



## **Activity and Movement Patterns of the Tortoise *Stigmochelys pardalis* in a Subtropical Savanna**

Authors: Monadjem, Ara, McCleery, Robert A., and Collier, Bret A.

Source: Journal of Herpetology, 47(2) : 237-242

Published By: Society for the Study of Amphibians and Reptiles

URL: <https://doi.org/10.1670/12-070>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## Activity and Movement Patterns of the Tortoise *Stigmochelys pardalis* in a Subtropical Savanna

ARA MONADJEM,<sup>1,2</sup> ROBERT A. MCCLEERY,<sup>3</sup> AND BRET A. COLLIER<sup>4</sup>

<sup>1</sup>All Out Africa Research Unit, Department of Biological Sciences, University of Swaziland, Private Bag 4, Kwaluseni Swaziland

<sup>3</sup>Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611 USA

<sup>4</sup>Institute of Renewable Natural Resources, Texas A&M University, College Station, Texas 77843 USA

**ABSTRACT.**—Radio-tracking studies of African tortoises have elucidated differences in spatial ecology in differing habitats. Our study aimed to demonstrate such patterns by radio tracking the Leopard Tortoise *Stigmochelys pardalis* in a subtropical savanna, northeast Swaziland. Activity of tracked tortoises was correlated with minimum temperatures and greater in the warm wet months compared with the cool, dry months. All tracked tortoises, however, remained active throughout the cool months, and none were observed entering a burrow or any other hibernaculum. The tortoises typically moved 0–89 m per day, with maximum daily movement of over 300 m. A dry river bed and game viewing road did not appear to obstruct the movement of the tortoises.

The activity patterns of ectothermic animals often show strong seasonality (Adolph and Porter, 1993), especially where fluctuations in ambient temperature vary (Christian and Weavers, 1996). Thermal differences may translate into differences in spatial ecology with consequences for the conservation and management of ectothermic populations. Home range and activity patterns are also expected to change with respect to seasonal fluctuations in climate (Ramsay et al., 2002).

Tortoises (family Testudinidae) show high levels of diversity and endemism in sub-Saharan Africa, but their spatial ecology has not been documented adequately (Boycott and Bourquin, 2000; Branch, 2008; McMaster and Downs, 2009). *Stigmochelys pardalis* (previously *Geochelone pardalis*) is distributed widely in southern and east Africa (Fritz et al., 2010). The home range and activity pattern of *S. pardalis* has been evaluated in a variety of habitats including the xeric Nama-Karoo, South Africa (McMaster and Downs, 2009), mesic valley thicket of the Eastern Cape, South Africa (Mason and Weatherby, 1995) and miombo/mopane woodland in Zimbabwe (Hailey and Coulson, 1996a). In the Nama-Karoo *S. pardalis* exhibited strong sex-related seasonal differences in activity, with greatly reduced activity in the cool winter months by both sexes (McMaster and Downs, 2009). In the same region, the species also made use of refuges and solar orientation to behaviorally ameliorate the effects of seasonal changes in ambient temperature (McMaster and Downs, 2006).

What emerges from these various studies is that home ranges and activity patterns of *S. pardalis* vary considerably across southern Africa, with a trend of increasing home range with aridity (McMaster and Downs, 2009), possibly as a result of decreasing food availability (Diemer, 1992).

Our main aim was to determine the seasonal activity pattern and home range of the Leopard Tortoise *S. pardalis* in a subtropical savanna, a contrasting habitat from those previously studied. We predicted that this tortoise would be more active and have a larger home range in the wet season and that it would decrease its home range during the cool, dry season when food may be less abundant and less nutritious and when cooler temperatures may pose physiological constraints on activity (McMaster and Downs, 2006).

### MATERIALS AND METHODS

**Study Area.**—We conducted the study at Mlawula Nature Reserve (26°11'S, 31°59'E, 160 m above sea level) in northeastern Swaziland. The climate is subtropical with hot, wet summers and dry, cool winters. Mean daily temperatures for January and July are 26°C and 18°C, respectively, whereas mean annual rainfall ranges from 550–725 mm. Rain falls predominantly during summer months (December to February), with winters (June through August) generally being dry. Mean monthly rainfall in January and July are 122.0 mm and 9.3 mm, respectively. The dominant vegetation is acacia savanna with *Acacia nigrescens*, *Acacia tortilis*, *Ziziphus mucronata*, *Sclerocarya birrea*, and *Dichrostachys cinerea* being characteristic trees (Monadjem et al., 2009, 2010).

