

Structure and projected decline of a Karoo dwarf tortoise population

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Abstract

Inconspicuous, secretive, or sparsely distributed species receive relatively little research attention, potentially leading to uncertainty about their status and lack of efforts to conserve them. Karoo dwarf tortoises (*Chersobius boulengeri*) are endemic to South Africa, spend most of the time in retreats at remote arid locations, and are seldom seen. We conducted a 3-year (2018–2020) mark-recapture study to investigate the size and structure of the only Karoo dwarf tortoise population currently known to exist. The population in the 16-ha core of our study site consisted primarily of adult males and females, at a density of 3.3 individuals/ha. Many individuals had severely worn shells and appeared old. Small individuals (straight carapace length <65 mm) represented just 8% of the population and were mostly recent hatchlings. Overall, tortoises had high estimated survival rates (0.77–0.95; lower 95% confidence limit for the smallest tortoises was 0.16), despite a 15-month drought. The lack of small individuals may reflect low levels of recruitment and population decline. Predation by corvids was an obvious threat to all size classes. We estimated that the local population across the 250-ha study area was 800–900 males and females, and recommend precautionary conservation measures focused on reducing human-subsidized avian predation.

KEYWORDS

Chersobius boulengeri, citizen science, corvids, demography, mortality, population dynamics, predation, recruitment

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Practical constraints on the observation of inconspicuous, secretive, or sparse species provide difficulties for field studies, limiting our understanding of population structure and dynamics, and rendering conservation requirements uncertain. For example, studies on bats have historically focused on species roosting or hibernating in groups in objects that can be easily observed by humans, whereas less attention has been given to inconspicuous species that are infrequently encountered (Weller et al. 2009). Similarly, research effort for cat species is biased towards large taxa, presumably because large species are charismatic and easier to study than small species (Brodie 2009). In naturally hidden marine ecosystems, lack of baseline data may lead to unsubstantiated optimistic assumptions about conservation statuses of populations and even cause unnoticed extinctions (Edgar et al. 2005). Ultimately, conservation efforts may not focus on species that need them most (Roberts et al. 2016, Tensen 2018), and important ecosystem roles that sparse species play may be lost (Lyons et al. 2005). To maximize effectiveness of conservation, researchers should explore study designs for inconspicuous, secretive, or sparse species of possible conservation concern (Hodge et al. 2017), and develop innovative approaches as needed (e.g., involving citizen scientists; Edgar et al. 2017).

Tortoises are among the most threatened vertebrate groups (Bombi et al. 2013, Lovich et al. 2018). Nevertheless, few populations have been thoroughly studied because of generally low population densities (Stevenson et al. 2007, Bondarenko and Peregontsev 2009, Sánchez et al. 2014), low levels of activity and secretive behavior (Hailey and Coulson 1999, Lawson 2006, Noss et al. 2013), and slow population changes as a result of longevity, delayed maturity, and low fecundity (Orenstein 2012, Loehr 2017). Lack of study and insight into characteristics of populations are particularly problematic in regions with high levels of species richness, such as the African continent where 39% of extant tortoise species live (Turtle Taxonomy Working Group 2017). Bombi et al. (2013) analyzed and recommended research and conservation priorities for African tortoises, identifying southern Africa as a priority region, with Karoo dwarf tortoises (*Chersobius boulengeri*) representing one of the taxa that might require conservation initiatives. The recently elevated conservation status of the Karoo dwarf tortoise by the International Union for Conservation of Nature, from vulnerable to endangered (Hofmeyr et al. 2018b), emphasizes this need for attention.

