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Habitat Use by the Rock-Dwelling Karoo Dwarf Tortoise, *Chersobius boulengeri*

Victor J. T. Loehr[1]

The global population status of many reptiles, particularly tortoises as one of the most threatened tetrapod groups, necessitates conservation efforts and study. Baseline information about habitat use can help formulate conservation strategies and improve effectiveness of surveys. I studied habitat use by Karoo Dwarf Tortoises (*Chersobius boulengeri*), an endangered South African endemic with only one population known to contain males, females, and juveniles, to aid conservationists in assessing which nature reserves (with incidental records) and potential new reserves may sustain populations, and to inform surveys for additional populations. Available microhabitats and rock types were mapped using an unmanned aerial vehicle. I analyzed the tortoise distribution and determined home range sizes (minimum convex polygons) and minimum daily movement distances of nine males and 16 females using radio transmitters. All fieldwork was conducted in spring 2018 and 2019, and in summer 2018, 2019, and 2020. Relatively high numbers of tortoises inhabited sills (i.e., exposed dolerite intrusions between sandstone) that contained ample retreats among boulders and rocks, whereas relatively few lived on level plateaus that might expose them to predatory birds. Despite their apparent preference of sills, tortoises were able to survive in home ranges that contained little sill microhabitat. Tortoises were rather sedentary, having small sexually and seasonally similar home ranges (1.10–1.14 ha) and movement distances (27.6–28.4 m/day), although their home ranges were larger than those of the related Speckled Dwarf Tortoise (*Chersobius signatus*), possibly as a result of different habitat productivities. Conservationists and surveyors should consider that sills appear important for Karoo Dwarf Tortoises, but generic rocky slopes may also harbor individuals. Future studies could address aspects that underlie microhabitat use, such as availability of retreats and vegetation, and integrate available information in a spatial model.

THERE are more threatened taxa in reptiles than in birds or mammals, and the number of data-deficient reptile taxa exceeds those in any tetrapod class (Cox et al., 2022). Moreover, most "lost" (i.e., possibly extinct) tetrapods are reptiles (Martin et al., 2023). To improve on this situation, considerable effort should be invested in specific studies on reptile species of high conservation concern. Conservation action and investigations benefit from baseline knowledge of how species use their habitats. For example, juvenile Smooth Snakes (*Coronella austriaca*) used habitat not inhabited by cannibalistic adults, requiring conservation of buffer zones to facilitate juvenile survival (Kolanek et al., 2019), and the rediscovered Barbados Leaf-Toed Gecko (*Phyllodactylus pulcher*) was more successful than introduced House Geckos (*Hemidactylus mabouia*) in exposed rocky habitat, emphasizing the need to conserve natural cliffs (Williams et al., 2020). In a protected national park, the identification of seasonal habitat use by Latifi's Viper (*Montivipera latifii*) informed the park's management procedures (Behrooz et al., 2015). Data on habitat use may also improve the spatial scope of surveys, such as for Desert Tortoises (*Gopherus agassizii*) that used habitats where they were previously assumed to be absent (Averill-Murray and Averill-Murray, 2005). Unfortunately, information on habitat use is unavailable for many reptiles.

Within reptiles, the proportion of turtles (order Testudines) threatened with extinction is similar to proportions in salamanders and monotremes, which are the most-threatened tetrapod groups (Cox et al., 2022). Thus, habitat studies are particularly relevant for turtles, and especially for tortoises (82% of evaluated extant species classified as Vulnerable, Endangered, or Critically Endangered; IUCN, 2022). Karoo Dwarf Tortoises (*Chersobius boulengeri*) are endemic to an arid range (Nama and Succulent Karoo biomes) in the Eastern, Northern, and Western Cape Provinces of South Africa (Boycott and Bourquin, 2000). They are small (maximum length 110 mm) and associated with rocky terrain (Boycott and Bourquin, 2000), where they were once considered abundant (Greig and Burdett, 1976; Boycott, 1989). More recent surveys suggest that populations are being extirpated, resulting in the species being classified as Endangered (Hofmeyr et al., 2018). At present, only one population is known to contain males, females, and juveniles (Loehr and Keswick, 2022). The deteriorating conservation status of the species amplifies the need for information about habitat use, to help conservationists assess if nature reserves with incidental records (i.e., Gamkapoort and Anysberg, and Karoo National Park; Hofmeyr et al., 2018) and potential new reserves are likely to sustain populations, and to inform surveys for additional populations.

I mapped the habitat of the single known Karoo Dwarf Tortoise population and investigated the distribution of individuals among microhabitats and rock types. In addition, I estimated home range sizes, determined which microhabitats and rock types they encompassed, and assessed minimum daily movement distances. The study was descriptive and aimed at providing baseline data for conservationists.