**Data Collection.**—We located and captured individual *S. pardalis* in the Siphiso valley at Mlawula Nature Reserve by walking or driving along the road network within the park, or by walking off road. All captured individuals were notched for individual identification (to avoid double counting), sexed, measured, and their mass determined. Sexing was based on the shape of the plastron (Schroeder and Robb, 2005). The following were recorded for each animal: mass, plastron length, straight carapace length, shell height, and shell width. A *t*-test (Zar, 1994) was used to test for differences between sexes in mass and measurements of *S. pardalis* captured during this study. The location of capture was recorded using a GPS, after which the tortoise was released at the point of capture.

In January/February 2010, eight *S. pardalis* were fitted with a Series 1800, flat-panel, glue-on VHF transmitter (Advanced Telemetry Systems, Isanti, MN), and individuals were released at the exact point of capture, usually within 30 min of capture.

We tracked tortoises on 65 days over a 9-month period between January and early September 2010. Greater effort (days of tracking per month) was made during the wet season in January through April (mean and range, 10.8 and 8–13 days/month) than during the cooler, dry season in June through August (5.0 and 4–7 days/month). We located tortoises by homing in (Fuller et al., 2005) on their locations with a radio-receiver (Biotrack Sika, Biotrack, Dorset, U.K.) and three element yagi antennas. Each location was marked using a Garmin 12, Global Positioning System. The date and time of each fix was also recorded, and a note was made on whether the tortoise was above ground and active, or in a burrow (and presumably inactive). Each tortoise was tracked until either the

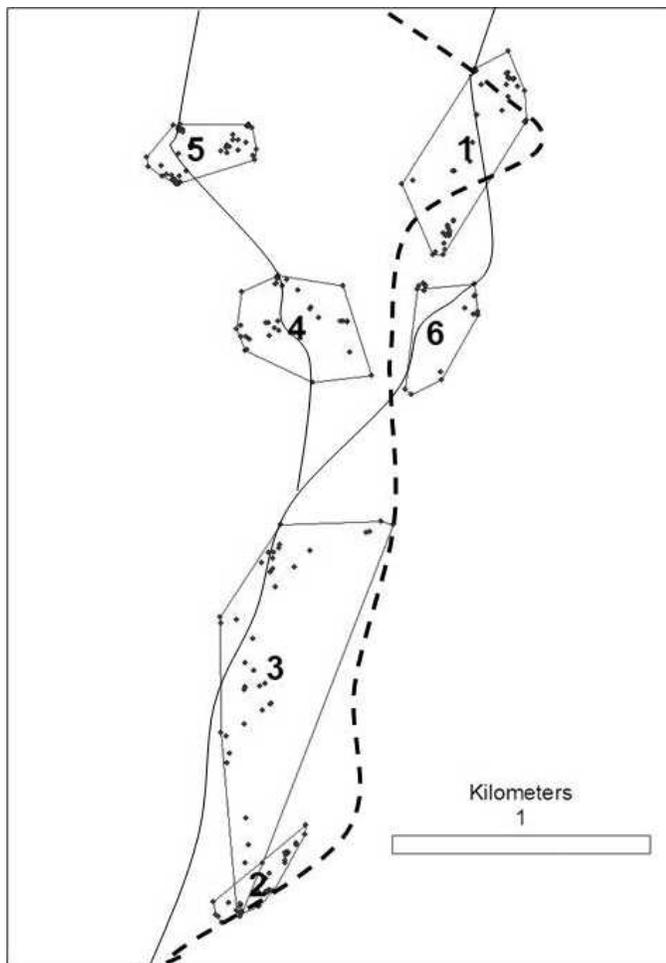
<sup>2</sup>Corresponding Author. E-mail: ara@uniswa.sz  
DOI: 10.1670/12-070

TABLE 1. Mass (g) and measurements (mm) of *Stigmochelys pardalis* captured in northeastern Swaziland.

