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Research article

Bimodal nesting season in Karoo dwarf tortoises (*Chersobius boulengeri*)

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Tortoises in arid, unpredictable regions may use a bet-hedging strategy of regularly laying small clutches regardless of actual environmental conditions, so that some hatchlings will emerge when conditions are favourable. Karoo dwarf tortoises (*Chersobius boulengeri*) are endangered in their arid, unpredictable range in South Africa, yet studies of reproduction are lacking. I used radiography and captive breeding to study reproduction in wild (n = 22, 2018–2022) and captive (n = 2, 2020–2023) individuals, expecting to find bet-hedging characteristics. My expectation was that females would regularly lay eggs in summer, when most rain falls. In addition, I expected that females would produce consistently large eggs and hatchlings capable of surviving their harsh environment. Indeed, females produced multiple clutches of large single eggs per year, some even during drought. However, the egg-laying season had a unique bimodal pattern in autumn and spring, possibly dispersing hatching events throughout the unpredictable rainfall season. Fecundity was low, approximately 5 eggs per year when resources were unlimited. The large eggs were usually wider than pelvic width, but egg size was nevertheless constrained by female size. Hatchling size correlated positively with egg size, confirming a potential survival benefit. Surprisingly, egg size decreased in successive clutches in a season, apparently to increase offspring frequency while resources were limited. Reproduction of Karoo dwarf tortoises is unlikely to offset current predation levels that contribute to their endangered status, thus predation reduction should be a conservation priority. Projected regional aridification due to climate change may pose a previously underestimated threat, because females lay fewer eggs during drought, females that lay eggs during drought may suffer increased mortality when body reserves cannot be restored, and hatchlings (particularly from late clutches) may have insufficient reserves for survival under aridified conditions. Conservation plans might focus on sites least affected by aridification.

Keywords: bet-hedging, drought, egg size, nesting phenology, radiography, reproduction

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Introduction

Species in environments with unpredictable offspring survivorship may bet-hedge reproductive investments, to maximise the long-term probability of producing surviving offspring (Slatkin 1974, Stearns 1976, Seger and Brockmann 1987). Bet-hedging may consist of regular production of small numbers of offspring, regardless of environmental conditions, to eventually produce more surviving offspring over a parent's lifetime than would single larger reproductive bouts that would risk total failure at times of unfavourable conditions. Reducing the variance and the mean of a fitness parameter (in this case fecundity) is a characteristic of all bet-hedging strategies (Seger and Brockmann 1987, Philippi and Seger 1989). Published examples include snail kites (*Rostrhamus sociabilis*) and black kites (*Milvus migrans*) that depend on unpredictable hydrological regimes for their prey and produce invariantly small clutches of eggs (Beissinger 1986, Sergio et al. 2011). Similarly, western box turtles (*Terrapene ornata luteola*) and desert tortoises (*Gopherus agassizii*), in areas with unpredictable rainfall and associated food availability, produce small mean clutch sizes that are similar among years (Nieuwolt-Dacanay 1997, Lovich et al. 2015). Although bet-hedging strategies may help species persist in unpredictable environments, eventual reproductive success is often affected by adjustments (e.g. number of clutches, brood reduction) in response to actual resource availability (Sergio et al. 2011, Lovich et al. 2015). This includes reducing egg size in response to scarce resources, before reducing egg number (Oro et al. 2023).

Dwarf tortoises in the genus *Chersobius* (maximum straight carapace lengths ~ 110 mm; Boycott and Bourquin 2000) appear to have a reproductive strategy consistent with bet-hedging. Dwarf tortoises are herbivorous (Schleicher and Loehr 2001, Loehr 2006, Loehr et al. 2023) and inhabit arid ranges with unpredictable rainfall and primary production in South Africa and Namibia (Schulze 1997, Boycott and Bourquin 2000). All three extant species produce single-egg clutches (Boycott and Bourquin 2000, Schleicher and Loehr 2001, Hofmeyr et al. 2005), a strategy that appears to have evolved in response to gradual aridification and increased unpredictability of rainfall in the region in the late Miocene (Hofmeyr et al. 2005). Consequently, the production of hatchlings is limited, but dispersed in time and space, increasing the probability that some hatchlings will survive. In addition, regular production of single-egg clutches enables females to adjust clutch frequency in response to available resources, and to produce eggs of a large size to potentially facilitate hatchling survival (Loehr et al. 2009). In speckled dwarf tortoises (*Chersobius signatus*), females with a high body condition produced larger eggs than did females with a low body condition, but egg size was relatively constant and unrelated to rainfall (Loehr et al. 2011).

Available information about reproduction in dwarf tortoises is mostly limited to speckled dwarf tortoises (Loehr et al. 2004, Hofmeyr et al. 2005, Loehr et al. 2011). The only published information about congeneric Karoo dwarf tortoises (*Chersobius boulengeri*) consists of a few incidental observations (Haagner 1990, Boycott and Bourquin 2000, Loehr 2017a, b, 2018), yet the endangered conservation status of Karoo dwarf tortoises (Hofmeyr et al. 2018b) requires conservation measures based on solid ecological data. Karoo dwarf tortoises are primarily threatened by habitat degradation due to overgrazing by livestock (Hofmeyr et al. 2018b). Remnant populations suffer from predation by corvids (Loehr 2022, Loehr and Keswick 2022) and baboons (Hofmeyr et al. 2018b), but assessment of predation in relation to reproductive potential is hampered by a lack of data on reproduction. In the harsh environment that Karoo dwarf tortoises inhabit, typically arid (annual rainfall ~ 165–295 mm) and unpredictable (coefficient of variation for rainfall ~ 35–38%) Nama Karoo in South Africa (Schulze 1997, Boycott and Bourquin 2000, Mucina et al. 2006), it might be challenging for populations to produce sufficient eggs and surviving offspring to offset predation, so studies are urgently needed. Moreover, climate change is projected to expand desert into the Nama Karoo, exacerbating challenges for the tortoises to overcome arid conditions (Hofmeyr et al. 2018b).