MATERIALS AND METHODS

Study site.—The study site consisted of a 16 ha core, with adjacent areas up to 250 m from the core area (Supplemental Fig. A; see Data Accessibility), in the Northern Cape Province of South Africa (coordinates recorded on the biodiversity database of CapeNature, Western Cape Province, South Africa). The site was rocky, with sparse vegetation comprising dwarf shrubs, forbs, grass tufts, succulents, and geophytes. On 26 February 2020, an unmanned aerial vehicle photographed the core area, after which I used Pix4Dmapper

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Table 1. Microhabitats and rock types at the core of a study site for Karoo Dwarf Tortoises (*Chersobius boulengeri*) in 2018–2020.

Microhabitat or rock type	Description
Sill	Exposed dolerite intrusion between sandstone, representing a more or less continuous layer of similar elevation, with large boulders and rocks. See also Supplemental Fig. B
Slope	Mountain slope between sills, littered with dolerite and sandstone rocks, and occasional dolerite boulders
Plateau	Relatively level area with dolerite or sandstone rocks
River bed	Narrow drainage path with exposed bedrock, and washed-down dolerite and sandstone rocks and wood
Dolerite	Red-, brown-, or black-colored igneous rock, often having rounded shapes (e.g., boulders)
Sandstone	Yellowish-colored sedimentary rock, often having flat, layered shapes

version 4.6.4 (Pix4D S.A., Prilly, Switzerland) to build an orthomosaic and a digital terrain model (DTM) with a spatial resolution of 0.38 × 0.38 m. The orthomosaic and DTM were imported into ArcMap 10.4.1 (Esri, Redlands, CA, USA) and used to manually delineate, at a scale of 1:125, microhabitats and rock types (Table 1) present at the core of the study site. I also created a digital elevation model (DEM) for the core and adjacent areas, by converting the DTM and an ASTER GDEM V2 raster (30 × 30 m; ASTER GDEM is a product of METI and NASA) into a triangular irregular network (TIN), and enhancing the TIN outside the core of the study site with 1,120 field-recorded GPS positions. The DEM was used to calculate effective surface areas and surface distances (i.e., accounting for elevational variation).

Because there are no long-term weather recordings for this area, I used modeled long-term data (30 years of hourly weather model simulations; Meteoblue, 2020. Climate (modelled). https://www.meteoblue.com/en/weather/forecast/modelclimate [accessed on 22 August 2020]) as comparison for temperatures and rainfall recorded by data-loggers (Hobo S-THB-M00x, RS3-B, and S-RGF-M002 connected to H21-USB; Onset Computer Corporation, Bourne, MA, USA) that I placed in the center of the study site.

Tortoise sampling.—Groups of 1–6 persons sampled the core study site and adjacent areas for Karoo Dwarf Tortoises in February–March 2018, 2019, and 2020 (summer), September–October 2018 (spring), and October 2019 (spring). In each period, we searched for hiding Karoo Dwarf Tortoises in holes under and among rocks during the day, ensuring that all holes present were frequently inspected. The species was easily identifiable, based on its dorso-ventrally compressed shell, uniformly brownish coloration of the carapace, and five claws on the front feet (Boycott and Bourquin, 2000). When a tortoise was found for the first time, we recorded its straight carapace length (SCL, to the nearest 0.01 mm) with digital calipers, its body mass (BM, to the nearest 1 g) with a digital balance, and its geographical position (to the nearest 3 m) with a GPS device. Tortoises were notched (Boycott and Bourquin, 2000) and photographed prior to release at the site of capture. When a tortoise was recaptured, we recorded its new GPS position.

In February–March 2018, I equipped the first nine males and 16 females encountered that had sufficient body mass (i.e., body mass at least ten times larger than equipment mass) with radio transmitters (type RI-2B with internal antenna; Holohil Systems, Carp, ON, Canada) placed onto the posterior costal scutes (equipment mass $\leq$9.7% of body mass). These tortoises were intensively tracked in October–November 2018, following a randomized experimental design in which I tracked two randomly selected tortoises each field-hour to record their GPS positions. I tracked each individual only once per day. Tortoises were also tracked and their GPS positions recorded in a non-randomized fashion (e.g., females tracked for radiography on several mornings) in February–March 2018 and 2019, and October 2019 (males and females), and in October–November 2018 and February–March 2020 (females). Transmitters of males and females were removed in February–March 2019 and 2020, respectively.

