapture sampling method and radio-telemetry. Density of tortoises was extremely low at  $0.017$  tortoises  $\text{ha}^{-1}$ , with a biomass of  $0.002 \text{ kg ha}^{-1}$ . Population density and biomass were lower compared with Leopard Tortoise populations in more mesic areas. This has implications for the understanding of fitness parameters and conservation of this species in semiarid areas.

Southern Africa has the greatest diversity of terrestrial tortoises (Family: Testudinidae) in the world, hosting a third of the world's 40 species (Boycott and Bourquin, 2000). Most of these southern African species have a restricted distribution and occur in arid to semiarid areas in the Cape Region, South Africa (Boycott and Bourquin, 2000). However, the largest of the African tortoises, the Leopard Tortoise, *Geochelone pardalis* (Bell, 1828), also has the widest distribution extending from southern to eastern Africa.

Evolution of body size is a trait of great significance in both ectotherms and endotherms in terms of ecophysiology as shown by numerous allometric studies (Chown et al., 2003). One facet is that sexual size dimorphism is important in determining fitness parameters in organisms like reptiles as it affects attainment of maturity, clutch size and egg size (Congdon and van Loben Sels, 1993). In addition, sexual size dimorphism may be related to intersexual variation in juvenile or adult growth rates or mortality (Willemssen and Hailey, 2001). Much research has focused on hatchling phenotype in reptiles and the influence of temperature, particularly on sex determination or differential mortality rates of males and females (Judd and Rose, 1983; Booth, 2006). However, in tortoise populations, size composition is skewed either to smaller sizes because of high recruitment rates with relatively large numbers of juveniles and subadults (Kabigumila, 2001a) or is biased to larger sizes because of adult longevity and low recruitment rates (Judd and Rose, 1983).

Despite its generally large size, the Leopard Tortoise shows variation in mean adult body size throughout Africa, with tortoises in the north (Republic of Somaliland) being of comparable size to insular giant tortoises (Hailey and Lambert, 2002). Those from Somaliland had similar juvenile growth rates and asymptotic sizes to other populations, and their large mean size was caused by high survival and continued linear growth after the asymptote (Hailey and Lambert, 2002). Leopard Tortoises in a protected area in northern Tanzania showed a paucity of smaller size classes as a consequence of few juveniles, although this may have been a consequence of drought or difficulty in locating small

tortoises in the dense vegetation (Kabigumila, 2001a). In contrast, Leopard Tortoise size ratios in an unprotected area in Tanzania were skewed toward juveniles and subadults as a consequence of an expanding human population (Kabigumila, 2001a).

However, in a study of *Testudo hermanni* in Greece, the adult size was considered adaptive and the result of variation in adult survival rates rather than juvenile survival (Willemssen and Hailey, 2001). In Zimbabwe, survival rates of Leopard Tortoises were lower than other tortoise species ( $0.72\text{--}0.80 \text{ y}^{-1}$ ; Hailey and Coulson, 1999). There was significant sexual size dimorphism with females being larger than males (Hailey and Coulson, 1999). Despite this, the population sex ratio was male-biased (Hailey and Coulson, 1999). This supported the prediction that sex ratios of tortoises are skewed and male-biased if females are larger (Lovich, 1996).

Population density of tortoises is also complex and can be affected by several factors, such as food and water availability, predation, recruitment, and population demography (Breitinger et al., 1994; Dean and Milton, 1999; Freilich et al., 2000; Coulson and Hailey, 2001). Leopard Tortoises occur in a range of habitats from grassland, savannah, tropical woodland and arid to semiarid Karoo (Boycott and Bourquin, 2000). Food and water resources in xeric areas are generally low and patchy in availability (Dean and Milton, 1999). In widespread tortoises, such as Leopard Tortoises, whose range extends from mesic to more xeric regions, and who cannot escape the adverse conditions, lower population densities are expected in the more xeric areas compared with mesic areas because of low recruitment rates and food availability.