Karoo dwarf tortoises are endemic to South Africa, where they inhabit isolated rocky ridges and outcrops in the southern interior (Boycott and Bourquin 2000), which support little human habitation. The tortoises are seldom

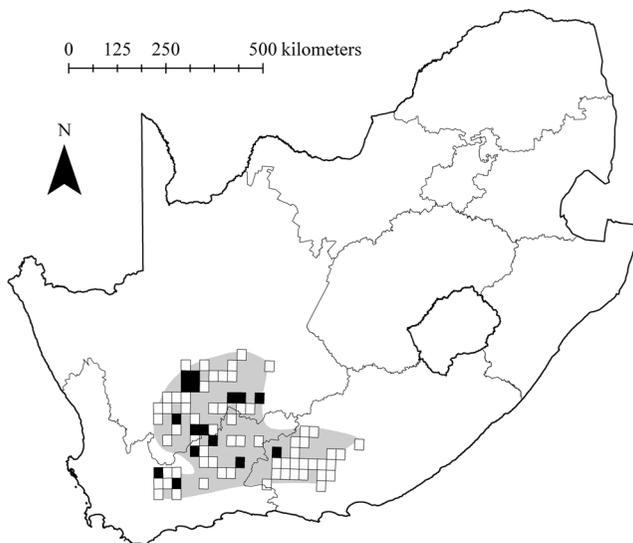


FIGURE 1 Distribution of Karoo dwarf tortoises in South Africa (grey shade), and quarter degree grid cells with records of live and dead individuals in 1881–2000 (white cells) and in 2000–2017 (black cells, representing 24 live individuals), based on combined museum and nature conservation databases. Figure modified from Hofmeyr et al. (2021)



seen (Figure 1) because of their small body size (max. length 110 mm; Boycott and Bourquin 2000), cryptic coloration (Boycott 1989), frequent inactivity (i.e., spending up to 90% of daytime in retreats; Loehr et al. 2021), and rarity. From 2005 until 2021, only 1 population was identified during surveys at 40 sites where the species had been located in the past (Hofmeyr et al. 2018b; J.-P. Le Roux, Endangered Wildlife Trust, unpublished data). Habitat degradation in nearly 50% of its range (Hoffman et al. 1999) may have contributed to local extinctions. Furthermore, predation by corvids may play a role, as seemed the case in a 66% decline for a population of congeneric speckled dwarf tortoises (*Chersobius signatus*; Loehr 2017). Because of their inconspicuousness, published information about Karoo dwarf tortoises is limited, is qualitative, and is based on incidental observations or museum material collected throughout the range of the species (Duerden 1907, Archer 1968, Boycott 1989, Haagner 1990, Van Wijk and Bates 1999). Quantitative studies on the structure and dynamics of populations are lacking, hampering potential conservation action.

Our objective was to quantify the only currently known Karoo dwarf tortoise population in terms of number of individuals, sex ratio, and size distribution, and to assess possible conservation strategies for the species. Based on the remoteness and low human population in the area, we expected that the population would be relatively dense and composed of male, female, and juvenile size classes each following Gaussian-distributions. In terms of conservation, we expected the population to be secure and not in need of specific measures.

STUDY AREA

We conducted the study at a remote (nearest village >65 km) study site in the Northern Cape Province, South Africa (coordinates recorded in the biodiversity database of CapeNature, Western Cape Province, South Africa, to avoid spread of sensitive locality data), composed of a 16-ha core and its surroundings. There are no long-term weather recordings for this area, but modeled long-term data (30 yr of hourly weather model simulations; Meteoblue 2020) produced average monthly minimum and maximum temperatures of 1–14°C and 14–30°C, and average annual rainfall of 162 mm, peaking in summer. We installed a rainfall datalogger (Hobo S-RGF-M002 connected to H21-USB; Onset Computer Corporation, Bourne, MA, USA) to monitor rainfall throughout the study. The study site is located in the Nama-Karoo biome (Mucina et al. 2006) and its topography consisted of northerly, north-easterly (core of the site), and easterly facing rocky slopes (~1,360–1,500 m above sea level) with dolerite ridges, and adjacent dolerite and sandstone plateaus. Vegetation type was classified as Upper Karoo Hardeveld (Mucina et al. 2006) and included sparse dwarf shrubs (e.g., asparagus [*Asparagus* spp.], doll's rose [*Hermannia* spp.], rooiganna [*Salsola calluna*]), grass tufts (particularly iron grass [*Aristida diffusa*]), succulents (e.g., aloe [*Aloe* spp.], crassula [*Crassula* spp.], haworthia [*Haworthiopsis venosa tessellata*], ice plant [*Stomatium* sp.]), and geophytes (e.g., slime lily [*Albuca* spp.], trachyandra [*Trachyandra* spp.]). Karoo dwarf tortoises shared their habitat with vertebrates such as western rock elephant-shrew (*Elephantulus rupestris*), variegated skink (*Trachylepis variegata*), Barnard's thick-toed gecko (*Pachydactylus barnardi*), and Karoo sand snake (*Psammophis notostictus*). The land was privately owned, fenced (not restricting wildlife), and used for sheep farming at a low stocking rate.