	Mean $\pm$ standard deviation (N)		t-test results	
	Male	Female	t-value	P-value
Mass	3,524 $\pm$ 922 (16)	4,910 $\pm$ 1,928 (16)	2.59	0.017
Straight carapace length (SCL)	280 $\pm$ 17.9 (21)	286 $\pm$ 51.3 (24)	0.54	0.593
Plastron length (PL)	245 $\pm$ 20.8 (22)	261 $\pm$ 39.2 (24)	1.69	0.1000
Shell height (SH)	146 $\pm$ 29.7 (22)	148 $\pm$ 25.9 (24)	0.34	0.737
Shell width (SW)	187 $\pm$ 51.3 (21)	200 $\pm$ 32.0 (24)	1.02	0.313

TABLE 2. Sex, mass (g), measurements (mm), number of fixes and home ranges (ha) of the six *Stigmochelys pardalis* tracked in northeastern Swaziland. The number assigned to each tortoise corresponds with those in Figure 1.

#	Sex	Mass	SCL	PL	SH	SW	Fixes	Months	Home range
1	Female	6,500	310	281	129	224	50	9	17.04
2	Female	5,500	320	290	166	225	37	4	3.80
3	Female	4,090	300	280	147	185	64	8	45.89
4	Male	5,000	300	280	195	215	39	5	14.14
5	Male	3,000	270	235	134	167	57	9	6.49
6	Male	2,500	270	230	124	161	15	2	7.09

FIG. 1. Home range as determined by minimum convex polygon (MCP) of six *Stigmochelys pardalis* radio-tracked in northeastern Swaziland. The numbers in the polygons refer to the tortoise and correspond with the numbers in Table 2. The solid lines indicate the position of gravel roads whereas the dashed line represents the Siphiso River bed.

transmitter stopped transmitting or was recovered dislodged from the tortoise.

We obtained weather data from the Mlula weather station (Royal Swaziland Sugar Corp.) located within 10 km of the study site.

**Data Analysis.**—We transferred GPS locations to a Geographic Information System (GIS) database to compute home ranges of the tortoises. We used Hawth's Tools extension version 3.27 (Beyer, 2004) for ArcGIS version 9.3 (ESRI, Redlands, CA, 2008) to calculate the 100% Minimum Convex Polygon (MCP) for each tortoise. We chose MCP as a measure of home range as it has been shown to be a conservative estimate (Rose and Judd, 1975) and allows for comparisons with other recent studies (McMaster and Downs, 2009). The distance moved between fixes was calculated using the "Calculate Movement Parameters" function in Hawth's Tools. To allow for a comparison of activity between months, we calculated a daily movement distance by dividing the number of days that the tortoises were tracked per month. This represents the absolute minimum distance that the tortoises would have travelled (i.e., a straight line between two fixes). On 113 occasions, fixes were taken one day (24 h) apart, allowing the calculation of the minimum distance moved in the course of one day. We calculated Pearson's correlation coefficient for the number of fixes and MCP (Zar, 1994) and used a *t*-test to test for differences between sexes in home-range size of *S. pardalis*. Two transmitters stopped functioning within 48 h of being fitted and both these individuals are excluded from all subsequent analyses, reducing the sample size to six individuals. All six were transmitting in January/February (during summer), but only four were transmitting in June through August (during winter).

## RESULTS

The morphological measurements of male and female *S. pardalis* captured in northeastern Swaziland did not differ (Table 1, *t*-test,  $P > 0.05$  for all comparisons), although female tortoises were heavier than males ( $t = 2.59$ ,  $P = 0.017$ ; Table 1).

Six tortoises were tracked for between 2 and 9 months (median: 6.5 months) (Table 2). The MCP of males and females