Little ecological information has been collected on the Leopard Tortoise despite its conspicuous size and wide distribution (Branch, 1984; Branch and Braack, 1987; McMaster 2001). Most data regarding Leopard Tortoise morphometrics are from observations of captive individuals (Archer, 1948; Jaques, 1969; Rall, 1988) or casual field observations (Rall, 1985). However, a few studies have investigated sex ratios, population estimates, density, mortality, and

morphometrics of Leopard Tortoises in the wild, although these studies were conducted in mesic areas in southern and central Africa, and there has been a lack of investigation in semiarid regions (Burger and Branch, 1994; Grobler, 1982; Mason et al., 2000; Kabigumila, 2001a,b).

Thus, the aim of this study was to determine the sex and age class distributions, population density, biomass, and morphometrics of Leopard Tortoises on farmland in the semiarid Nama-Karoo biome. We expected that Leopard Tortoises in the Nama-Karoo would show an increased body size compared with those from more mesic areas because of survival rates of older individuals or as a mechanism to deal with the extreme fluctuations in temperature and resources. In addition, we expected that Leopard Tortoises would be found in lower densities compared with more mesic areas as a consequence of the latter.

#### MATERIALS AND METHODS

Leopard Tortoises were studied in a 5500-ha area in the De Aar District, which is situated in the Nama-Karoo biome, South Africa (31°04'S, 23°41'E). The area comprises mixed commercial sheep and game farms of 26,000 ha and grassy dwarf shrubland (Palmer and Hoffman, 1997). The average annual rainfall is low (200–400 mm), with its highest rainfall in late summer and autumn. Daily temperatures are variable and range from 5–39°C in spring (September through November) and summer (December through February) and from –5–26°C in autumn (March through May) and winter (June through August).

Leopard Tortoises were located by riding transects on horseback in the study area twice daily. Date, time, type of activity, and the geographical position of all tortoises were recorded using a handheld Trimble Navigation GeoExplorer II Geographical Position System (GPS) unit. Individual tortoises were marked using a coded sequence of notches filed into their marginal scutes following Branch (1984). All tortoises were sexed and weighed, and various morphometric characteristics were recorded. Measurements (to the nearest 1 mm) were taken of curved carapace length, curved carapace width, carapace side length, straight carapace height, length, and width, and the distance between the two front marginal shields (i.e., the front marginal shield gap). Tortoises were broadly placed into age classes based on body mass as adult, subadult, or hatchlings. If male tortoises weighed < 5 kg, and females < 10 kg, they were considered subadults.

In addition to opportunistic sightings, eight female and six male tortoises were fitted with unique-frequency radio transmitters weighing 60 g (< 1% body mass), powered by a 3.6 V lithium battery, with a one-fourth wavelength stainless steel tracer wire antennae. The latter was potted in moulded PVC tubing and attached to the carapace with dental acrylic. The transmitters were made locally by the University of KwaZulu-Natal Electronics Centre. Telemetered tortoises were tracked with YAESU (California) transceivers and a Yagi antenna. Telemetered Leopard Tortoises were located twice daily for three-month periods from October 1997 to April 1999. The radio-telemetry was used as a tool to locate the tortoises to determine presence and abundance as suggested for species where sighting is affected by season, habitat or behaviour (Díaz et al., 2006).

Descriptive statistics, *t*-tests and Chi-squared tests were calculated using STATISTICA software (Statsoft, Tulsa, OK). Population size of Leopard Tortoises was estimated using the Jolly-Seber mark-recapture equation and using Method B table (following Krebs, 1989; Zar, 1996). Density of Leopard Tortoises was calculated as a function of a 5500-ha area using (1) the total number of tortoises located, (2) the estimated population size, and (3) the number of male and female tortoises. Similarly, Leopard Tortoise biomass (total mass in kilogram of tortoises per hectare) was estimated for all tortoises, as well as for males and females using mean body mass.