Calculations and statistics.—For first captures of males and females at the core of the study site, I used contingency table analysis to test if their distributions among microhabitats and rock types were proportional to microhabitat and rock type effective surface areas. I applied Yates's correction in tests with one degree of freedom and completed all tests with average expected frequencies $>$5 (Zar, 1999). There were too few juveniles (i.e., individuals that were smaller than the smallest males with plastral concavities and large tails; Boycott and Bourquin, 2000) to include in any of the analyses.

I estimated effective home range sizes as 100% minimum convex polygons (MCPs) based on tortoise GPS positions and the DEM. MCPs were selected as measure for home ranges due to relatively small sample sizes (Seaman et al., 1999; Boyle et al., 2009) and to facilitate comparison with previous work on congeneric Nama and Speckled Dwarf Tortoises (*C. solus* and *C. signatus*, respectively; Cunningham and Simang, 2007; Loehr, 2015). To assess the effect of the number of available GPS positions on home range size (i.e., whether a plateau breakpoint was reached; Haenel et al., 2003), I used segmented linear regression (Oosterbaan, 1994). I compared MCPs between males and females with a *t*-test. Furthermore, I calculated and compared intra- and intersexual overlaps of MCPs using paired *t*-tests.

For MCPs that were mostly ($>$95% of MCP) situated inside the study site core (i.e., the area for which microhabitats and rock types were mapped), I calculated proportions of MCPs containing specific microhabitats or rock types and analyzed the effects of sex and microhabitat or rock type on proportions using two-way repeated-measurements analysis of variance (RM ANOVA) followed by Student-Newman-Keuls (SNK) *post hoc* tests. In addition, I compared proportions of microhabitats or rock types within MCPs with proportions of microhabitats or rock types present among GPS positions on which the MCPs were based, by means of two-way RM ANOVA. For data with non-normal distributions, I checked if one-way RM ANOVA conducted separately for each microhabitat or rock type would yield different results.

Minimum daily movement distances (MDMDs) were calculated as effective distances (based on the DEM) between

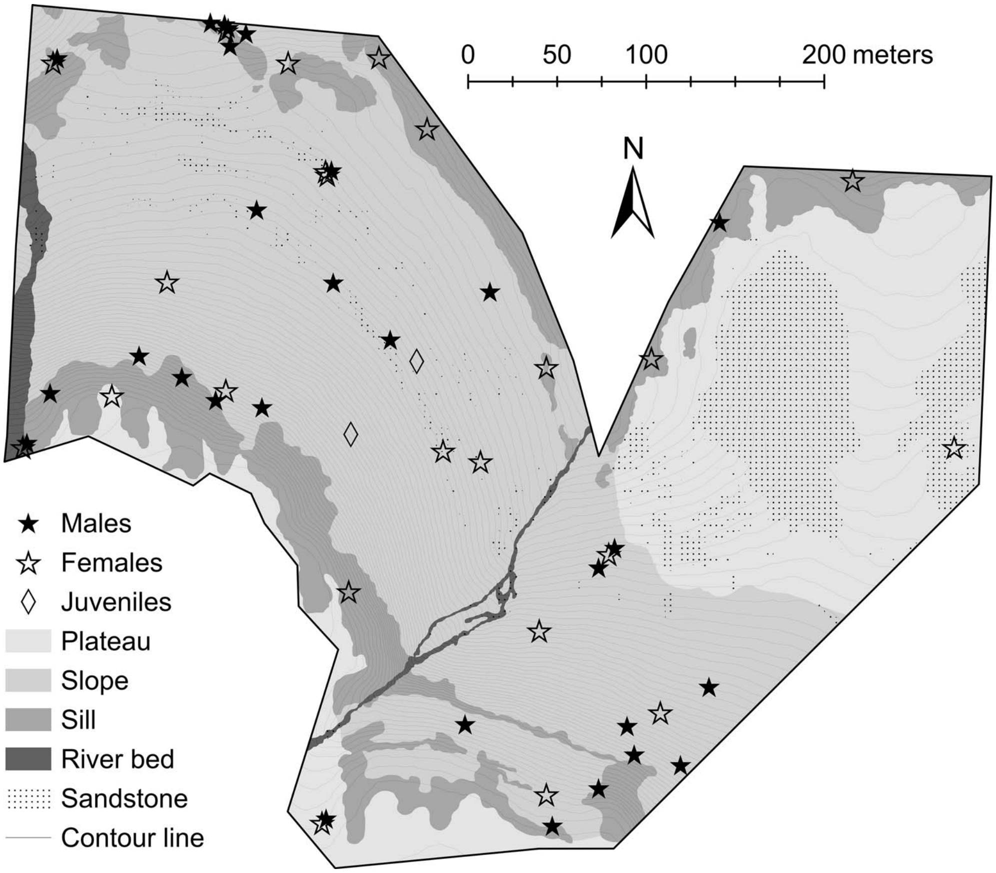

Fig. 1. Core of a Karoo Dwarf Tortoise (*Chersobius boulengeri*) study site in 2018–2020, with plateau, slope, sill, and river bed microhabitats. Dominant rock type at the site was dolerite, except where dots indicate sandstone. Contour lines represent equal elevations ranging from 1,373 (northeast) to 1,445 (southwest) meters above sea level. Star and diamond symbols are locations where 54 individual tortoises were encountered for the first time.