From 2018 to 2023, I studied reproduction in a wild population of Karoo dwarf tortoises, and in individuals that had been transferred to captivity. I expected to find a reproductive strategy consistent with the bet-hedging concept: 1) females laying multiple single-egg clutches, in the season of the highest mean rainfall and resource availability (i.e. February–March; Meteoblue 2020), and 2) females producing eggs regardless of actual rainfall. Similar to speckled dwarf tortoises (Loehr et al. 2011), I expected that egg size would relate to female size, but otherwise would be quite constant, to produce consistently large hatchlings capable of surviving their harsh environment. To identify potential conservation requirements, I qualitatively assessed the implications of reproductive strategy in light of observed predation pressure and projected climate change.

Material and methods

Study site and recordings in the wild

The study site consisted of a rocky mountain slope (~ 1400 m a.s.l.) with adjacent plateaus, exposed dolerite sills, and dry river beds in the Northern Cape Province of South Africa (Loehr 2023b; due to the sensitivity of this population the coordinates are withheld here, but are recorded on the biodiversity database of CapeNature, Western Cape Province, South Africa). Long-term modelled (30 years of hourly weather simulations) climatic conditions show that the site is arid (annual rainfall 162 mm, largely falling in summer), with mean minimum and maximum monthly temperatures ranging between 1–14 and 14–30°C, respectively (Meteoblue 2020). I placed dataloggers (Hobo S-THB-M00x, RS3-B, and S-RGF-M002 connected to H21-USB; Onset Computer Corporation, Bourne, MA, USA) in the centre of the study site to record temperature and rainfall during this study.

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Between 20 February and 8 March 2018, I captured 16 female tortoises through inspection of holes under and among rocks. Females were equipped with radio transmitters (type RI-2B with internal antenna; Holohil Systems, Carp, ON, Canada), which were glued onto the posterior costal scutes (equipment mass ≤ 9.7% of body mass) to not obstruct mating. In summer (20 February and 8 March 2018, and 12 March 2019) and in spring (2 October, 19 October, and 7 November 2018, and 9 October 2019), females were tracked, transported by hiking and driving to the nearest radiography facility (~ 185 km), radiographed dorso-ventrally at 50 kV for 0.25 s at 50 mA with 6–10 tortoises placed on each radiograph, and released at the location of capture within 24 h after tracking. Prior to release, females were offered drinking water to replenish voided urine. On 8 March 2018, two opportunistically captured females were also radiographed, whereas two females with transmitters were found dead on 9 October 2019, and the signal of one female was lost on 7 November 2018. In autumn (13 April 2022), after all transmitters had been removed in March 2020, I captured and radiographed four females, one of which had been radiographed previously. All radiographed females appeared mature, based on the lack of male characteristics (e.g. large tail, concave plastron; Boycott and Bourquin 2000) and straight carapace lengths that exceeded minimum male straight carapace length (Loehr and Keswick 2023).

Each year in February, and for each female not captured by radiotelemetry, I used digital sliding callipers to record to the nearest 0.01 mm straight carapace length (SCL), maximum shell width (SW), maximum shell height (SH), and plastron length (PL). Shell volume (SV, cm^3) was calculated as $\pi \times SCL \times SW \times SH/6000$ (Loehr et al. 2004). Because all females appeared mature, I assumed that growth would be negligible within years. Body mass (BM) was recorded on each radiography date, and used to calculate body condition (BC) as BM/SV (Loehr et al. 2004). Radiographs were inspected for females gravid with shelled eggs, and successive clutches were distinguished based on the level of egg calcification (e.g. successive radiographs of a female showing a heavily and lightly calcified egg indicated different clutches) and egg dimensions. For each female on the radiographs, I measured PL and pelvic width (PW, mm, at the largest gap between the ilia), and for each egg I measured egg length (EL, mm) and egg width (EW, mm), to the nearest 0.01 mm. Egg volume (EV, cm^3) was calculated as $\pi \times EL \times EW^2/6000$ (Coleman 1991). I estimated egg mass (EM) based on egg density of captive eggs in this study, and subtracted EM from female BM to calculate BC of gravid females excluding egg mass. Measurements of radiographs were performed using either DICOM files (MiViewer ver. 10.25.0, MillenSys, Cairo, Egypt) or bitmaps with scale bar (ImageJ ver. 1.50i, LOCI, University of Wisconsin, Madison, WI, USA). I verified recordings by comparing PL on radiographs with actual PL. One radiograph (13 April 2022) was not available as DICOM or bitmap with scale bar, so I used the ratio between PL on the radiograph and actual PL to determine the scale.

Husbandry and recordings in captivity

In March 2019, I captured two females and two males outside the core of the study site and transported them to indoor facilities in the Northern Hemisphere (Netherlands), for study until 2023. Both females had very low body masses and appeared emaciated by drought. Consequently, I provided a Northern Hemisphere seasonal cycle (i.e. March representing spring), delaying unfavourable winter conditions (Loehr 2023a). Females were individually housed in well-structured enclosures, fed ad libitum on a fibre-rich diet low in sugars and proteins, and seasonal cycles of temperatures and photoperiod mimicked those in the wild (Loehr 2023a). Enclosure temperatures were monitored with Pt100 sensors (Yageo Nexensos, New Taipei City, Taiwan) connected to a controller (Siemens LOGO!, Munich, Germany). Males were occasionally introduced in female enclosures to mate.

When an egg had been produced, it was excavated immediately. I measured EL and EW to the nearest 0.01 mm with digital sliding callipers, and recorded egg mass (EM) to the nearest 0.1 g with a digital balance. Egg dimensions were used to calculate EV (Coleman 1991). Eggs were transferred to an incubator (IPP30plus, Memmert, Schwabach, Germany), where they incubated at a diurnal temperature cycle, interrupted by a 20-day period in a constant-temperature incubator (INCU-Line IL 10, VWR International, Amsterdam, Netherlands, retrofitted with a CAREL ir33 temperature controller, CAREL Industries, Padova, Italy) to control offspring sex assuming temperature-dependent sex determination (Bull 1983, Loehr 2023a). Initially, the diurnal temperature cycle ranged from 28.0 to 33.0°C, but this was changed to 26.0–31.0°C from 10 September 2021 onwards to reduce the development of supernumeral scutes. During the constant-temperature phase (incubation days 30–50 for the first two eggs, 23–43 for all other eggs), eggs were incubated at 30°C (to produce males) or 33.0°C (to produce females), but the latter temperature was reduced to 32.5°C from 4 April 2023 onwards. I ensured that incubation treatments were evenly distributed among eggs from the two females. After hatching, hatchlings were placed on wet tissue for 12–24 h, after which I measured SCL, SW, SH, and BM, enabling calculation of SV using the equation that had been used for adults. At the end of this study, husbandry and breeding was continued in a studbook under the auspices of Dwarf Tortoise Conservation (IJsselstein, Netherlands) and the European Studbook Foundation (Sneek, Netherlands), with the aim to develop an ex situ assurance population (Zippel et al. 2011).