#### RESULTS

*Number, Sex, and Age Distribution of Tortoises Captured.*—Observations of Leopard Tortoise activity were made on 3958 occasions over the total search time of 2615 person-hours. Number of Leopard Tortoises caught and number of observations per season with regard to sex and age distributions of the tortoises are shown in Table 1. A total of 92 (40 males and 52 females) Leopard Tortoises was caught. A male to female sex ratio of 1:1.3 was found when all age classes were grouped. This was not significantly different from a sex ratio of unity ( $\chi^2 = 0.818$ ,  $df = 1$ ,  $P = 0.37$ ). A total of 62 adults (19 males and 43 females; 1:2.3 sex ratio) were captured, 26 subadults (18 males and eight females; 1:0.44 sex ratio) and only four hatchlings (Table 1). However, some males classified as subadults were later found to be sexually active. Also there was a bias because of the different mass classes used for males and females. Therefore, it seems that age classes are contentious and that this differentiation is inappropriate.

TABLE 1. Number of Leopard Tortoises captured and the number of observations of these tortoises per season with regard to sex and age class distributions on farmland in the Nama-Karoo, South Africa from October 1997 through April 1999.

	Spring	Summer	Autumn	Winter	Total
Tortoises captured <sup>a</sup>	34	53	4	1	92
Captured males	20	17	3	0	40
Captured females	14	36	1	1	52
Captured adults	20	39	2	1	62
Captured subadults	13	12	1	0	26
Captured hatchlings	1	2	1	0	4
Number of observations <sup>b</sup>	1208	1240	637	814	3899
Observed males	498	523	264	316	1601
Observed females	710	717	373	498	2298
Observed adults	964	1063	521	588	1121
Observed subadults	243	175	115	226	758
Observed hatchlings	1	2	1	0	4

<sup>a</sup>"Captured" is the first sighting and marking of a tortoise.

<sup>b</sup>"Observed" is the repeated sighting of all of the marked tortoises.

The majority of Leopard Tortoises were caught in spring (37%) and summer (58%), with males being caught more frequently in spring and females more frequently in summer (Table 1). Table 1 shows records of both recaptured and telemetered tortoises. Most Leopard Tortoises were observed in summer and spring, with a similar number of observations of male and females in summer and spring (Table 1). Most adult observations were in spring and summer; however, observations of subadults were more frequent in spring and winter (Table 1). Hatchlings were never recaptured; hence, capture and observation frequencies were the same (Table 1).

*Morphometrics.*—As a consequence of the bias in determining subadults and adults Leopard Tortoises as mentioned above, these were grouped for analyses of their morphometrics, and juveniles were excluded. Adult female Leopard Tortoises were significantly heavier than males (Table 2). In addition, adult females

were also significantly larger than males for the other size measurements taken (Table 2).

Body mass and straight carapace lengths of Leopard Tortoises (excluding juveniles) captured and measured were plotted as frequency distributions to show differences in body size in terms of sex (Fig. 1). Frequency distribution of male body mass was negatively skewed compared to the females (Fig. 1A). Furthermore, more females had a greater body mass than males (Fig. 1A). Male carapace length was negatively skewed (Fig. 1B). Most females had straight carapace lengths of about 40 cm, whereas most males were about 35 cm in length (Fig. 1B).

*Population Size and Density.*—Using the Jolly-Seber method of population estimation, a population size of  $57.6 \pm 4.0$  Leopard Tortoises was estimated on farmland in the Nama-Karoo, South Africa, from monthly sightings and recapture from October 1997 through April 1999. In addition, 98% of tortoises marked were

TABLE 2. Differences in morphological characters between female and male Leopard Tortoises (adult and subadults combined and excluding juveniles) captured on farmland in the Nama-Karoo, South Africa from October 1997 through April 1999.