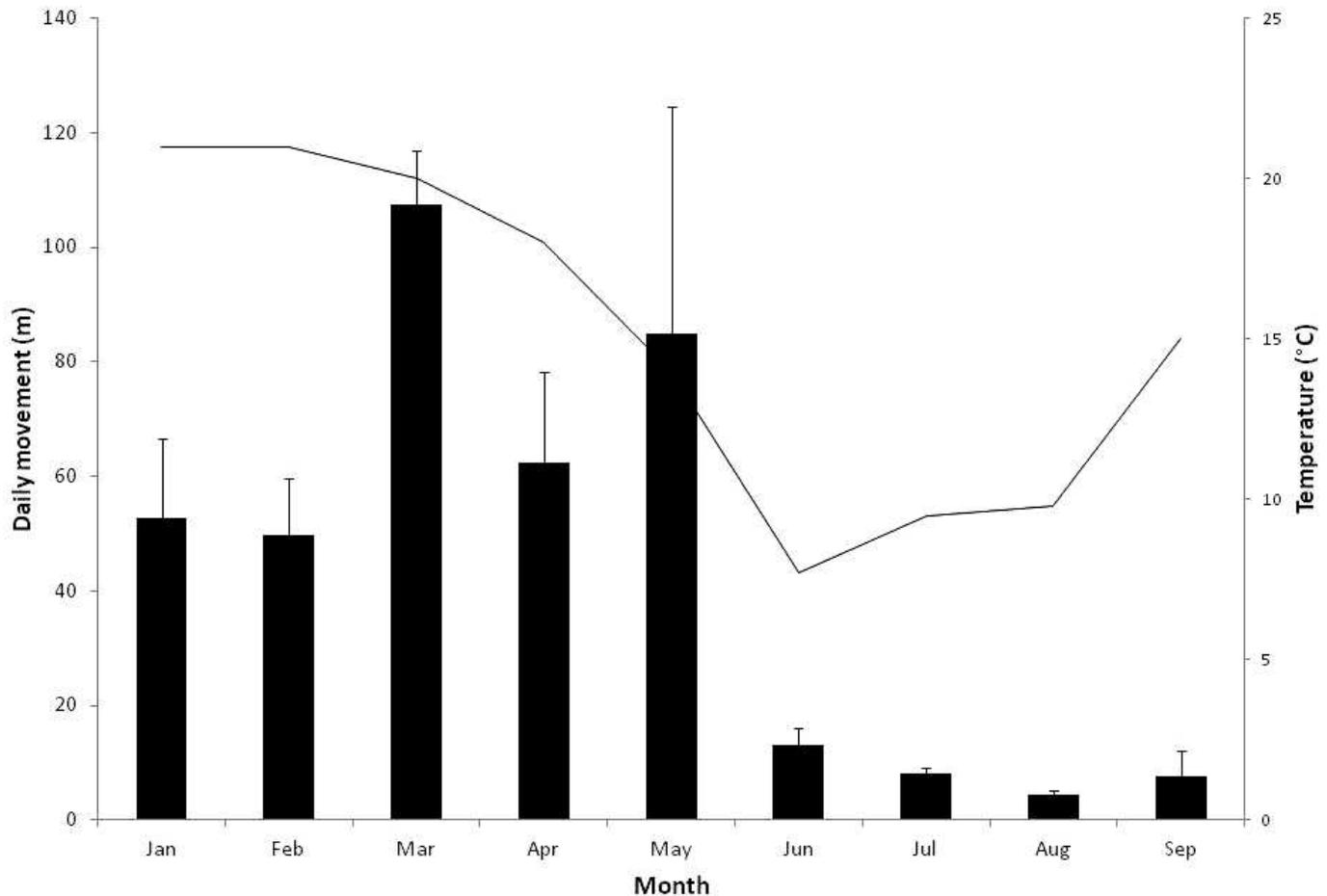


FIG. 2. Activity pattern, as measured by daily distance moved ( $\pm$  SE), of six radio-tracked *Stigmochelys pardalis* between January and September 2010, in northeastern Swaziland. The line shows the mean monthly minimum temperatures during the study period.

did not differ ( $t = 1.03$ ,  $P = 0.413$ ,  $df = 4$ ) and, therefore, were combined for all subsequent analyses. No correlation was observed between MCP and number of fixes ( $r = 0.613$ ,  $P = 0.196$ ). The mean MCP ( $\pm$  SE) of the six tortoises was 13.49 ha ( $\pm 6.93$  ha) (Fig. 1). The largest home range was that of the smallest female and exceeded 45 ha (Table 2). The smallest range (covering almost 4 ha) was that of a female that was only tracked for 4 months. However, a male tracked for 9 months had a home range of just 6.49 ha. In all but one case, tracking ended because of transmitter failure. In one case, the transmitter became dislodged from the tortoise.

The four tortoises that still had working transmitters in winter (June through August) were all above ground and moved regularly, although over shorter distances (Fig. 2). Only a single tortoise was suspected of having entered a burrow. The transmitter of this individual was recovered at the entrance of a hole in the ground, but the tortoise was not resighted after this time.

Tortoise activity (daily distance moved) was high between January and May, declining sharply in June and remaining low until the end of the study in September (Fig. 2). Activity was correlated with mean minimum temperature ( $r = 0.670$ ,  $P = 0.048$ ). The mean total distance moved by the six tortoises was 2,419 m but varied considerably (1,122–4,306 m) and was correlated with the number of fixes ( $r = 0.860$ ,  $P = 0.028$ ). The tortoises generally kept within a definable home range, moving a mean ( $\pm$  SE) maximum distance of 655 m ( $\pm 177$  m) from the

point of capture. The majority of movements were between 0 and 89 m ( $N = 81$  or 71.7%), with a maximum distance of 367 m, although only a few movements of more than 200 m ( $N = 9$  or 8.0%) were recorded (Fig. 3).