Statistics

For recordings in the wild, I assessed the presence of gravid and nongravid females among seasons, and analysed variation in egg dimensions. Some eggs were present on multiple radiographs; in that case I used the largest recorded egg dimensions, because egg size can only be underestimated (i.e. long axis not parallel to film plane, or egg asymmetrical in

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cross-sectional width). To be consistent, I also used the largest value for PW. I used linear mixed models (LMM) for all analyses, because many females were recorded multiple times during the study. In all models, female was included as random effect (random intercept) to group non-independent data as 'nuisance parameter' (Gomes 2022). I started with fully parameterised models, and removed interactions among fixed effects, and covariates, to assess AIC differences. Models with the lowest AIC were used to generate fixed effect test statistics, and to estimate model parameters. To compare BC among gravid and nongravid females (including and excluding EM for gravid females) and seasons, I used LMM with reproductive status (gravid or nongravid), and autumn and spring radiography dates (2 October 2018, 19 October 2018, 7 November 2018, 9 October 2019, and 13 April 2022), as fixed effects. To test if egg dimensions differed among successive clutches in spring 2018, and if egg dimensions depended on body size and condition, I used LMM with clutch number as fixed effect, and SCL (for EL and EW) or SV (for EV) and BC as covariates. I also analysed if EL and EW depended on PW, using LMM with PW as covariate.

For recordings in captivity, I assessed how egg production was distributed among seasons, and used the same LMM approach as for recordings in the wild (i.e. captive females were recorded multiple times within the study) to analyse clutch frequencies, incubation periods, and egg dimensions among seasons and years. The LMM approach included the use of a random intercept for the two captive females in all models, because LMM is relatively insensitive to few random effect levels (Gomes 2022). Poisson generalised linear mixed models (P-GLMM) for frequency data compared autumn and spring clutch frequencies among years, with season and year as fixed effects. Seasonal differences of incubation period were tested with LMM, using season (autumn or spring) as fixed effect. I tested differences of EL, EW, and EV among successive clutches in a season, with clutch number and season (autumn or spring) as fixed effects, and SCL (for EL and EW) or SV (for EV) as covariate. In addition, I used LMM to test if captive egg dimensions differed from wild egg dimensions, with origin (captive or wild) as fixed effect, and SCL (for EL and EW) or SV (for EV) as covariate. Dependencies of captive hatchling SV and BM on EV and EM, respectively, were analysed with LMM that used EV or EM as covariate.

To ensure that LMM met assumptions of linearity, normality, and homoskedasticity, I visually assessed Q–Q plots, residual histograms, and residual-predicted scatter plots. Furthermore, I used Shapiro–Wilk tests to verify normality. In two instances, I accepted slightly non-normally distributed residuals ($p \geq 0.014$), because of the relative robustness of LMM for non-normality (Knief and Forstmeier 2021). When appropriate, LMM were followed by Bonferroni-corrected post hoc tests. Statistical test results were considered significant at $p < 0.05$. All tests were completed in jamovi ver. 2.4.1.0 (the jamovi project, www.jamovi.org). Means are presented with standard errors (SE), unless indicated that standard deviations (SD) were used.

Results

Reproduction in the wild

Radiographed females had SCL and SV size ranges of 77.6–103.12 mm and 89.77–188.07 cm^3, respectively. Because the smallest gravid female had an SCL and SV of 85.60 mm and 111.51 cm^3, respectively, a smaller (SCL 77.6 mm, SV 89.77 cm^3) nongravid female that might have been immature was excluded from all further analyses. Females were gravid in October–November (spring) and in April (autumn), but not in February–March (summer; Fig. 1A). All gravid females contained single eggs, and gravid females had a higher BC than nongravid females (Table 1; mean ± SD = 1.19 ± 0.087 for gravid and 1.10 ± 0.084 g/cm^3 for nongravid females). In October–November 2018, 16 of 17 radiographed females developed at least one egg, and seven females developed a second egg that was recorded 17–36 days after the first clutch. In contrast, only two of 14 radiographed females were gravid on 9 October 2019 (Fig. 1), after a 12-month drought period that

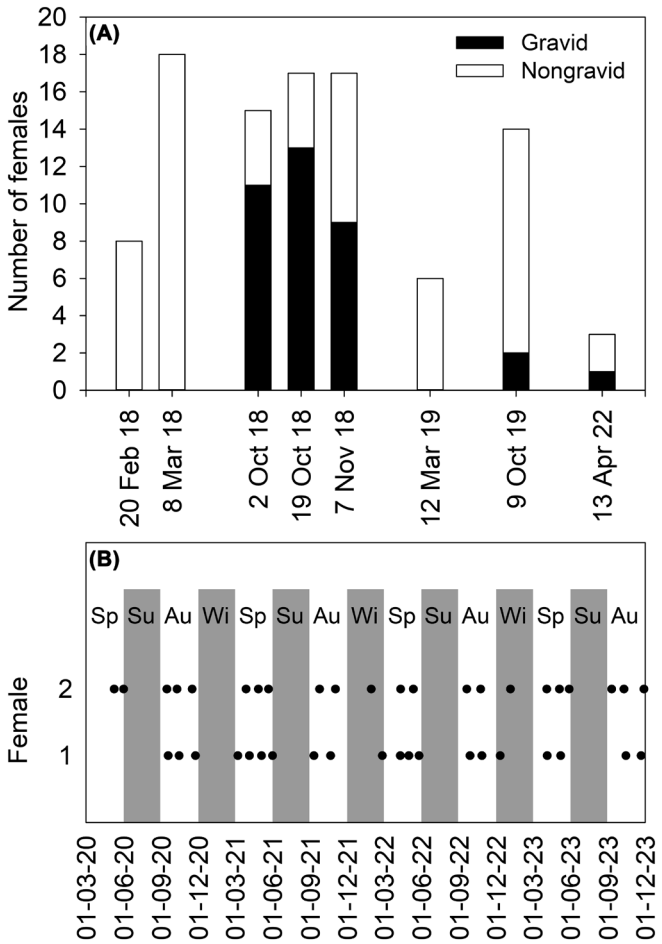


Figure 1. Reproductive status of 25 wild (Southern Hemisphere) radiographed female Karoo dwarf tortoises (*Chersobius boulengeri*) in 2018–2022 (A), and eggs (circles) produced by two captive (Northern Hemisphere) Karoo dwarf tortoises relative to meteorological spring (Sp), summer (Su), autumn (Au), and winter (Wi) 2020–2023 (B).