any two different GPS positions recorded for a given tortoise within 19–29 hours (i.e., MDMD > 0), and averaged for each individual. I compared MDMDs of males and females with a Mann-Whitney *U* test. In addition, I compared MDMDs of males and females that had data for spring and summer among sexes and seasons using two-way RM ANOVA.

Contingency table analysis was completed in Microsoft Excel 2021, segmented linear regression in SegReg (Oosterbaan, 2013), and all other analyses in SigmaPlot 12.0 (Systat Software, San Jose, CA, USA). I report means with standard deviations (SD), and considered results statistically significant when $P < 0.05$.

RESULTS

Study site core and tortoise distribution.—The elevational range of the 16 ha core of the study site was 72 m, mostly northeast-facing (Fig. 1), and its effective surface area was 16.6 ha. Slopes were most prevalent (55.5% of the core's effective surface area; Fig. 1), followed by plateaus (27.2%), sills (15.6%; Supplemental Fig. B; see Data Accessibility), and river beds (1.7%). Most of the core had dolerite rock (90% of effective surface area), whereas sandstone (10%) was concentrated on a large plateau and as a semicontinuous layer of similar elevation on the western mountain slope (Fig. 1).

Monthly mean minimum and maximum temperatures from February 2018 to March 2020 were, respectively, 0.0–5.2°C and 1.0–7.0°C higher than long-term modeled temperatures. For February to September 2018, rainfall was 145% of long-term modeled rainfall. Thereafter, rainfall was very low (27% of long-term modeled rainfall) in the October 2018–May 2019 rainfall season. Besides some scattered rainfall events, drought continued until December 2019. In response to weather conditions, plants at the study site were green in February–March 2018, October–November 2018, and February–March 2020, providing food and cover for the tortoises, but green vegetation was mostly absent in February–March 2019 and October 2019.

At the core of the site, we found 29 males (SCL 82.0±10.5 mm, BM 91.1±29.5 g), 23 females (SCL 93.0±8.2 mm, BM 150.7±32.2 g), and 2 juveniles (SCL 45.7±17.1 mm, BM 24.5±19.1 g; Fig. 1). Males and females were not distributed proportionally to effective surface areas of microhabitats ($\chi^2_3 = 24.62$, $P < 0.001$; Fig. 2A). In particular, sills yielded relatively many tortoises, whereas plateaus yielded relatively few tortoises. Areas with dolerite and sandstone rock contained male and female tortoises proportionally to rock type effective surfaces ($\chi^2_1 = 0.77$, $P = 0.38$; Fig. 2B).

Home ranges and movements.—Males and females with radio transmitters were tracked 21–35 and 28–36 times during this study, respectively (Table 2). Most tracking records were made in October–November 2018 (Table 2). MCP size increased with the number of GPS positions that were included, until a plateau breakpoint was reached at 15.6 positions for males (segmented linear regression, $F_{3,167} = 39.83$, $P < 0.001$), and 30.0 positions for females ($F_{3,416} = 107.71$, $P < 0.001$). Consequently, I calculated MCPs for males in October–November 2018 (excluding one male that had fewer than 16 GPS positions) and for all tracking records combined, whereas I calculated MCPs for females only for all tracking records combined (excluding one female that had fewer than 30 GPS positions). In October–November 2018, male MCPs ranged from 0.22 to 1.62 ha (mean 0.67±0.43 ha, $n = 8$).