No apparent barriers to the movement of the tortoises were observed in our study area. The dry Siphiso River bed was crossed by at least one of the tortoises. Five of the tortoises also crossed a gravel game-viewing road that passed through the area. The boundaries of the MCPs of the six tortoises did not coincide with the roads, but three of the individuals had home ranges ending along the dry river bed (Fig. 1).

#### DISCUSSION

This study has demonstrated clear differences in the activity patterns and movement of six *S. pardalis* between seasons in a subtropical savanna. The distances moved by the tracked tortoises dropped sharply at the beginning of June, which also represents the beginning of the cool, dry season. Minimum temperatures vary considerably throughout the year at Mlawula, and drop well below 10°C at the beginning of June. Tortoise activity is closely related to ambient temperature; for example, *Chersina angulata* in a winter-rainfall region of South Africa was never active below 14°C (Ramsay et al., 2002). Perhaps of greater interest is that these tortoises remained above ground and active throughout the cool, dry winter months, indicating that they were not hibernating. This species

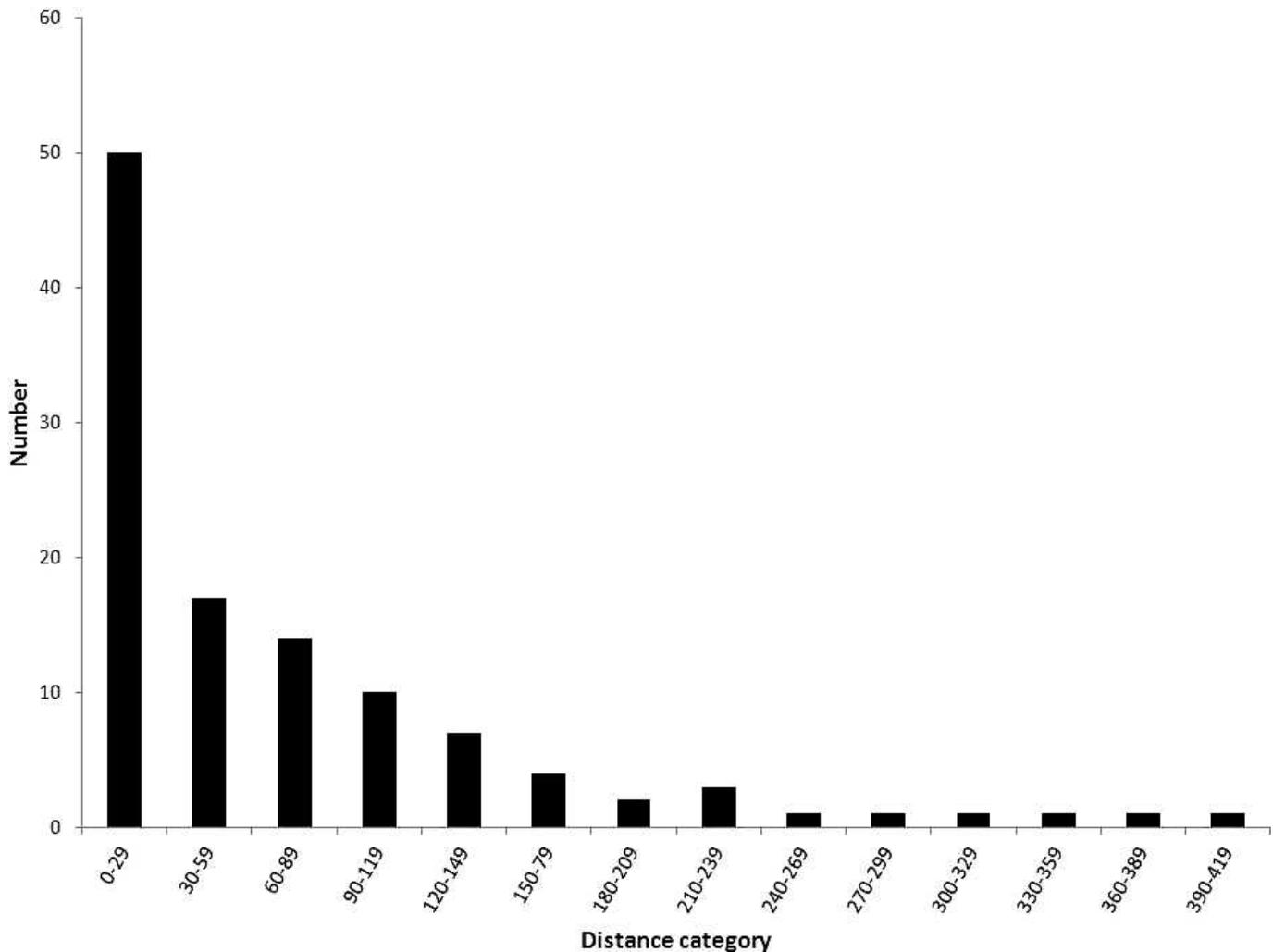


FIG. 3. The distance between 113 paired fixes taken one day apart presented as a histogram, showing the minimum distance moved in a 24-h period by *Stigmochelys pardalis* in northeastern Swaziland.

is not known to dig burrows (Boycott and Bourquin, 2000) but rests up among boulders and bushes (Grobler, 1982; Hailey and Coulson, 1995). In the Nama-Karoo of South Africa, where night time temperatures can drop below 10°C in three of the four seasons, *S. pardalis* regulates its exposure to the cold by behavioral means (McMaster and Downs, 2006). The smaller *Kinixys spekii*, which occurs sympatrically with *S. pardalis* in our study area, is known to hibernate (Hailey and Coulson, 1996b). Considering the substantial age- and sex-related differences in mass in *S. pardalis*, it would be interesting to ascertain the role of size in the thermoregulatory behavior of this species.