METHODS

Field recordings and marking

We intensively searched the 16-ha core of the study site for Karoo dwarf tortoises during 5-week sampling periods in austral summer 2018 (14 Feb–22 Mar), 2019 (12 Feb–20 Mar), and 2020 (11 Feb–17 Mar). In addition, we searched the core briefly from 30 January–3 February 2017 (summer), 2 October–8 November 2018 (spring), and 8–11 October 2019 (spring). We conducted searches in surrounding areas (up to 3,500 m from the core) incidentally. Field-time was

maximized by mobilization of volunteers recruited in African, American, European, and Oceanic conservation, herpetocultural, and zoo communities. In all cases, we targeted tortoises hiding in holes under or among rocks. We instructed volunteers to inspect all holes on the site, demonstrated various types of holes (e.g., holes concealed by shrubs or rocks), showed them how to thoroughly inspect holes, and evaluated volunteer effectiveness by regular duplication of inspections. Furthermore, we maintained strict time schedules for breaks and monitored success rates of volunteers. When we captured a tortoise for the first time, we categorized it as male or female based on the presence of a large tail and plastron concavity in males (Boycott and Bourquin 2000), or as juvenile if it was too small for confident sex determination. Furthermore, we examined its carapace and categorized individuals with smooth, worn scutes, faded scute rings, thickened scute edges, and concave scute centers as old (Grover and DeFalco 1995, Medica et al. 2012; Figure 2B). We recorded its global positioning system (GPS) location to the nearest 3 m and used digital calipers to measure to the nearest 0.01 mm its straight carapace length (SCL; straight-line distance between the nuchal and supracaudal scutes), maximum shell width (MSW), and maximum shell height (MSH). We calculated shell volume (SV; cm^3) as $\pi \times \text{SCL} \times \text{MSW} \times \text{MSH} / 6,000$ (Loehr et al. 2007a).

Before releasing a tortoise at the site of capture, we notched its marginal scutes (Boycott and Bourquin 2000), but we marked tortoises with $\text{SCL} \leq 40.57$ mm with a small and inconspicuous dot of nail polish to avoid shell damage. We photographed all tortoises' carapaces and plastrons for identification purposes. When we recaptured a tortoise, we identified it, recorded its GPS location, recorded its shell dimensions if recaptured for the first time in a sampling period, and released it. We entered all GPS locations in ArcMap 9.3 (Esri, Redlands, CA, USA) to assess if tortoises were in or outside the core of the study site. We equipped 9 males and 17 females with radio-transmitters but did not include observations of tortoises tracked using telemetry in the current study; thus, all captured and recaptured tortoises were located without telemetry or precapture knowledge of their locations.