Morphological Character	Males					Females					<i>t</i>
	Mean	SE	Min	Max	<i>N</i>	Mean	SE	Min	Max	<i>N</i>	
Curved carapace length (cm)	47.5	11.0	6.2	63.0	39	55.9	7.4	22.5	69.5	51	-6.06***
Curved carapace width (cm)	45.4	10.9	6.5	61.7	39	54.6	7.2	22.0	66.5	51	-6.47***
Carapace side length (cm)	32.8	7.8	5.0	46.6	39	39.1	5.4	15.5	49.0	51	-6.00***
Straight carapace height (cm)	16.8	4.6	2.4	27.0	32	20.5	3.2	7.0	26.0	48	-5.20**
Straight carapace length (cm)	35.4	10.3	5.2	47.0	23	42.8	4.7	28.0	49.5	35	-3.05**
Straight carapace width (cm)	23.0	6.3	4.5	31.0	23	30.3	4.6	21.0	43.0	35	-6.09***
Front marginal shield gap (cm)	7.2	1.9	1.3	12.0	39	8.3	1.4	3.2	11.0	51	-4.31**
Mass (kg)	7.6	3.3	4.4	15.9	32	15.2	5.3	5.6	18.8	43	-7.33***

$P < 0.005^{**}$ ,  $P < 0.0001^{***}$ .