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Table 1. Fixed effect parameter estimates with standard errors, 95% confidence intervals and test statistics for final linear mixed models with dependent variables egg length (EL), egg width (EW), egg volume (EV), female body condition (BC) and BC excluding egg mass (EM), fixed effects reproductive status (gravid and nongravid), radiography date, clutch number (Clutch #) and origin (wild and captive), and covariates straight carapace length (SCL), shell volume (SV), BC and pelvic width (PW), for 26 wild and 42 captive Karoo dwarf tortoise (*Chersobius boulengeri*) eggs produced by 17 wild (2018–2022, South Africa) and two captive (2020–2023, Netherlands) females. Captive data were only included in models containing origin as fixed effect. Radiography dates 1–5 are 2 October, 19 October, and 7 November 2018, and 9 October 2019 and 13 April 2022, respectively. p values (in bold when significant) were calculated using Satterthwaite approximations, and confidence intervals were calculated using the Wald method.

	Estimate	SE	95% CI	t	p	n
BC ~ 1 + Reproductive status + Radiography date + (1 | Female)						67
Intercept	1.15	0.014	1.12–1.17	80.57	**< 0.001**	
Status (gravid–nongravid)	0.070	0.018	0.035–0.10	3.91	**< 0.001**	
Radiography date 2–1	−0.016	0.020	−0.054–0.023	−0.79	0.44	
Radiography date 3–1	−0.074	0.020	−0.11 to −0.034	−3.66	**< 0.001**	
Radiography date 4–1	−0.092	0.024	−0.14 to −0.045	−3.87	**< 0.001**	
Radiography date 5–1	−0.052	0.044	−0.14–0.035	−1.17	0.25	
BC excluding EM ~ 1 + Radiography date + (1 | Female)						67
Intercept	1.10	0.014	1.073–1.13	79.47	**< 0.001**	
Radiography date 2–1	−0.0067	0.019	−0.045–0.031	−0.36	0.72	
Radiography date 3–1	−0.062	0.019	−0.10 to −0.025	−3.24	**0.002**	
Radiography date 4–1	−0.072	0.020	−0.11 to −0.032	−3.53	**< 0.001**	
Radiography date 5–1	−0.033	0.042	−0.12–0.050	−0.79	0.44	
EL ~ 1 + Clutch # + (1 | Female)						23
Intercept	35.83	0.66	34.53–37.13	53.94	**< 0.001**	
Clutch # (2–1)	−2.28	1.13	−4.50 to −0.059	−2.01	0.086	
EW ~ 1 + Clutch # + SCL + BC + Clutch #:SCL + Clutch #:BC + SCL:BC + Clutch #:SCL:BC + (1 | Female)						23
Intercept	25.40	0.38	24.65–26.15	66.60	**< 0.001**	
Clutch # (2–1)	−0.32	0.54	−1.38–0.74	−0.60	0.58	
SCL	0.23	0.10	0.032–0.43	2.28	**0.040**	
BC	5.46	4.28	−2.93–13.84	1.28	0.23	
Clutch # × SCL	0.41	0.15	0.12–0.69	2.82	0.052	
Clutch # × BC	3.55	6.12	−8.43–15.54	0.58	0.60	
SCL × BC	0.18	0.81	−1.40–1.77	0.23	0.83	
Clutch # × SCL × BC	−1.91	1.01	−3.88–0.062	−1.90	0.14	
EV ~ 1 + Clutch # + SV + (1 | Female)						23
Intercept	11.65	0.33	11.00–12.30	35.14	**< 0.001**	
Clutch # (2–1)	−1.69	0.43	−2.53 to −0.86	−3.97	**0.006**	
SV	0.030	0.019	−0.0080–0.067	1.54	0.15	
EL ~ 1 + PW + (1 | Female)						26
Intercept	36.41	0.56	35.32–37.50	65.59	**< 0.001**	
PW	0.12	0.37	−0.60–0.85	0.33	0.74	
EW ~ 1 + PW + (1 | Female)[%]						26
Intercept	25.26	0.20	24.86–25.66	124.48	**< 0.001**	
PW	0.35	0.14	0.089–0.62	2.62	**0.015**	
EL ~ 1 + Origin + SCL + (1 | Female)						68
Intercept	37.30	0.37	36.58–38.02	100.94	**< 0.001**	
Origin (wild–captive)	0.66	1.40	−2.09–3.40	0.47	0.66	
SCL	0.15	0.095	−0.032–0.34	1.62	0.16	
EW ~ 1 + Origin + SCL + Origin:SCL + (1 | Female)						68
Intercept	25.35	0.50	24.37–26.34	50.46	**< 0.001**	
Origin (wild–captive)	1.05	1.00	−0.92–3.02	1.04	0.32	
SCL	0.26	0.076	0.11–0.41	3.37	**0.002**	
Origin × SCL	−0.35	0.15	−0.65 to −0.049	−2.28	**0.032**	
EV ~ 1 + Origin + SV + (1 | Female)						68
Intercept	13.48	0.18	13.13–13.83	76.15	**< 0.001**	
Origin (wild–captive)	−0.64	0.54	−1.70–0.42	−1.18	0.24	
SV	0.034	0.0092	0.016–0.052	3.74	**< 0.001**	

[%] Residuals not normally distributed (SW test, p = 0.036).

had only 33% of mean rainfall (Fig. 2). Gravid and nongravid female BC differed among radiography dates in autumn and spring 2018, 2019, and 2022, with higher body conditions on 2 and 19 October 2018 compared to 7 November 2018 and 9 October 2019 (Table 1, post hoc tests $p \leq 0.046$). When EM was subtracted from gravid female BM, reproductive status was not retained in the models, but BC differences among radiography dates remained (Table 1, post hoc tests $p \leq 0.045$).