FIGURE 2 Shell variation (A–C) in a population of Karoo dwarf tortoises, Northern Cape Province, South Africa, 2018–2020, and an adult female Karoo dwarf tortoise (red arrow) demonstrating crypsis in its habitat (D)



Statistics and mark-recapture analysis

We recorded numbers of captured male, female, and juvenile tortoises, and examined the sex ratio with a χ^2 test. We evaluated size distributions of males and females in the population with Shapiro-Wilk tests. We calculated means for SCL and SV of males, females, and juveniles, and compared them using Kruskal-Wallis (KW) tests followed by Dunn's *post hoc* tests.

We estimated apparent survival (ϕ) and recapture probabilities (p) for the open tortoise population at the core of the study site based on our searches in February–March 2018, 2019, and 2020 using the Cormack-Jolly-Seber (CJS) formulation in Program MARK (version 9.0; White and Burnham 1999). We were unable to model time-dependence because of insufficient data, and assumed constant p because our standardized methodology (all field personnel received the same training and evaluation) did not rely on tortoise activity (Karoo dwarf tortoises spend most of daytime in retreats; Loehr et al. 2021), and sampling effort was similar among years. We expected apparent survival to depend on SV and sex, so we used $\phi(SV \times sex) p(.)$ as our starting model. We assessed goodness of fit (GOF) of the starting model by examining Fletcher's variance inflation factor, \hat{c} (Fletcher 2012), after which we removed the covariate SV from the model, conducted a bootstrap analysis (100 simulations), and estimated \hat{c} by dividing model deviance and \hat{c} by mean simulation deviance and \hat{c} , respectively. We adjusted \hat{c} in Program MARK to the largest estimated value. We built derived models by removing SV and sex, and ranked models based on adjusted Akaike's Information Criterion (AIC_c; Sugiura 1978, Hurvich and Tsai 1989). We tested robustness of model ranking by manually increasing \hat{c} from 1.0 to 2.0 in 4 steps of 0.25. Finally, we estimated ϕ and p as model-averaged values (Buckland et al. 1997).

To estimate population size and the number of tortoises entering the core of the study site, we used the POPAN formulation in Program MARK (Schwarz and Arnason 1996). We translated the most parsimonious CJS model to a time-independent POPAN starting model, in which the additional POPAN parameters probability of entrance (pent) and super-population size (N ; representing all individuals entering the core of the study site prior to and during the study) were allowed to depend on sex. We assessed GOF of the starting model by examining Fletcher's \hat{c} ; additional GOF tests for the POPAN starting model were not available. We built derived models by removing sex, ranked models using Akaike's Information Criterion, and tested robustness of ranking by manual adjustments (1.0 to 2.0) of \hat{c} . We also verified that model-averaged ϕ and p estimates were similar to those produced by the CJS model.

We conducted statistical tests, except Program MARK modeling, in SigmaPlot 12.0 (Systat Software, San Jose, CA, USA). We considered statistical test results significant if $P < 0.05$ and report standard errors (SE) unless indicated otherwise.

RESULTS

The study site experienced temporal variation in rainfall. February–September 2018 had above-average rainfall (148 mm compared to a modeled long-term average of 102 mm), resulting in abundance of food (i.e., green vegetation) and active tortoises that were relatively heavy in February–March and October–November 2018. Because of a drought that followed from October 2018 to December 2019 (64 mm compared to 206 mm), green vegetation was absent in February–March 2019, and many tortoises (particularly females) had low body masses and were lethargic. High rainfall in January–February 2020 (106 mm compared to 39 mm) restored plant growth, resulting in active and heavy tortoises in February–March 2020.

We located 52 male, 37 female, and 5 juvenile Karoo dwarf tortoises on the study site, representing an equal sex ratio ($\chi^2_{1} = 2.53$, $P = 0.11$). Searches in the surroundings of the site's core were not systematic, but we were unable to find any tortoises $>1,200$ m from the core, and inhabited areas were restricted to north-easterly and easterly facing mountain slopes. Most tortoises had relatively plain beige to reddish-brown carapaces (Figure 2). All juveniles were uniformly beige. Six individuals (6%) had black edges on the vertebral and costal scutes

(Figure 2A). Older carapacial sections had olive shades (Figure 2B–C), and 36% of the males and females had worn, smooth scutes with faded scute rings, thickened scute edges, and concave scute centers indicative of old age (Figure 2B). Despite the generally plain coloration, tortoises were camouflaged and usually overlooked when active in their rocky habitat (Figure 2D).