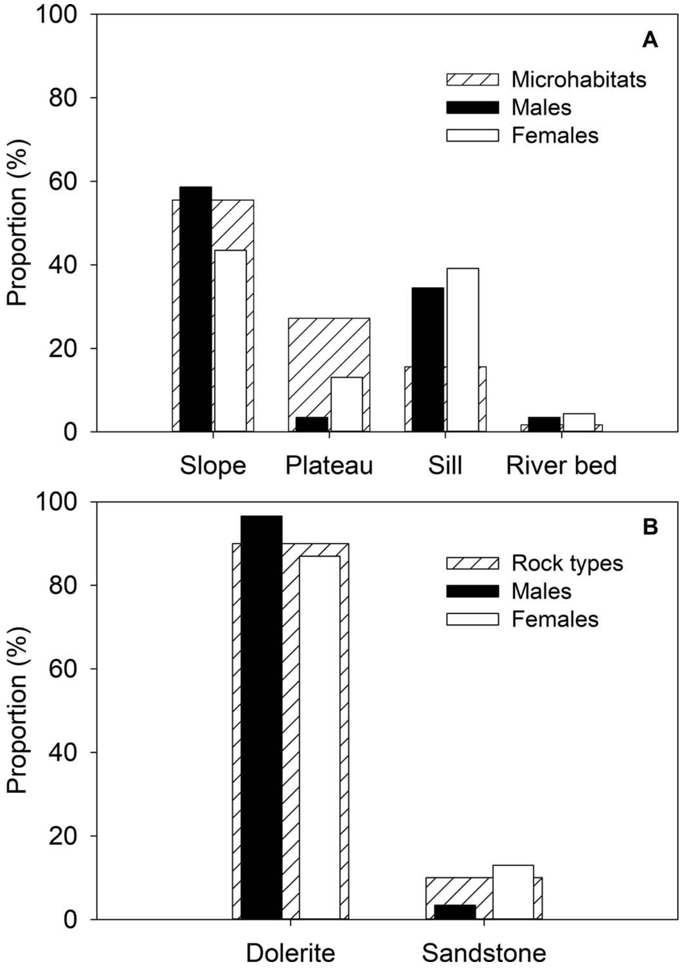

Fig. 2. Proportions of the effective surface area (shaded bars) of the core of a Karoo Dwarf Tortoise (*Chersobius boulengeri*) study site that were characterized as slope, plateau, sill, and river bed microhabitats (A), or as dolerite and sandstone rock types (B), and proportions of the total number of unique males (black bars, $n = 29$) and females (white bars, $n = 23$) that were encountered in each microhabitat (A) or rock type (B) in 2018–2020.

MCPs of two males overlapped each other 69% and 82%, but there was no overlap among MCPs of other males. For all tracking records combined, MCPs of males and females had similar sizes (*t*-test, $t_{22} = 0.19$, two-tailed $P = 0.86$; Table 3). Male MCPs overlapped MCPs of females more than MCPs of other males (paired *t*-test, $t_8 = 3.35$, two-tailed $P = 0.010$; Table 3, Supplemental Fig. A; see Data Accessibility). In contrast, female MCPs overlapped MCPs of males and other females similarly ($t_{14} = 0.32$, two-tailed $P = 0.76$; Table 3, Supplemental Fig. A; see Data Accessibility).

Three males and seven females had MCPs that were situated mostly (>95% of MCP) inside the core of the study site (Supplemental Fig. A; see Data Accessibility). Microhabitats within these MCPs did not represent habitat use of all individuals with transmitters, because the sample excluded multiple MCPs that contained substantial amounts of plateau and sill microhabitat (Fig. 1 and Supplemental Fig. A; see Data Accessibility). MCPs of the three males (0.81–1.89 ha) and seven females (0.27–1.43 ha) contained more slope than other microhabitats (two-way RM ANOVA, $F_{3,24} = 172.50$, $P < 0.001$, *post hoc* tests $P < 0.001$; Fig. 3A–B). Proportions of MCPs containing specific microhabitats were similar between sexes ($F_{1,24} = 2.21$, $P = 0.18$), and interaction between sex and microhabitat was not significant ($F_{3,24} = 0.37$, $P = 0.78$). MCPs contained more dolerite than sandstone rock types (two-way RM ANOVA, $F_{1,8} = 2663.07$, $P < 0.001$, *post hoc* test $P < 0.001$; Fig. 3C–D), without sexual variation ($F_{1,8} = 0.00$, $P = 1.00$) or interaction between sex and rock type ($F_{1,8} = 1.26$, $P = 0.29$). For the three males and seven females, proportions of MCPs consisting of specific microhabitats or rock types were similar to proportions microhabitats or rock types present among the GPS positions on which MCPs were based (two-way RM ANOVA, $F_{1,\geq 2} \leq 1.00$, $P \geq 0.36$; Fig. 3A–D), and interaction with microhabitat or rock type ($F_{\geq 1,\geq 2} \leq 2.19$, $P \geq 0.19$) was absent. The latter two-way RM ANOVA for microhabitats and rock types violated the assumption of normality ($P < 0.001$ and $P = 0.017$, respectively), but one-way RM ANOVA ($F_{1,\geq 2} \leq 1.59$, $P \geq 0.26$) confirmed two-way RM ANOVA results.