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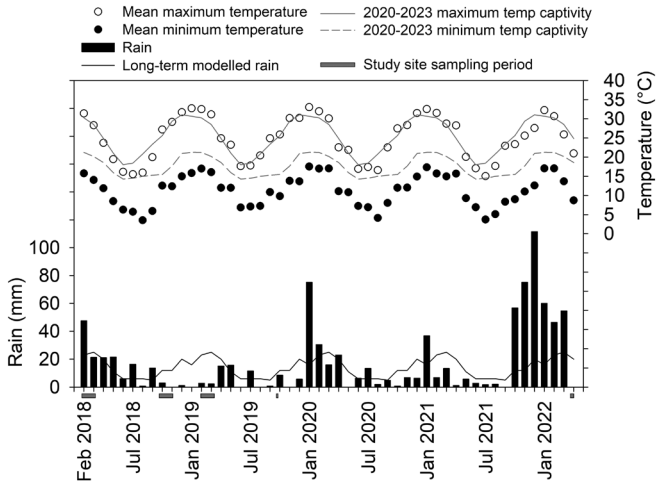


Figure 2. Mean monthly minimum and maximum temperatures, and monthly rainfall, at a Karoo dwarf tortoise (*Chersobius boulengeri*) study site (Southern Hemisphere) between February 2018 and April 2022. Black lines represent modelled long-term monthly rainfall (Meteoblue 2020). Grey lines represent monthly minimum and maximum temperatures, averaged for May 2020–December 2023, for two captive (Northern Hemisphere) female Karoo dwarf tortoises; Northern Hemisphere months were converted to Southern Hemisphere equivalents.

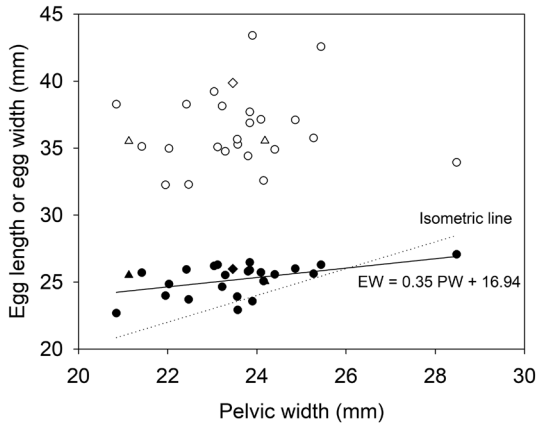


Figure 3. Egg length (open symbols) and egg width (EW, filled symbols) in relation to female pelvic width (PW) for eggs produced by 25 wild female Karoo dwarf tortoises (*Chersobius boulengeri*) in spring 2018 (circles), spring 2019 (triangles), and autumn 2022 (diamond). The solid line represents a significant relationship identified by linear mixed models, and the dotted line isometry between egg width and pelvic width. The relationship between egg length and pelvic width was not significant.

In October–November 2018, EL and EW were similar among successive clutches, but EV was larger in first than in second clutches (Table 1 and 2). Comparison of the significance levels of the EL and EW models ($p = 0.086$ and 0.56, respectively, Table 1) suggests that the decrease in EV was mostly due to EL. There was significant correlation between EW and SCL, and between EV and SV, but BC did not appear to affect egg dimensions (Table 1). Mean (± SD) EV relative to SV was 8.3 ± 0.21%. Egg width, but not EL, strongly correlated with PW (Table 1), and EW exceeded PW in all but three eggs (Fig. 3). Moreover, many of the larger females (i.e. relatively large PW) contained eggs that were wider than PW (Fig. 3).

During fieldwork, I observed sexual interaction, egg-laying, and recent hatchlings. In February–March, males and females were frequently found sharing retreats, whereas all individuals were solitary in October–November and in April. Egg-laying was observed in two females, on 5 and 17 October 2018. Nests were dug at partly shaded locations among shrubs and rocks, and nest depth was 60 mm. In summer (21 February 2018, and 3 and 19 March 2019) and spring (8 October 2019), recent hatchlings were encountered. All hatchlings were in direct proximity of an eggshell, had incompletely closed plastrons, and natal scutes without additional annuli.

Reproduction in captivity

The two females that were transferred to captivity had initial SCL of 104.6 and 108.2 mm, and initial SV of 173.7 and 203.7 cm^3. The females showed little growth during the study, eventually reaching an SCL of 105.2 and 110.6 mm, and an SV of 176.5 and 218.4 cm^3. Mean monthly maximum temperatures in the enclosures were similar to those in the wild, but mean monthly minimum temperatures were higher than in the wild, especially in winter (Fig. 2). Egg production started 13 months after releasing the females in their enclosures. Single-egg clutches were laid in two distinct egg-laying seasons (Fig. 1B); autumn (10 September–11 December) and spring (25 February–1 June). Within egg-laying seasons, each female laid 2–4 eggs separated by 21–49 days. Autumn and spring egg-laying seasons were separated by 101–162 days, except in two instances (29 January 2022 and 5 January 2023) when one female laid an egg in between the autumn and spring egg-laying seasons (Fig. 1B). These two eggs were excluded from analyses of seasonal differences.

Clutch frequencies were similar among years and seasons (Table 3; mean ± SD = 2.5 ± 0.97 clutches per season). Eggs had similar EL, EW, and EV between autumn and spring, but EW and EV depended on SCL and SV, respectively (Table 3). Within autumn and spring, EL and EV were larger in first clutches than in second (EL) and third (EL and EV) clutches, whereas EW was similar among clutches (Table 2 and 3). In contrast to the length of the eggs, EW and EV depended on female SCL and SV, respectively (Table 3). Captive females produced eggs of similar EL, EW, and EV as wild females (Table 2 and 3).

Thirteen of the autumn eggs and nine of the spring eggs hatched. There was no significant effect of season on incubation period (Table 3; mean ± SD = 86.5 ± 5.23 days). Eggs with a larger EV or EM produced hatchlings with a larger SV or BM, respectively (Table 3).