Males, females, and juveniles differed significantly in SCL (KW test; $H_2 = 48.99$, $P \leq 0.001$); SCL was greater in females than in males and juveniles, and greater in males than in juveniles (Table 1). Mean SV also differed among groups ($H_2 = 60.62$, $P \leq 0.001$), and was greater in females than in males and juveniles (Table 1). Straight carapace lengths ranged from 31.3 mm to 102.5 mm, but 92% of tortoises had carapaces >65 mm (Figure 3). The smallest (male) individual from which the sex could be confidently identified had an SCL of 53.7 mm. Female SCL sizes were Gaussian-distributed (Shapiro-Wilk test; $W = 0.85$, $P = 0.066$), whereas male SCL sizes were skewed towards larger individuals ($W = 0.27$, $P = 0.013$).

Within the 16-ha core of the study site, we located 32 male, 21 female, and 1 juvenile Karoo dwarf tortoises, representing an equal sex ratio ($\chi^2_1 = 2.28$, $P = 0.13$). Most were located in February–March 2018–2020, when we searched for 478, 457, and 473 person-hours, respectively. Despite the abundance of potential retreats and use of

TABLE 1 Means, standard deviations (SD), ranges, and sample sizes (n) of straight carapace length (mm) and shell volume (cm^3) for male, female, and juvenile Karoo dwarf tortoises, Northern Cape Province, South Africa, 2018–2020

	\bar{x}	SD	Range	n
Straight carapace length				
Males	82.5	8.67	53.7–94.8	52
Females	93.5	7.04	63.6–102.5	37
Juveniles	39.4	10.84	31.3–57.7	5
Shell volume				
Males	88.6	22.03	32.0–138.3	52
Females	141.7	24.82	46.1–180.5	37
Juveniles	15.0	11.03	8.1–34.3	5

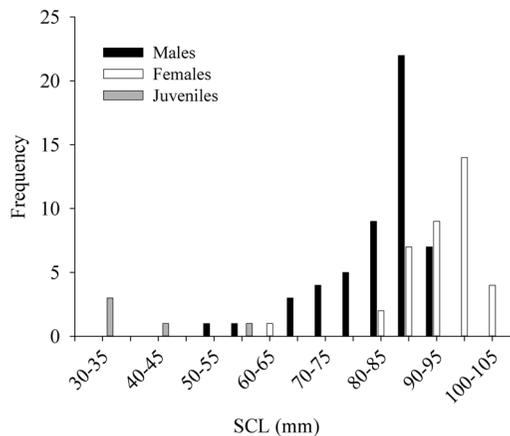


FIGURE 3 Straight carapace length (SCL) distributions of 52 males, 37 females, and 5 juveniles in a population of Karoo dwarf tortoises, Northern Cape Province, South Africa, 2018–2020



multiple retreats by each tortoise, most individuals captured in February–March 2018 were recaptured in February–March 2019 and 2020 (Table 2). Moreover, many individuals were recaptured multiple times within each February–March sampling period (annual averages for males and females were 1.5–2.6 times and 1.5–3.3 times, respectively). We excluded the single juvenile (SCL = 57.7 mm) from population modeling. Fletcher's \hat{c} for the CJS starting model was 1.45, indicating reasonable GOF. This was confirmed by bootstrap simulations, after removing SV from the starting model, which indicated a reasonable chance to encounter deviances as large or greater than the deviance of the starting model without inclusion of SV ($P = 0.33$). Furthermore, bootstrap results estimated \hat{c} values of 0.96–1.14. Manual increases of \hat{c} did not change ranking of derived models, so we adjusted \hat{c} in Program MARK to 1.14.