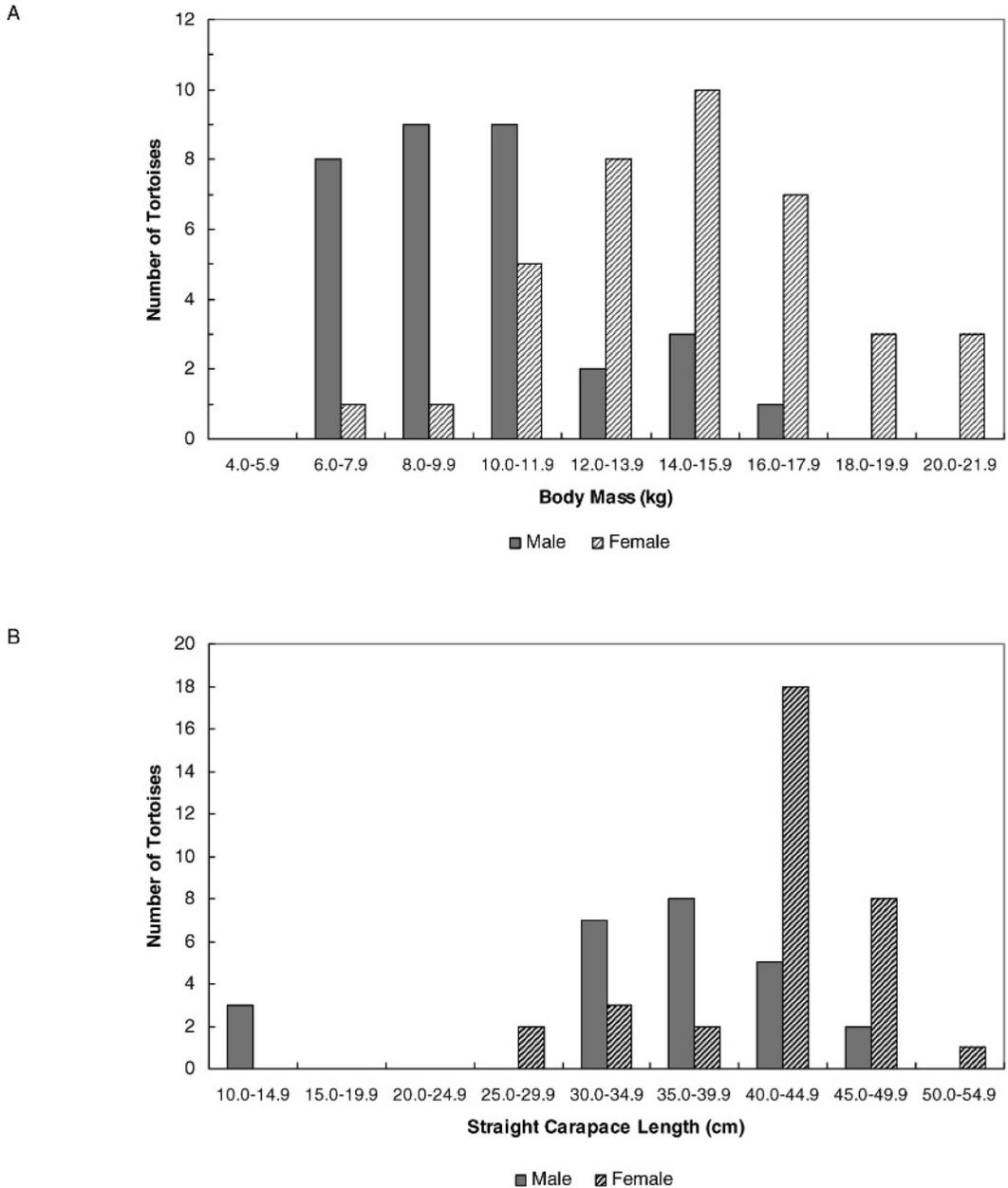


FIG. 1. Frequency distribution of (A) body mass (kg) and (B) straight carapace length (cm) for male and female Leopard Tortoises on farmland in the Nama-Karoo, South Africa.

recaptured at least twice. Density was calculated over 5500 ha as (1) 0.017 tortoises  $\text{ha}^{-1}$  using the total number of tortoises caught, (2) 0.010 tortoises  $\text{ha}^{-1}$  using the estimated population size, and (3) 0.007 males  $\text{ha}^{-1}$  and 0.009 females  $\text{ha}^{-1}$  using estimated population size.

Biomass of Leopard Tortoises on farmland in the Nama-Karoo was 0.002  $\text{kg ha}^{-1}$  for all tortoises using the mean mass (Table 2),

0.001  $\text{kg ha}^{-1}$  for males and 0.003  $\text{kg ha}^{-1}$  for females, using their respective mean masses.

#### DISCUSSION

*Locating Terrestrial Tortoises.*—Generally, it appears that capture and sighting frequency of terrestrial tortoises vary with sampling effort, time, season, size of the species and habitat type

(Coulson and Hailey, 2001; Kabigumila, 2001a,b; Willemsen and Hailey, 2001). In the present study, despite similar sampling effort over seasons, most Leopard Tortoises were sighted and captured during spring and summer. These Leopard Tortoises were active earlier and for longer periods in warmer temperatures (McMaster, 2001) and, therefore, were more easily sighted in spring and summer, compared with autumn and winter. In addition, during spring, summer and autumn tortoises drank and fed at livestock watering points, where they were easily visible (McMaster, 2001). In winter, tortoises hibernated and retreated to refuges where they were cryptic and easily overlooked (McMaster, 2001). Radio telemetry allowed for the location of Leopard Tortoises with transmitters fitted year-round; hence, the observational data obtained during autumn and winter. This supports the importance of radiotelemetry as a tool to determine presence and abundance of tortoises, particularly in species where sighting is affected by season, habitat or behaviour (Díaz et al., 2006).

*Complexities of Age, Sex, and Size Distribution of Terrestrial Tortoises.*—There are problems with distinguishing age class categories based on size or mass in terrestrial tortoises. We initially based age classes on mass, but after finding some subadult males sexually active, we grouped subadults and adults in further analyses. Other workers have similarly distinguished only between juveniles and adults (including subadults; Lambert, 1982; Meek, 1985).

The age class structure of Leopard Tortoises on farmland in the Nama-Karoo was skewed with few juveniles. The low number of hatchlings caught may be because of the difficulty of sighting them in the field but may also indicate a population skewed toward adults. This may imply a lack of juvenile recruitment, which may be a result of high predation, low egg fertility, or high juvenile mortality. Further investigation is needed to determine whether there is a paucity of juveniles and hatchlings in the population or whether they were merely overlooked in sampling. Similarly, in an unprotected area in Tanzania, few juvenile Leopard Tortoises were found (Kabigumila, 2001a), and this was attributed to sight as well as drought. No juvenile Leopard Tortoises were found in the Mountain Zebra National Park, South Africa, and it was concluded that predation on juveniles caused the population to consist primarily of adults (Grobler, 1982). However, other factors may have skewed the population toward adults, such as fences limiting the immigration of adults out of the park. Meek (1985) reported that many populations of land tortoises have

age and size frequencies skewed toward large and older individuals in conjunction with low recruitment rates of 1–5%. As in our study, it generally appears that terrestrial tortoises show skewed age distributions as a result of low recruitment. This is probably because of the high vulnerability at low sizes and decreased vulnerability at large sizes combined with a long life span (mostly at larger sizes).