Discussion

The objective of this study was to elucidate the reproductive strategy of Karoo dwarf tortoises, and to provide reproductive

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Table 2. Means (± SD) for egg length (mm), egg width (mm), and egg volume (cm^3) of successive clutches (1–4) in autumn and spring produced by two captive female Karoo dwarf tortoises (*Chersobius boulengeri*) in the Netherlands from 2020 to 2023, and of successive clutches (1–2) produced by 16 female Karoo dwarf tortoises in the wild in spring 2018. Significant differences among successive clutches as identified by linear mixed models are indicated.

	n	Egg length	Egg width	Egg volume
Clutch (captive)				
1	15	39.3 ± 1.13	27.0 ± 0.70	15.0 ± 0.94
2	15	37.3 ± 1.60	27.1 ± 1.21	14.4 ± 1.48
3	8	36.1 ± 2.79	26.6 ± 1.29	13.5 ± 2.02
4	2	35.0 ± 1.97	27.0 ± 1.64	13.4 ± 2.38
		1 > 2 = 3		1 > 3
Clutch (wild)				
1	16	37.0 ± 2.88	25.5 ± 1.10	12.6 ± 1.33
2	7	34.9 ± 1.89	24.7 ± 1.15	11.2 ± 1.39
				1 > 2

data to inform conservation. Combining wild and captive studies was essential to achieve this objective. Captive females unexpectedly produced eggs in autumn, which led to the sampling of wild females in autumn 2022. In addition, information such as incubation periods and relationships between egg and hatchling dimensions could not be gathered in the wild, because virtually no nesting females were encountered.

Mating season

Although identification of a mating season was not a specific aim of this study and mating was never observed in the wild, results suggest that mating at the study site occurred in summer. Male–female couples sharing retreats were frequently encountered in summer, but never in autumn or spring. Several other species, such as radiated tortoises (*Astrochelys radiata*; Leuteritz and Ravolanaivo 2005) and Hermann's tortoises (*Testudo hermanni*; Loy and Cianfrani 2010) mate in summer however, observations of mating in wild chelonians are relatively rare and identifying mating seasons may require innovative approaches (e.g. citizen science; Hughes et al. 2023). Summer mating activity in Karoo dwarf tortoises, in the presence of water, food, and protective plant cover, might help offset some of the energy costs and predation risks associated with mating behaviour (Mueti Ngwava et al. 2024).

Nesting season

Contrary to my expectation, Karoo dwarf tortoises did not produce eggs in the season of the highest mean rainfall and resource availability (i.e. summer), but showed a bimodal nesting season in autumn and spring. Captive females consistently corroborated limited field data of egg production in autumn. The only two eggs that one of the captive females produced in winter were probably due to year-round availability of water and food, and 10°C higher average minimum winter temperatures compared to conditions in the wild. In contrast, the study site had virtually no rainfall and plant growth in winter, while absolute minimum temperatures dropped below zero, providing poor conditions for egg-laying. Bimodal nesting seasons are uncommon in tortoises. Although many taxa have discontinuous egg-laying patterns (Kuchling 1999), these are usually unimodal. In temperate zones, tortoises generally nest from spring to summer (e.g. desert tortoises [Lovich et al. 2015], spur-thighed tortoises [*Testudo graeca*; Díaz-Paniagua et al. 1996], Hermann's tortoises [Bertolero et al. 2007], steppe tortoises [*Testudo horsfieldii*; Lagarde et al. 2002]). In tropical zones, unimodal nesting seasons relate to temperature and rainfall patterns (e.g. red-footed tortoises [*Chelonoidis carbonarius*; Pritchard and Trebbau 1984, summarised by Kuchling 1999], giant tortoises [*Geochelone gigantea*; Bourn 1977], pancake tortoises [*Malacochersus tornieri*; Mueti Ngwava et al. 2024]). Some other taxa have nearly year-round egg-laying periods, with extended nesting seasons of 8–11 months (e.g. angulate tortoises [*Chersina angulata*; Hofmeyr 2004], geometric and tent tortoises [*Psammobates geometricus* and *P. tentorius*, respectively; Leuteritz and Hofmeyr 2007]). In terrapins, bimodal nesting seasons in autumn and spring are more common (e.g. broad-shelled turtles [*Chelodina expansa*; Booth 1998], chicken turtles [*Deirochelys reticulata*; Buhlmann et al. 1995], common musk turtles [*Sternotherus odoratus*; Thiem and Gienger 2022]). However, bimodal nesting seasons in terrapins are primarily the result of oviducal egg-retention. Karoo dwarf tortoises produced multiple single-egg clutches in autumn and spring, ruling out the possibility that egg-production was due to shelled eggs that had been retained from the previous season.

Bimodal nesting by Karoo dwarf tortoises might disperse hatching events throughout the unpredictable rainfall season. If eggs were laid in summer, they would hatch at the end of the rainfall season (based on the captive mean incubation period), when plant growth quickly ceases, accelerated by the onset of frost (Mucina et al. 2006). Eggs laid in spring will probably incubate similar to captive eggs and hatch in the second half of the rainfall season. However, eggs produced in autumn are unlikely to develop during the cold winter months (e.g. cold torpor or facultative diapause; Ewert and Wilson 1996, Rafferty and Reina 2012) and may hatch in the beginning of the next rainfall season. Dispersal of emerging hatchlings throughout the rainfall season will increase the chance that some offspring will encounter favourable environmental conditions. The recently born hatchlings that I observed at the beginning and half way through the rainfall season confirm that hatching of Karoo dwarf tortoise eggs occurs scattered throughout the rainfall season.

The bimodal nesting season of Karoo dwarf tortoises challenges a previous suggestion that small body size and associated physical restrictions on fecundity might contribute to a unimodal nesting season in speckled dwarf tortoises (Hofmeyr et al. 2018a), because Karoo dwarf tortoises have a similar body size (Boycott and Bourquin 2000). Other factors may be more important determinants of nesting season modality. The inferred benefits of bimodal nesting for Karoo dwarf tortoises might not materialise for speckled dwarf tortoises, due to the different (winter) rainfall pattern in the range of the latter species (Esler et al. 2010).