The 2 most parsimonious models (71% support from the data; Table 3) indicated that apparent survival (ϕ) was similar in males and females, and was related to SV (63% support from the data, including the most parsimonious

TABLE 2 Encounter histories for 32 male, 21 female, and 1 juvenile Karoo dwarf tortoises, Northern Cape Province, South Africa, 2018, 2019, and 2020. Format of encounter histories follows White and Burnham (1999; e.g., 1 1 0 indicates that individuals were encountered in 2018 and 2019 but not in 2020

Encounter history	Number of males	Number of females	Number of juveniles
1 0 0	4	2	1
1 1 0	1	3	0
1 1 1	12	10	0
1 0 1	3	2	0
0 1 0	3	0	0
0 1 1	3	2	0
0 0 1	6	2	0

TABLE 3 General and derived Cormack-Jolly-Seber (CJS) models with Akaike's Information Criterion values (AIC), change in AIC (Δ AIC), weights (w_i), estimable model parameters (K), and deviances, generated to estimate apparent survival (ϕ) and recapture rate (p) for 32 male and 21 female Karoo dwarf tortoises, Northern Cape Province, South Africa, 2018–2020. Model variables for ϕ included shell volume (SV) and sex, whereas parameter p was assumed constant. The POPAN models were adapted from the most parsimonious CJS model to estimate ϕ , p , probability of entrance (pent), and super-population size (N). Parameters pent and N included the model variable sex. Akaike's Information Criterion values were corrected for the CJS models, but not for the POPAN models

Models	AIC	Δ AIC	w_i	K	Deviance
CJS models					
$\phi(SV) p(.)$	87.27	0.00	0.44	2	83.09
$\phi(.) p(.)$	88.29	1.02	0.27	2	84.11
$\phi(SV \times \text{sex}) p(.)$	89.01	1.74	0.19	3	82.65
$\phi(\text{sex}) p(.)$	90.17	2.90	0.10	3	83.81
POPAN models					
$\phi(SV) p(.) \text{pent}(.) N(.)$	120.50	0.00	0.39	4	112.12
$\phi(SV) p(.) \text{pent}(\text{sex}) N(.)$	120.78	0.28	0.34	5	110.21
$\phi(SV) p(.) \text{pent}(.) N(\text{sex})$	122.64	2.14	0.13	5	112.06
$\phi(SV) p(.) \text{pent}(\text{sex}) N(\text{sex})$	122.69	2.20	0.13	6	109.89

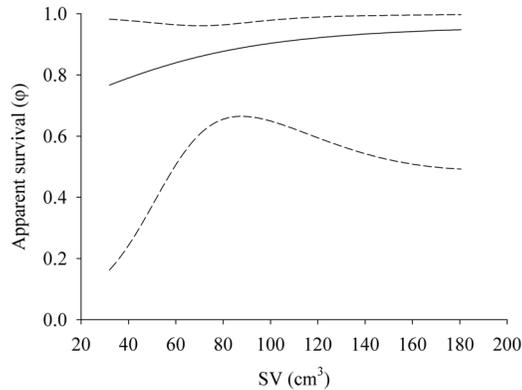


FIGURE 4 Model-averaged relationship between apparent annual survival (ϕ) and shell volume (SV) for Karoo dwarf tortoises, Northern Cape Province, South Africa, 2018–2020, based on Cormack-Jolly-Seber models including 32 males and 21 females. Dashed lines represent 95% confidence intervals

model; Table 3). Mean model-averaged ϕ was 0.95 ± 0.075 for males and 0.95 ± 0.073 for females, and recapture probability (p) was 0.82 ± 0.080 . Relative to SV, ϕ ranged from 0.77 to 0.95, but confidence intervals indicated that considerably lower rates were also possible, particularly for small individuals that were under-represented in the dataset (Figure 4).