Other studies have found that, where females were larger than males, there was a skewed sex ratio with fewer females (Lovich, 1996; Judd and Rose, 1983; Hailey and Coulson, 1999). Despite the greater size of females in the present study, there was an insignificant difference in the 1:1.3 male:female sex ratio (excluding juveniles). In contrast, there was a significantly female-biased sex ratio of 1:1.75 males:females in Leopard Tortoises in the Mountain Zebra National Park, South Africa (Grobler, 1982). Both *Gopherus polyphemus* and *T. hermanni* showed apparent seasonal differences in the sex ratio obtained (Hailey et al., 1984; Diemer, 1992). Similarly, *G. polyphemus* showed variation in sex ratios among habitats (Breininger et al., 1994). Thus, the sex ratio of males to females in terrestrial tortoises may be biased by several factors, including season, habitat type, and female to male size.

In the present study, female Leopard Tortoises were significantly heavier (about twice as heavy) than males. In addition, they were larger than males with regard to all morphological characters measured (Table 2). Similarly female Leopard Tortoises in Thicket Biome, South Africa, were also larger than the males (Mason et al., 2000). However, these tortoises were smaller in size than those observed in the present study (Mason et al., 2000). Again female Leopard Tortoises (mean mass 12.2 kg, maximum 16.4 kg) in the Mountain Zebra National Park weighed more than males (mean mass 10.5 kg, maximum 18.4 kg) but only 1.2 times (Grobler, 1982). These tortoises, however, were larger than males and females in the present study. In Zimbabwe, female Leopard Tortoises were 1.7 times heavier than males (Hailey and Coulson, 1999). Consequently, female Leopard Tortoises seem to be consistently larger than males regardless of habitat; however, the mean mass and total lengths of both males and females vary between sites. Although Leopard Tortoises appear larger in more xeric areas (Hailey and Lambert, 2002; present study), more data are required along an aridity gradient to determine this. Furthermore, Leopard Tortoises may be larger in a more extreme environment to buffer the effects of extreme temperatures by decreasing the surface:volume ratio. In addition, Leopard Tortoises have the largest body

mass and size compared with other xeric-dwelling chelonians both in south and eastern Africa (Boycott and Bourquin, 2000; Diemer, 1992; Meek, 1985).

Southern Africa is characterized by an unpredictable environment with daily and seasonal temperature fluctuations as well as variations in precipitation on a seasonal or temporal interannual basis and spatially (Schulze, 1997). Consequently, food availability for most animals is also in flux. Fluctuations in the thermal environment may elicit different physiological, behavioural and ecological responses (Seebacher et al., 2004). In many species, there is limited variation in physiological traits; and for many traits, there is a continuum of variation and specialization, yet clear physiological "strategies" can be identified (Chown et al., 2003). As mentioned, the evolution of body size is a trait of great significance in ectotherms (Chown et al., 2003). In particular, size in reptiles is important in determining fitness parameters such as clutch size and egg size and in determining variation in juvenile or adult growth rates or mortality. In addition, increased size in Leopard Tortoises reflects survival of a few in the more unpredictable and extreme xeric habitats.

*Low Resource Availability Influences Terrestrial Tortoise Density.*—The population of Leopard Tortoises on farmland in the Nama-Karoo was estimated to be  $57.6 \pm 4.0$  tortoises. This density was extremely low at  $0.017$  tortoises  $\text{ha}^{-1}$  using all tortoises caught and at  $0.010$  tortoises  $\text{ha}^{-1}$  using the population estimate. Leopard Tortoises in the Addo Elephant National Park, South Africa, had a population of 85 tortoises per 100 ha (i.e.,  $0.85$  tortoises  $\text{ha}^{-1}$ ; Branch and Braack, 1987). This is an order of magnitude greater than the density found in the present study. Similarly, the biomass calculated for Leopard Tortoises in the present study was an extremely low ( $0.002$  kg  $\text{ha}^{-1}$  for all tortoises,  $0.001$  kg  $\text{ha}^{-1}$  for males and  $0.003$  kg  $\text{ha}^{-1}$  for females). In comparison, Leopard Tortoises in the Addo Elephant National Park had a biomass of  $6.02$  kg  $\text{ha}^{-1}$  (Mason et al., 2000). Thus, it seems evident that density is strongly influenced by habitat type and productivity. Similarly, the density of *G. polyphemus* was found to be influenced by habitat type (Breininger et al., 1994) and environmental effects (Kushlan and Mazzotti, 1984), whereas extreme environmental conditions influenced the density of *Gopherus agassizii* (Freilich et al., 2000).