Male and female MDMDs were available for February–March and October–November 2018. For all records combined, MDMDs were similar between sexes (Mann-Whitney test, $U = 59.0$, $P = 0.48$; Table 3). MDMDs for five males and nine females that were recorded in February–March as well as in October–November 2018 were similar among sexes and seasons (two-way RM ANOVA, $F_{1,12} \leq 1.82$, $P \geq 0.20$).

DISCUSSION

Karoo Dwarf Tortoises are seldom seen (Loehr and Keswick, 2022) and only a few studies have been conducted. Previous workers have qualitatively described their habitat as "rocky ridges and outcrops" (Boycott and Bourquin, 2000) or "dolerite ridges" (Branch, 2008). The present study provides quantitative details on tortoise habitat use, which may assist conservationists and surveyors to assess if locations may sustain populations. Karoo Dwarf Tortoises inhabited slopes, plateaus, sills, and river beds. I found a relatively large number of individuals in sills, which are a marked characteristic of the Karoo landscape. Sills contained ample retreats under and among boulders and rocks, which appear important for a diurnal tortoise that spends 80–90% of daytime in retreats (Loehr et al., 2021). In contrast to sills, plateaus harbored few Karoo Dwarf Tortoises. This species (Loehr, 2022; Loehr and Keswick, 2022) and other tortoises (Kristan and Boarman, 2003; Loehr, 2017; Segura et al., 2020) are depredated by birds, and relatively open plateaus expose them to predators. The low frequency of tortoises that I observed on plateaus may reflect past predation or avoidance by the tortoises. The sandstone nature of much of the plateau microhabitat did not seem to play a role, as Karoo Dwarf Tortoises used dolerite and sandstone areas according to availability. It is unlikely that the time of the day that observations were made affected microhabitat use (e.g., tortoises shuttling among microhabitats for thermoregulation), because the species typically remains in retreats for multiple days in a row, has brief activity periods of <1 h in the late afternoon, and displays thermoregulatory behavior inside retreats (Loehr et al., 2021).

Despite the relatively large number of Karoo Dwarf Tortoises in sills, individuals were able to survive in home ranges that consisted mostly of slopes or plateaus and contained little or no sill. This was not an artifact of the tendency of MCPs to include areas that are not actually used

Table 2. Means (x̄), standard deviations (SD), ranges, and sample sizes (*n*) for the numbers of GPS positions recorded for male and female Karoo Dwarf Tortoises (*Chersobius boulengeri*), and for a subsample consisting of individuals with home ranges (minimum convex polygons, MCP) situated mostly (>95% of MCP) inside the core of the study site, in 2018–2020. Data for October–November 2018 are presented separately for records originating from a randomized experimental design (see text for details) that generated most GPS positions in this study, and for all October–November 2018 records combined.

	Males				Females			
	x̄	SD	Range	*n*	x̄	SD	Range	*n*
All individuals								
Feb–Mar 2018	9.7	3.4	7–17	9	9.3	2.4	5–12	16
Oct–Nov 2018[a]	16.8	3.2	9–20	9	16.8	1.1	15–19	16
Oct–Nov 2018	16.8	3.2	9–20	9	19.8	1.1	19–22	16
Feb–Mar 2019	1.2	0.4	1–2	9	1.7	0.7	1–3	15
Oct 2019	0	–	0–0	0	1	0	1–1	13
Feb–Mar 2020	0	–	0–0	0	1.4	0.7	1–3	12
Study total	27.7	4.1	21–35	9	32.6	2.2	28–36	16
Individuals with MCPs situated mostly inside study site core								
Feb–Mar 2018	7.7	1.2	7–9	3	9.3	2.3	7–12	7
Oct–Nov 2018[a]	16.7	0.6	16–17	3	17.3	1.1	16–19	7
Oct–Nov 2018	16.7	0.6	16–17	3	20.3	1.1	19–22	7
Feb–Mar 2019	1.3	0.6	1–2	3	1.6	0.5	1–2	7
Oct 2019	0	–	0–0	0	1	0	1–1	6
Feb–Mar 2020	0	–	0–0	0	1.5	0.8	1–3	6
Study total	25.7	0.6	25–26	3	33.3	1.8	30–35	7

[a] Randomized experimental design

(Burgman and Fox, 2003), because GPS positions were similarly distributed. I was unable to test if tortoises preferred home ranges with specific microhabitats (e.g., sills), because many individuals had home ranges that were entirely or partly outside the core area for which microhabitats had been mapped. Nevertheless, my finding that the most common microhabitats (northeast-facing slopes and plateaus) can sustain Karoo Dwarf Tortoises suggests that, within the species' range, a relatively large area is available to them.