The home ranges of the six tracked tortoises were spaced widely across the Siphiso Valley. No differences were observed in home-range size of male and female tortoises, despite the larger mass of females, corroborating the findings of other studies (Hailey and Coulson, 1999; Mason et al., 2000). McMaster and Downs (2009) reported considerable overlap in home ranges of individual *S. pardalis* regardless of age or sex and suggested that this species was not territorial. The individual tortoises, however, did appear to have a distinct home range, remaining within approximately 0.6 km of the point of capture. A similar observation was made by McMaster and Downs (2009) for *S. pardalis* in the Nama-Karoo. The

TABLE 3. Home range of *Stigmochelys pardalis* in various habitats across its African range. Annual rainfall is taken from WorldClim (Hijmans et al., 2005; www.worldclim.org).

Country	Habitat	Home range (ha)	Rainfall (mm)	Reference
South Africa	Nama-Karoo	205.4	300	McMaster and Downs (2009)
Tanzania	Grassland/ Savanna	160.0	895	Bertram (1979)
South Africa	Valley thicket	106.4	524	Mason and Weatherby (1995)
Zimbabwe	Miombo/Mopane	26.0	656	Hailey and Coulson (1996a)
Swaziland	Acacia savanna	13.5	657	This study

average MCP of the six tortoises (13.49 ha) is close to the home range predicted for an herbivorous mammal (11.1 ha; calculated by Hailey and Coulson [1996a] based on the equation in Lindstedt et al. [1986]). This is in contrast to most other studies of *S. pardalis*, which have reported far larger home-range sizes (see Table 3). Variation in home-range size has been proposed to be linked with rainfall (McMaster and Downs, 2006); however, no correlation between home-range size and annual rainfall was observed in the five studies for which such data are available ( $r = -0.326$ ,  $P = 0.593$ ; Table 3). The largest home ranges are by tortoises inhabiting the driest site (Nama-Karoo), but the site with the highest rainfall had tortoises with the second largest home range. Rainfall is known to be important in the reproduction and growth (Loehr et al., 2007, 2011) and energetics (Peterson, 1996; Henen et al., 1998) of arid zone tortoises, but this pattern may not hold in other biomes (Swingland and Stubbs, 1985; Diaz-Paniagua et al., 2001). In an African context, perhaps a better (or additional) correlate of home-range size may be soil fertility (sensu Fritz and Duncan, 1994), but this has yet to be examined with respect to tortoises.