In summary, female Leopard Tortoises on farmland in the Nama-Karoo, South Africa, were larger than males, but the sex ratio did not differ from unity. These Leopard Tortoises were larger in size compared to other popula-

tions in more mesic areas. In addition, Leopard Tortoise densities and biomass in this study were low compared to populations in other habitats. This has implications for the understanding of fitness parameters and the conservation of this species in semiarid areas.

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#### LITERATURE CITED

- ARCHER, W. H. 1948. The mountain tortoise. *African Wildlife* 2:75–78.
- BOOTH, D. T. 2006. Influence of incubation temperature on hatchling phenotype in reptiles. *Physiological and Biochemical Zoology* 79:274–281.
- BOYCOTT, R. C., AND O. BOURQUIN. 2000. *The South African Tortoise Book: A Guide to the Southern African Tortoises, Terrapins and Turtles*. Southern Book Publishers, Johannesburg, South Africa.
- BRANCH, W. R. 1984. Preliminary observations on the ecology of the Angulate Tortoise (*Chersina angulata*) in the eastern Cape Province, South Africa. *Amphibia-Reptilia* 5:43–55.
- BRANCH, W. R., AND H. H. BRAACK. 1987. Reptiles and amphibians of the Addo Elephant National Park. *Koedoe* 30:61–111.
- BREININGER, D. R., P. A. SCHMALZER, AND C. R. HINKLE. 1994. Gopher Tortoise (*Gopherus polyphemus*) densities in coastal scrub and slash pine flatwoods in Florida. *Journal of Herpetology* 28:60–65.
- BURGER, M., AND W. R. BRANCH. 1994. Tortoise mortality caused by electrified fences in the Thomas Baines Nature Reserve. *South African Journal of Wildlife Research* 24:32–37.
- CHOWN, S. L., A. ADDO-BEDIAKO, AND K. J. GASTON. 2003. Physiological diversity: listening to the large scale signal. *Functional Ecology* 17:568–572.
- CONGDON, J. D., AND R. C. VAN LOBEN SELS. 1993. Relationships of reproductive traits and body size with attainment of sexual maturity and age in Blanding's Turtles (*Emydoidea blandingi*). *Journal of Evolutionary Biology* 6:547–557.
- COULSON, I. M., AND A. HAILEY. 2001. Low survival and high predation in the African Hingeback Tortoise *Kinixys spekii*. *African Journal of Ecology* 39:383–392.
- DEAN, W. R. J., AND S. J. MILTON. 1999. *The Karoo: Ecological Patterns and Processes*. Cambridge University Press, Cambridge.
- DIAZ, J. A., C. MONTASTERIO, AND A. SALVADOR. 2006. Abundance, microhabitat selection and conservation of Eyed Lizards (*Lacerata lepida*): a radiotelemetric study. *Journal of Zoology (London)* 268:295–301.