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Table 3. Fixed effect parameter estimates with standard errors, 95% confidence intervals and test statistics for final linear mixed models with dependent variables egg length (EL), egg width (EW), egg volume (EV), clutch frequency, incubation period, hatchling shell volume (SV) and hatchling body mass (BM), fixed effects clutch number (Clutch #), season (autumn and spring), year, and covariates straight carapace length (SCL), SV, EV, and egg mass (EM), for 40 Karoo dwarf tortoise (*Chersobius boulengeri*) eggs produced by two females in captivity in the Netherlands from 2020 to 2023. p values (in bold when significant) were calculated using Satterthwaite approximations, and confidence intervals were calculated using the Wald method.

	Estimate	SE	95% CI	T[&]	p	n
Clutch frequency ~ 1 + Year + Season + (1 | Female)						40
Intercept	0.91	0.16	0.60–1.22	5.70	**< 0.001**	
Year 2021–2020	0.32	0.47	−0.59–1.23	0.69	0.49	
Year 2022–2020	0.32	0.47	−0.59–1.23	0.69	0.49	
Year 2023–2020	0.22	0.47	−0.71–1.15	0.47	0.64	
Season (spring–autumn)	~ 0	0.32	−0.62–0.62	~ 0	1.00	
EL ~ 1 + Clutch # + SCL + Season + Clutch #:SCL + (1 | Female)						40
Intercept	35.86	1.04	33.82–37.90	34.45	**< 0.001**	
Clutch # 2–1	−2.09	0.64	−3.34 to −0.84	−3.28	**0.003**	
Clutch # 3–1	−3.23	0.76	−4.73 to −1.74	−4.24	**< 0.001**	
Clutch # 4–1	−8.54	4.10	−16.58 to −0.51	−2.09	**0.045**	
Season (spring–autumn)	−0.25	0.57	−1.36–0.86	−0.44	0.67	
SCL	0.67	0.49	−0.30–1.64	1.35	0.19	
Clutch # 2-1 × SCL	−0.10	0.26	−0.60–0.40	−0.39	0.70	
Clutch # 3-1 × SCL	0.60	0.34	−0.072–1.27	1.75	0.090	
Clutch # 4-1 × SCL	2.21	1.95	−1.61–6.02	1.13	0.27	
EW ~ 1 + Clutch # + SCL + Season + Season:SCL + (1 | Female)						40
Intercept	26.81	0.56	25.71–27.90	47.83	0.107	
Clutch # 2–1	0.13	0.30	−0.46–0.71	0.43	0.67	
Clutch # 3–1	−0.35	0.36	−1.05–0.35	−0.98	0.33	
Clutch # 4–1	−0.59	0.66	−1.88–0.70	−0.90	0.37	
Season (spring–autumn)	−0.25	0.27	−0.76–0.27	−0.93	0.36	
SCL	0.42	0.14	0.14–0.69	2.97	0.051	
Season × SCL	0.25	0.11	0.032–0.46	2.25	**0.031**	
EV ~ 1 + Clutch # + Season + SV + Clutch #:SV + Season:SV + (1 | Female)						40
Intercept	12.80	1.14	10.56–15.04	11.22	0.087	
Clutch # 2–1	−0.62	0.44	−1.48–0.23	−1.42	0.17	
Clutch # 3–1	−1.52	0.52	−2.55 to −0.49	−2.90	**0.007**	
Clutch # 4–1	−6.78	3.16	−12.96 to −0.59	−2.15	**0.040**	
Season (spring–autumn)	−0.33	0.39	−1.09–0.44	−0.84	0.41	
SV	0.13	0.049	0.035–0.23	2.68	**0.021**	
Clutch # 2-1 × SV	0.011	0.023	−0.035–0.056	0.46	0.65	
Clutch # 3-1 × SV	0.040	0.029	−0.016–0.097	1.41	0.17	
Clutch # 4-1 × SV	0.26	0.17	−0.078–0.60	1.51	0.14	
Season × SV	0.043	0.021	0.0024–0.085	2.07	**0.047**	
Incubation period ~ 1 + Season + (1 | Female)[%]						22
Intercept	86.24	1.10	84.09–88.39	78.53	**< 0.001**	
Season (spring–autumn)	−3.37	2.20	−7.67–0.94	−1.53	0.14	
Hatchling SV ~ 1 + EV + (1 | Female)						23
Intercept	11.04	0.29	10.46–11.61	37.85	**0.021**	
EV	0.75	0.15	0.47–1.03	5.19	**< 0.001**	
Hatchling BM ~ 1 + EM + (1 | Female)						23
Intercept	10.97	0.12	10.74–11.20	94.73	**< 0.001**	
EM	0.80	0.091	0.62–0.98	8.80	**< 0.001**	

[%] Residuals not normally distributed (Shapiro–Wilk test, p = 0.014).
[&] *z* for clutch frequency Poisson generalised linear mixed model.

Clutch size and frequency

This study (n = 66) confirms incidental observations (Haagner 1990, Boycott and Bourquin 2000, Loehr 2017, 2018) of Karoo dwarf tortoises producing exclusively single-egg clutches. Physically, females could probably accommodate multiple eggs, because similar-sized captive speckled dwarf tortoise females rarely produce two-egg clutches (Van Loon 2018), and gravid speckled dwarf tortoise females can contain multiple follicles of pre-ovulatory size (Hofmeyr et al. 2018a). The selective advantages of single-egg clutches might be similar for both species, given the similarities between their arid and unpredictable environments. Single-egg clutches maximise the dispersal of eggs and offspring in time and space (Loehr et al. 2009), which is in agreement with my expectation that Karoo dwarf tortoises would hedge their

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reproductive bets (eggs). Single large eggs may also produce large hatchlings, capable of surviving their harsh environment (Hofmeyr et al. 2018a). Another advantage of single-egg clutches might be the flexibility they offer for females to decide at each egg whether to invest in reproduction (ovulation and oviposition) or in maintenance (follicular atresia; Kuchling 1999, Hofmeyr et al. 2018a). The shallow nests that I found raise the question of whether Karoo dwarf tortoise females would be physically capable of digging nests deep enough to accommodate multiple eggs.