Home ranges of Karoo Dwarf Tortoises were small compared to other tortoises (0.28–195 ha based on 25 species; Slavenko et al., 2016), yet more than three times larger than in Speckled Dwarf Tortoises (Loehr, 2015), and more than twice as large as in Nama Dwarf Tortoises (based on a small sample size of 5–11 GPS positions for five tortoises; Cunningham and Simang, 2007). In a meta-analysis of home ranges in chelonians, it was suggested that home range size relates to environmental productivity, topography, and habitat size, rather than on phylogeny, body mass, sex, diet, habitat, and social structure (Slavenko et al., 2016). Karoo Dwarf Tortoises are closely related to Speckled and Nama Dwarf Tortoises (Hofmeyr et al., 2017), and these species have similar mean body masses (males and females sampled for home range studies 83–91 and 139–155 g, respectively; Cunningham and Simang, 2007; V.J.T. Loehr, unpubl.). In addition, all three species inhabit rocky mountain slopes (Boycott and Bourquin, 2000; Branch, 2008). Thus, within suitable habitat, environmental productivity may explain interspecific differences in dwarf tortoise home range sizes. Indeed, unlike Speckled Dwarf Tortoises that have access to dense (annual) vegetation cover due to relatively reliable winter rains (Desmet, 2007; Esler et al., 2010), vegetation cover at the Karoo Dwarf Tortoise study site was always low, possibly requiring tortoises to use larger home ranges to find food.

Tortoises generally are not territorial, as indicated by overlapping home ranges (Harless et al., 2009; Loehr, 2015; Bernheim et al., 2019; Ward et al., 2021). Less overlap among male Karoo Dwarf Tortoises, compared to females, may have resulted from the large physical spaces between males that were equipped with radio transmitters (Supplemental Fig. A; see Data Accessibility); 22% of the males and 66% of the females present at the core of the study site (Loehr and Keswick, 2022) were tracked, so several overlapping home ranges may have been missed. However, male Karoo Dwarf Tortoises vigorously attack, ram, and bite other males, and may chase subordinate males for >10 m (Supplemental Video A; see Data Accessibility). Consequently, male Karoo Dwarf Tortoise home ranges may have little overlap.

Table 3. Means (x̄), standard deviations (SD), ranges, and sample sizes for home range sizes (minimum convex polygons, MCP), intra- and intersexual overlaps among home ranges, and minimum daily movement distances (MDMD) of male and female Karoo Dwarf Tortoises (*Chersobius boulengeri*) in 2018–2020. Calculations are based on 21–35 and 30–37 GPS positions for males and females, respectively.

	Males				Females			
	x̄	SD	Range	*n*	x̄	SD	Range	*n*
MCP (ha)	1.14	0.48	0.28–1.89	9	1.1	0.61	0.27–2.30	15
Overlap with males (%)	15.2	27.4	0.0–72.3	9	35.8	29	0.0–85.9	15
Overlap with females (%)	58.3	37.3	0.0–96.4	9	32.6	35.3	0.0–97.5	15
MDMD (m)	27.6	18.8	6.5–71.6	9	28.4	9.7	16.6–53.5	16