Although the tortoises generally only moved about 50 m in 24 h, they were on occasion capable of significantly longer movements. Three separate movements of over 300 m were observed, exhibited by three different tortoises (with a fourth tortoise moving 293 m), showing that such movements are typical (and not attributable to idiosyncratic differences). These movements are rather short by comparison to those reported for the same species in the xeric Nama-Karoo, where individuals moved up to a maximum of 8 km in a day (McMaster and Downs, 2009). The greatest distance moved by any tortoise in this study was approximately half the maximum daily distance reported above for the Nama-Karoo (McMaster and Downs, 2009). Although differences in sampling methods may account for some of this difference, it is not likely to explain this order of magnitude difference. Daily movements (77 m for females and 93 m for males) in valley bush were greater, but comparable, with our study (Mason and Weatherby, 1995). By comparison, *S. pardalis* moved long distances daily (435 m) in Zimbabwe, which was related to the need to ingest sodium, which was only available at isolated sodic sites (Hailey and Coulson, 1996a). Calcium is also critical for tortoise growth (Fledelius et al., 2005), but its effect on daily movement or microhabitat selection has yet to be determined for *S. pardalis*. This species appears to select forbs with high water content (Kabigumila, 2001) and is able to alter its digestion in response to water availability (McMaster and Downs, 2008), which may facilitate its survival in water scarce habitats.

*Acknowledgments.*—This is the 20th communication of the All Out Africa Research Unit ([www.alloutafrica.org](http://www.alloutafrica.org)). We thank E. Franklin, M. SurrIDGE, and M. Ngwenya for tracking the tortoises. K. Roques and C. Fellner provided logistic support. N. Dlamini, Senior Warden, Swaziland National Trust Commission, provided permission for us to work at Mlawula.

## LITERATURE CITED

- ADOLPH, S. C., AND W. P. PORTER. 1993. Temperature, activity and lizard life histories. *American Naturalist* 142:273–295.
- BERTRAM, B. 1979. Homing by a Leopard Tortoise in the Serengeti. *African Journal of Ecology* 17:245–247.
- BEYER, H. L. 2004. Hawth's Analysis Tools for ArcGIS [Internet]. Available from: <http://www.spatial ecology.com/htools>. Accessed December 2009.
- BOYCOTT, R. C., AND O. BOURQUIN. 2000. *The South African Tortoise Book: A Guide to Southern African Tortoises, Terrapins and Turtles*. Southern Book Publishers, Hilton, South Africa.
- BRANCH, B. 2008. *Tortoises, Terrapins and Turtles of South Africa*. Struik, Cape Town, South Africa.
- CHRISTIAN, K. A., AND B. W. WEAVERS. 1996. Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. *Ecological Monographs* 66:139–157.
- DIAZ-PANIAGUA, C., C. KELLER, AND A. C. ANDREU. 2001. Long-term demographic fluctuations of the Spur-Thighed Tortoise *Testudo graeca* in SW Spain. *Ecography* 24:707–721.
- DIEMER, J. E. 1992. Home range and movements of the tortoise *Gopherus polyphemus* in Northern Florida. *Journal of Herpetology* 26:158–165.
- FLEDELIUS, B., G. W. JORGENSEN, H. E. JENSEN, AND L. BRIMER. 2005. Influence of the calcium content of the diet offered to Leopard Tortoises (*Geochelone pardalis*). *Veterinary Record* 156:831–835.
- FRTZ, H., AND P. DUNCAN. 1994. On the carrying capacity for large ungulates of African savanna ecosystems. *Proceedings of the Royal Society, London B* 256:77–82.
- FRTZ, U., S. R. DANIELS, M. D. HOFMEYR, J. GONZALEZ, C. L. BARRIO-AMOROS, P. SIROKY, A. K. HUNSDORFER, AND H. STUCKAS. 2010. Mitochondrial phylogeography and subspecies of the wide-ranging sub-Saharan Leopard Tortoise *Stigmochelys pardalis* (Testudines: Testudinidae)—a case study for the pitfalls of pseudogenes and GenBank sequences. *Journal of Zoological Systematics and Evolutionary Research* 48:348–359.
- FULLER, M. R., J. J. MILLSPAUGH, K. E. CHURCH, AND R. E. KENWARD. 2005. Criteria for gender and age. In C. E. Braun (ed.), *Techniques for Wildlife Investigations and Management*. 6th ed., pp. 377–417. The Wildlife Society, Bethesda, MD.
- GROBLER, J. H. 1982. *The Leopard Tortoise in the Mountain Zebra National Park*. Koedoe 25:49–53.
- HAILEY, A., AND I. M. COULSON. 1995. Habitat associations of the tortoises *Geochelone pardalis* and *Kinixys spekii* in the Sengwa wildlife research area, Zimbabwe. *Herpetological Journal* 5:305–309.
- . 1996a. Differential scaling of home-range area to daily movement distance in two African tortoises. *Canadian Journal of Zoology* 74:97–102.
- . 1996b. Temperatures and the tropical tortoise *Kinixys spekii*: tests of thermoregulation. *Journal of Zoology, London* 240:537–549.
- . 1999. The growth pattern of the African tortoise *Geochelone pardalis* and other chelonians. *Canadian Journal of Zoology* 77:181–193.
- HENEN, B. T., C. C. PETERSON, I. R. WALLIS, K. H. BERRY, AND K. A. NAGY. 1998. Effects of climatic variation on field metabolism and water relations of desert tortoises. *Oecologia* 117:365–373.
- HIJMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES, AND A. JARVIS. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978.
- KABIGUMILA, J. 2001. Sighting frequency and food habits of the Leopard Tortoise, *Geochelone pardalis*, in northern Tanzania. *African Journal of Ecology* 39:276–285.
- LINDSTEDT, S. L., B. J. MILLER, AND S. W. BUSKIRK. 1986. Home range, time, and body size in mammals. *Ecology* 67:413–418.
- LOEHR, V. J. T., M. D. HOFMEYR, AND B. T. HENEN. 2007. Growing and shrinking in the smallest tortoise, *Homopus signatus signatus*: the importance of rain. *Oecologia* 153:479–488.
- LOEHR, V. J. T., B. T. HENEN, AND M. D. HOFMEYR. 2011. Reproductive responses to rainfall in the Namaqualand Speckled Tortoise. *Copeia* 2:278–284.
- MASON, M. C., AND C. A. WEATHERBY. 1995. Home Range of *Geochelone pardalis* and *Chersina angulata*. 2 Sympatric Genera in the Eastern Cape, South Africa. 4th HAA Symposium on African Herpetology, St. Lucia. Kwa Zulu-Natal.
- 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., AND C. T. DOWNS. 2006. Do seasonal and behavioral differences in the use of refuges by the Leopard Tortoise (*Geochelone pardalis*) favour passive thermoregulation? *Herpetologica* 62:37–46.