Clutch frequency was invariable among years and seasons for captive females, but so was resource availability. Under these circumstances, Karoo dwarf tortoise females produced a mean of 2.5 clutches in autumn and spring with a maximum of seven eggs per year. Thus, fecundity was higher than for two female speckled dwarf tortoise females kept under similar conditions from 1999 to 2004 (mean ± SD = 3.2 ± 0.94 eggs per year; V. J. T. Loehr, unpubl.). Karoo dwarf tortoises may have evolved for higher fecundity in their slightly higher productive environment compared to the speckled dwarf tortoise range (Esler et al. 2010). In the wild, female Karoo dwarf tortoises were capable of producing multiple clutches in a season, yet my study design was unable to determine how many. Body condition differences among radiography dates suggest that gravid and nongravid females contained stored resources at the beginning of the spring 2018 sampling period, which they used for egg-production towards the end of spring 2018. In spring 2019, during an extensive drought, most females appeared to forego egg-production, because few females were gravid in comparison to the same period in 2018 and females had low body conditions. Egg-production during drought by some females is consistent with reproductive patterns of other tortoise species in arid regions (Loehr et al. 2011, Lovich et al. 2018, Rodríguez-Caro et al. 2021), and is typical for the bet-hedging strategy used by Karoo dwarf tortoise females.

Egg size

Relationships of egg size with female body size and pelvic width indicate that large eggs are important for Karoo dwarf tortoises. Females produced eggs that were very large for their body size (8.3% of shell volume), a trait they share with speckled dwarf tortoises (8.5–8.8% of shell volume; Loehr et al. 2011, Hofmeyr et al. 2018a). Consequently, as in speckled dwarf tortoises, most eggs (including both eggs recorded during drought) were wider than pelvic width, requiring pelvic kinesis during oviposition (Loehr et al. 2011). The importance of large eggs may exert through offspring size, because large eggs produced large hatchlings. Potential survival benefits of a large hatchling size can be unpredictable (Congdon et al. 1999, Paterson et al. 2014). However, hatchling desert tortoise survival was related to hatchling size (in absence of predation; Nafus et al. 2015), and a large hatchling size may provide emerging hatchlings with resources in unpredictable environments (Wallis et al. 1999), optimise locomotory performance (Myers et al. 2007), and reduce predation (Janzen et al. 2000). Thus, the large egg and hatchling sizes in Karoo dwarf tortoises may benefit hatchling survival.

Despite the importance of large eggs for Karoo dwarf tortoises, egg size differed among females of different sizes and among successive clutches. In chelonians, egg size is often positively correlated with female size (Kuchling 1999), in part due to constraints on egg size imposed by pelvic aperture in small females (Congdon and Gibbons 1987, Macip-Ríos et al. 2013). Pelvic kinesis enabled Karoo dwarf tortoise females to overcome morphological constraints to some degree, but the increase of egg width with pelvic width among the largest females showed that pelvic width was a constraint across the female size range. What came as a surprise were up to 11% differing egg volumes in successive clutches in a season, both in the wild and in captivity, because of potential effects on hatchling survival. Tortoises may adjust egg size in response to accumulated resources (i.e. female body condition; Loehr et al. 2011, Averill-Murray et al. 2018). I was unable to detect a relationship between egg size and body condition in Karoo dwarf tortoises, but assume that females traded off offspring size and number within the limitation of available resources. The production of eggs significantly smaller than obtainable within the constraints of female body size emphasises the importance of frequent offspring for Karoo dwarf tortoises. These results also suggest that the ad libitum diet of the captive females may have contained insufficient nutrients (e.g. proteins) to consistently develop maximum egg sizes.

Different egg sizes among successive clutches were due to egg length, whereas egg width was fairly constant. This suggests a benefit of a large egg width, because a reduction of egg width could potentially reduce risks for females associated with the production of eggs wider than pelvic width (e.g. egg breakage during oviposition). Egg width was not a strong determinant of hatchling shell volume (Supporting information). Therefore, the benefit of a large egg width might be its contribution to a somewhat round egg shape, less prone to water loss during incubation due to the relatively small surface to volume ratio.

Conservation implications

During this 4-year investigation, the study population of Karoo dwarf tortoises declined > 22%, most likely due to predation (Loehr 2022). Moreover, the population contained virtually no juveniles to replace depredated adults (Loehr and Keswick 2022). In response to these dynamics, and because the population is one of only two known extant populations that might be viable, conservation measures are being planned (Endangered Wildlife Trust 2024). I found a low mean fecundity of five eggs per female per year, when resources were unlimited. Under natural resource limitations, fecundity will be lower and translate to a slow population recovery. Thus, conservation measures and population monitoring should persist for a long time. Furthermore, the low fecundity of Karoo dwarf tortoises is unlikely to offset current high predation levels (Loehr 2022), as appears to be the case

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in other tortoise taxa affected by high predation levels (desert tortoises [Berry et al. 2013], speckled dwarf tortoises [Loehr 2017], spur-thighed tortoises [Segura et al. 2020]), so reduction of predation should be a conservation priority.

The reproductive strategy of Karoo dwarf tortoise females to disperse large eggs and offspring in time and space, even during drought, and to sacrifice hatchling size to offspring number, might be incompatible with regional climate change projections. Much of the Karoo dwarf tortoise range is projected to aridify (Hannah et al. 2002, CSIR 2019), yet effects on fauna are understudied (Hoffman et al. 2021). Aridification may affect Karoo dwarf tortoises in multiple ways: 1) aridification will result in reduced egg production, because fewer females will accumulate sufficient resources to reproduce, as has also been observed in desert tortoises (Henen 1997) and speckled dwarf tortoises (Loehr et al. 2011), 2) female mortality may increase, because some females will reproduce during drought and be unable to restore body reserves under aridified conditions, as observed in desert tortoises (Lovich et al. 2023), and 3) hatchlings, particularly smaller individuals from later clutches in a season, may be unable to survive drier conditions, similar to desert tortoise hatchlings (Wallis et al. 1999) and speckled dwarf tortoise hatchlings (Loehr et al. 2011). Predictive modelling studies on spur-thighed tortoises have shown that combined effects of decreased reproduction and survival due to increased drought may extirpate populations (Rodríguez-Caro et al. 2021).

Expected survival threats for Karoo dwarf tortoises related to their reproduction add to known threats caused by habitat degradation and predation (Hofmeyr et al. 2018b). I recommend that conservation plans consider regional climate change projections and prioritise measures, including surveys and monitoring, in areas in the Karoo dwarf tortoise range that may be least affected by aridification.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.stqjq2ccd (Loehr 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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