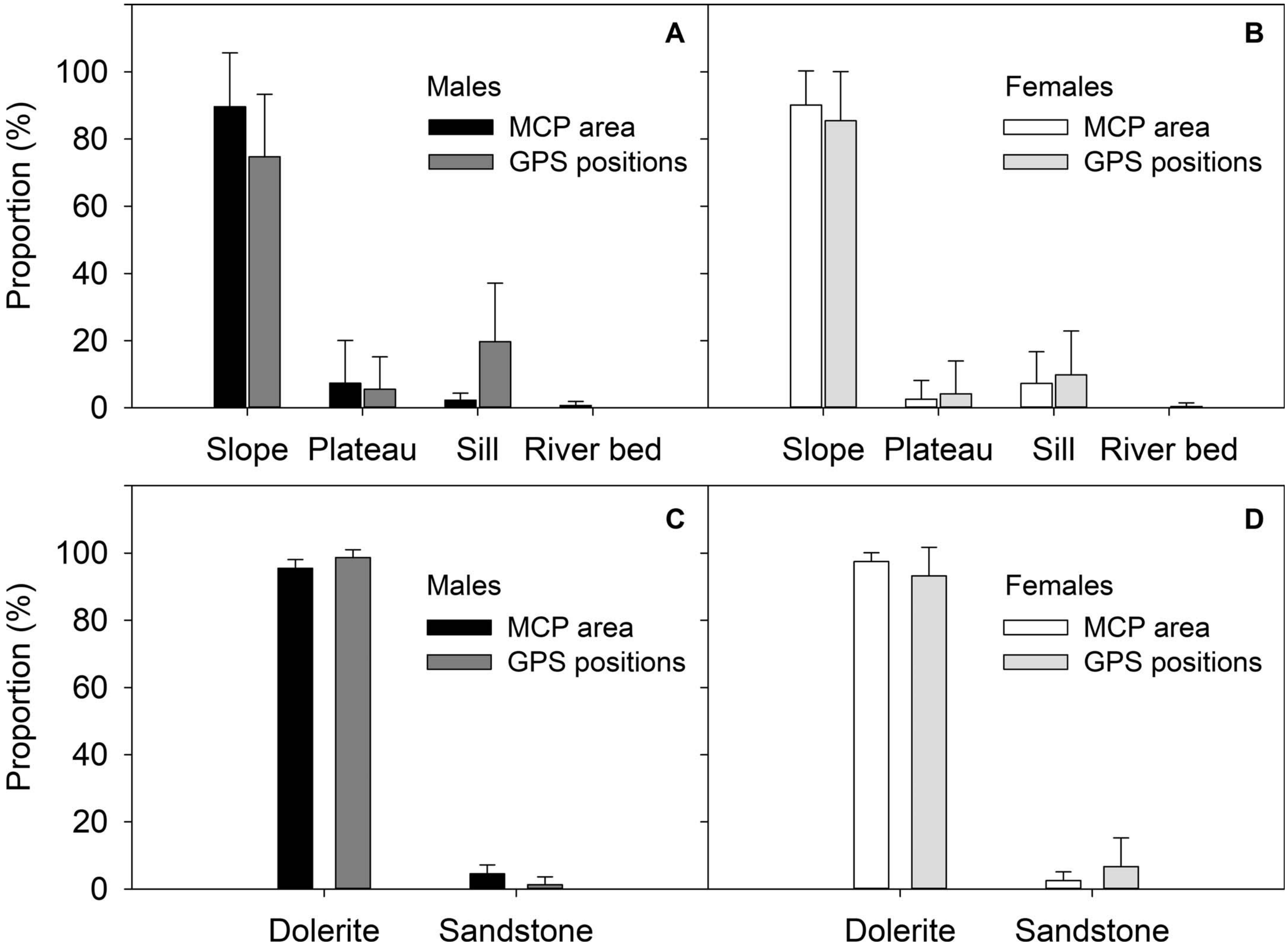

Fig. 3. Mean proportions and standard deviations of home ranges (minimum convex polygons, MCP), and of GPS positions, representing specific microhabitats (A–B) or rock types (C–D), for three male (A and C) and seven female (B and D) Karoo Dwarf Tortoises (*Chersobius boulengeri*) in 2018–2020.

MDMDs are a coarse proxy of actual movement distances (Iglay et al., 2006). Despite inherent underestimation of actual movement distances, MDMDs can provide insight into how tortoises use their home ranges (Lagarde et al., 2003; Rozylowicz and Popescu, 2013), and even provide insight into conservation statuses of populations (Guyer et al., 2012). Male and female Karoo Dwarf Tortoises had similar MDMDs, which were near ranges of MDMDs in other tortoises (Geffen and Mendelssohn, 1988; Franks et al., 2011; Rozylowicz and Popescu, 2013). MDMDs in Karoo Dwarf Tortoises may reflect distances among suitable retreats (i.e., most GPS positions were for hiding tortoises; Loehr et al., 2021), but the distribution of retreats was not recorded in the current study. Although recordings were made during the summer mating season, males did not seem to travel greater distances than females to find mates, as has been found in other tortoise species (Lagarde et al., 2003; Hofmeyr et al., 2012). Despite similar MDMDs in male and female Karoo Dwarf Tortoises, associated predation risks may be larger for males that represent the smaller sex, because avian predation appeared to be targeted at smaller individuals (Loehr and Keswick, 2022).

Karoo Dwarf Tortoise populations are threatened range-wide (Hofmeyr et al., 2018). My study used simple measures of microhabitat and rock type to highlight the importance of sills for this species, and also indicates that it can survive in other microhabitats (e.g., plateaus). Future studies should address other aspects of their habitat such as retreat availability and fine-scale vegetation composition (Del Vecchio et al., 2011). The rather sedentary habits of Karoo Dwarf Tortoises, as indicated by small MCPs and MDMDs, emphasize the importance of habitat suitability for population conservation. Eventually, spatial models may integrate available data (Andersen et al., 2000) and improve information available for conservation actions.

DATA ACCESSIBILITY

The data from this study are available upon request. Supplemental material is available at https://www.ichthyologyandherpetology.org/h2022059. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and

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