Our POPAN starting model, translated from the most parsimonious CJS model, was $\phi(SV) p(.) \text{pent}(\text{sex}) N(\text{sex})$. The POPAN starting model had a reasonable GOF, as indicated by Fletcher's \hat{c} of 1.81. Derived models indicated similar support for sex-dependent and constant probability of entrance into the population (pent), and little support for sex-dependent super-population size (N ; Table 3). Model-ranking was unaffected by manual increases of \hat{c} . Model-averaged estimates of ϕ (0.96 ± 0.050) and p (0.87 ± 0.059) were similar to CJS model-averaged estimates. Values of pent were 0.13 ± 0.045 for males and 0.083 ± 0.043 for females, revealing that 87–92% of the tortoises were already present at the core of the study site before the study started. The POPAN models estimated that the population at the core consisted of 32.18 ± 0.71 (95% CI = 30.79–33.57) males and 21.08 ± 0.66 (95% CI = 19.78–22.39) females, and that 4.18 ± 1.51 males and 1.78 ± 0.93 females entered the population between 2018 and 2020.

DISCUSSION

Our effort to maximize person-hours by deploying volunteers was successful in mitigating practical constraints caused by the remote location of the study population and the inconspicuousness of Karoo dwarf tortoises. The high recapture probability from 2018 to 2020 indicated that we were able to capture most of the male and female tortoises that were present at the core of the study site. Consequently, we were able to generate meaningful quantitative data on the structure of the population, enabling inferences with regard to conservation. Deploying volunteers in scientific tortoise studies is not new (Rose and Judd 2014, Cayot 2021), yet its success factors have received little attention. We consider our selection of volunteers in the conservation, herpetocultural, and zoo communities (i.e., producing persons with strong conservation values for tortoises; Campbell and Smith 2006), and provision of training and evaluation during sampling (Stylinski et al. 2020), to be factors that contributed to high recapture rates. Towards the end of sampling periods, we instructed volunteers how to deal with information they had obtained (e.g., GPS coordinates embedded in photographs) to reduce risks associated with the spread of sensitive locality data (Quinn 2021).



Populations of long-lived species may appear of little conservation concern because of the persistent presence of adult and reproducing individuals, masking processes such as lack of recruitment and inbreeding depression that can eventually lead to extinction (Thompson 1983, Reichert et al. 2016, Taylor et al. 2017). The Karoo dwarf tortoise population in this study had originally been identified based on the capture of 8 adult individuals during a survey of 24 person-hours, leading to the conclusion that it “could be considered viable” (Hofmeyr et al. 2018b:4). Our population analysis challenges the notion that this population is viable because it consisted primarily of adult individuals, 36% of which appeared old, and contained few small (SCL < 65 mm) males, females, and juveniles. Moreover, 3 of the 5 juveniles that we located were recent hatchlings (Loehr 2018). Tortoise populations may not necessarily require large juvenile components because adults can reproduce over many years, but authors reporting populations with 5–56% juveniles (Judd and Rose 1983, Meek 1985, McMaster and Downs 2006) cautioned that their percentages were probably underestimates because small tortoises might have been overlooked (Pike et al. 2008). In contrast, we are confident that our estimate that 5% of the study population was juveniles was accurate because of our frequent and thorough inspections of virtually all available retreats at the core site. The lack of small individuals may retard recruitment into adult life stages, considering the low fecundity and growth in dwarf tortoises. We have little information for Karoo dwarf tortoises, but speckled dwarf tortoises produce ≤ 3 eggs/year (Hofmeyr et al. 2018a) and require 6–7 years for hatchlings to grow to an SCL of 65 mm (Loehr et al. 2007b). The size composition of the Karoo dwarf tortoise population was similar to a population of speckled dwarf tortoises that had declined by 66% (Loehr 2017: Figure 1). Declines in chelonian populations due to insufficient recruitment and aging adults appear common (Epperson and Heise 2003, Smith et al. 2013, Van Dyke et al. 2019, Segura et al. 2020, Price et al. 2021), and we consider lack of recruitment a survival threat for Karoo dwarf tortoises.