- DIEMER, J. E. 1992. Demography of the tortoise *Gopherus polyphemus* in northern Florida. *Journal of Herpetology* 26:281–289.
- FREILICH, J. E., K. P. BURNHAM, C. M. COLLINS, AND C. A. GARRY. 2000. Factors affecting population assessments of desert tortoises. *Conservation Biology* 14:1479–1489.
- GROBLER, J. H. 1982. The Leopard Tortoise in the Mountain Zebra National Park. *Koedoe* 25:49–53.
- HAILEY, A., AND I. M. COULSON. 1999. The growth pattern of the African tortoise *Geochelone pardalis* and other chelonians. *Canadian Journal of Zoology* 77:181–193.
- HAILEY, A., AND M. R. K. LAMBERT. 2002. Comparative growth patterns in Afrotropical giant tortoises (Reptilia Testudinidae). *Tropical Zoology* 15:121–139.
- HAILEY, A., E. A. PULFORD, AND D. STUBBS. 1984. Summer activity patterns of *Testudo hermanni* Gmelin in Greece and France. *Amphibia-Reptilia* 5:69–78.
- JAQUES, J. 1969. Hatching and early life of the mountain tortoise. *African Wildlife* 23:95–104.
- JUDD, F. W., AND F. I. ROSE. 1983. Population structure, density and movement of the Texas tortoise (*Gopherus berlandi*). *Southwest Naturalist* 28:387–398.
- KABIGUMILA, J. 2001a. Size composition and sex ratio of the Leopard Tortoise (*Geochelone pardalis*) in Northern Tanzania. *African Journal of Ecology* 39:393–395.
- . 2001b. Sighting frequency and food habits of the Leopard Tortoise, *Geochelone pardalis*, in Northern Tanzania. *African Journal of Ecology* 39:276–285.
- KREBS, C. J. 1989. *Ecological Methodology*. HarperCollins, New York.
- KUSHLAN, J. A., AND F. J. MAZZOTTI. 1984. Environmental effects on a coastal population of Gopher Tortoises. *Journal of Herpetology* 18:231–239.
- LAMBERT, M. 1982. Studies on the Growth, structure and abundance of the Mediterranean Spur-Thighed Tortoise *Testudo graeca* in field populations. *Journal of Zoology (London)* 196:165–189.
- LOVICH, P. J. 1996. Possible demographic and ecological consequences of sex ratio manipulation in turtles. *Chelonian Conservation Biology* 2:114–117.
- MASON, M. C., G. I. H. KERLEY, C. A. WEATHERBY, AND W. R. BRANCH. 2000. Angulate and Leopard Tortoises in the Thicket Biome, Eastern Cape, South Africa: populations and biomass estimates. *African Journal of Ecology* 38:147–153.
- McMASTER, M. K. 2001. The Status and Ecology of the Leopard Tortoise (*Geochelone pardalis*) on Farmland in the Nama-Karoo. Unpubl. master's thesis, University of Natal, Pietermaritzburg, South Africa.
- MEEK, R. 1985. Aspects of the ecology of *Testudo hermanni* in southern Yugoslavia. *British Journal of Herpetology* 6:437–445.
- PALMER, A. R., AND M. T. HOFFMAN. 1997. Nama-Karoo. In R. M. Cowling, D. M. Richardson, and S. M. Pierce (eds.), *Vegetation of Southern Africa*, pp. 167–188. Cambridge University Press, Cambridge.
- RALL, M. 1985. Ekologiese waarnemings van'n bergskilpadpopulasie, *Geochelone pardalis* Bell, 1828, soos aangeteken in die soetdoring-natuurreservaat in die Oranje-Vrystaat. *Koedoe* 28:47–60.
- . 1988. Observations on the growth of the Leopard Tortoise *Geochelone pardalis* in captivity. *Journal of Herpetological Association of Africa* 35:7–8.
- SCHULZE, R. E. 1997. *South African Atlas of Agrohydrology and Climatology*. Water Research Commission, Pretoria, South Africa.
- SEEBACHER, F., J. SPARROW, AND M. B. THOMPSON. 2004. Turtles (*Chelodina longicollis*) regulate metabolic enzyme activity in response to seasonal variation in body temperature. *Journal of Comparative Physiology B* 174:205–210.
- WILLEMSSEN, R. E., AND A. HAILEY. 2001. Variation in adult survival rate of the tortoise *Testudo hermanni* in Greece: implications for the evolution of body size. *Journal of Zoology* 255:43–53.
- ZAR, J. H. 1996. *Biostatistical Analysis*. 3rd ed. Prentice Hall, Englewood Cliffs, NJ.

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