- . 2008. Digestive parameters and water turnover of the Leopard Tortoise. *Comparative Biochemistry and Physiology, Part A*. doi: 10.1016/j.cbpa.2008.06.007.
- . 2009. Home range and daily movement of Leopard Tortoises (*Stigmochelys pardalis*) in the Nama-Karoo, South Africa. *Journal of Herpetology* 43:561–569.
- MONADJEM, A., A. RESIDE, J. CORNUT, AND M. R. PERRIN. 2009. Roost selection and home range of an African insectivorous bat *Nycteris thebaica* (Chiroptera, Nycteridae). *Mammalia* 73:353–359.
- MONADJEM, A., T. RAABE, B. DICKERSON, N. SILVY, AND R. MCCLEERY. 2010. Roost use by two sympatric species of *Scotophilus* in a natural environment. *South African Journal of Wildlife Research* 40:73–76.
- PETERSON, C. C. 1996. Ecological energetics of the desert tortoise (*Gopherus agassizii*): effects of rainfall and drought. *Ecology* 77: 1831–1844.
- RAMSAY, S. L., M. D. HOFMEYR, AND Q. I. JOSHUA. 2002. Activity patterns of the Angulate Tortoise (*Chersina angulata*) on Dassen Island, South Africa. *Journal of Herpetology* 36:161–169.
- ROSE, F. L., AND F. W. JUDD. 1975. Activity and home range size of the Texas Tortoise, *Gopherus berlandieri*, in South Texas. *Herpetologica* 31: 448–456.
- SCHROEDER, M. A., AND L. A. ROBB. 2005. Criteria for gender and age. In C. E. Braun (ed.), *Techniques for Wildlife Investigations and Management*. 6th ed., pp. 303–338. The Wildlife Society, Bethesda, MD.
- SWINGLAND, I. R., AND D. STUBBS. 1985. The ecology of a Mediterranean tortoise (*Testudo hermanni*): reproduction. *Journal of Zoology, London* 205:595–610.
- ZAR, J. H. 1994. *Biostatistical Analysis*. 3rd ed. Prentice-Hall, Englewood Cliffs, NJ.

Accepted: 11 July 2012.