Circumstantial evidence suggests that the paucity of small tortoises and possible decline of the population was related to predation. The study site was patrolled by white-necked ravens (*Corvus albicollis*) daily in all years and seasons, and by pied crows (*Corvus albus*) less frequently. Both species are tortoise predators (Hockey et al. 2005, Fincham and Lambrechts 2014), pied crows especially in arid regions (Durà i Franch 2017). Corvids in general affect tortoise demographics (Boarman 2003, Berry et al. 2013, Segura et al. 2020) and were a likely cause of decline in a speckled dwarf tortoise population (Loehr 2017). We found 3 dead adult Karoo dwarf tortoises with shattered shells next to large boulders on which they were probably dropped by birds (Hockey et al. 2005, Branch 2008). Depredated (or scavenged) juveniles are often transported to bird nests or perches (Mendelssohn and Geffen 1995, Boarman 2003, Fincham and Lambrechts 2014, Durà i Franch 2017), which were not present at the study site. Despite our frequent and long-term presence until after sunset, we rarely directly observed other potential predators or signs that such species were present. Alternative factors that could have affected the proportion juveniles in the population were less likely. Reproductive studies, conducted simultaneously, ruled out lack of egg production as a cause (V. J. T. Loehr, Dwarf Tortoise Conservation, unpublished data), and the hatchlings that we captured indicated that at least some eggs incubated successfully. Drought may have been detrimental to juvenile Karoo dwarf tortoises, but juvenile speckled dwarf tortoises appear to have comparable survival rates in years with and without drought (Loehr 2010). Likewise, adult Karoo dwarf tortoises had high apparent survival rates despite drought.

Densities of various tortoise species vary from 0.01–57 individuals/ha (Leuteritz et al. 2005, Rouag et al. 2007, Asefa et al. 2020), depending on habitat productivity, and natural and human perturbations. The low productivity of the arid Karoo dwarf tortoise habitat (based on long-term grazing capacity presented by Esler et al. 2010) suggests a population density at the lower end of the global range. The 3.3 individuals/ha that we report at the core of the study site was lower than the density of 16–21 resident individuals/ha that Loehr (2010) recorded for speckled dwarf tortoises in a Karoo habitat with a lower productivity than our site (Esler et al. 2010). Therefore, the relatively low density of individuals that we located supports our suspicion that the Karoo dwarf tortoise population may be in decline. Extrapolation of the core across the approximately 250 ha where we found tortoises at the study site leads to an estimate of 800–900 males and females for the entire local population.



MANAGEMENT IMPLICATIONS

Given the size and remoteness of the Karoo dwarf tortoise's range, we expect that future surveys will discover additional populations beyond the single known extant population we studied. Populations throughout the range appear to be declining in viability and are in danger of extirpation. The results of our demographic study support the implementation of precautionary conservation measures for the Karoo dwarf tortoise range in the Nama Karoo that are attempting to reduce corvid numbers. These include removal of obsolete telephone poles and windmills (i.e., potential nesting sites); livestock carcasses, roadkills, and uncovered landfills (i.e., potential food sources); and uncovered water containers, spillage, and shallow troughs (i.e., accessible water sources) that are attractions for corvids. It is paramount that surveys are conducted to identify additional Karoo dwarf tortoise populations, and that their population dynamics be investigated for local and range-wide conservation actions.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

ETHICS STATEMENT

Handling of tortoises was permitted by the Northern Cape Department of Environment and Nature Conservation, South Africa (permit FAUNA 0950/2017). In addition, our methods were approved by the Senate Research Committee of the University of the Western Cape, South Africa (registration number 04/4/11).

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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