Population ecology of Psammobates oculifer in a semi-arid environment

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Abstract

We studied the ecology of *Psammobates oculifer* over 13 months near Kimberley, South Africa, to ascertain if the population's life history traits conform to chelonian patterns in arid environments. Capture rates were highest in spring and lowest in winter when environmental conditions were respectively most and least favourable for tortoise activity. Body condition did not change from autumn to spring, but reached lower values during the summer drought. Capture effort averaged 5 hours/tortoise, which corresponds closely to that of species with low population densities in arid regions. Population size structure was skewed towards adults, indicative of low recruitment and/or low juvenile survivorship. Females were larger and heavier than males, confirming sexual dimorphism in this species. Body size of cohorts scaled to annuli counts, indicating a close correspondence between body size and age. Telemetered adults deposited one or no growth ring in the year of study; consequently, annuli counts could underestimate adult age. Regression analyses showed that male and female growth rates did not differ, but males matured at a smaller size and younger age than females. The smallest male showing reproductive behaviour had 12 annuli and a shell volume of 157 cm^3, while similar measures for females were 14 annuli and 185 cm^3. The sex ratio of the population did not differ from 1:1 but the bias towards males in spring, and towards females in autumn, indicates that studies limited to particular seasons can misrepresent life history traits of populations. We concluded that the life history of *P. oculifer* conforms to chelonian patterns in arid regions.

Introduction

The evolution of life history traits is determined by the organism's environment while it is constrained by trade-offs and phylogeny (Stearns 1992). Life history characteristics generally fall on a fast-slow continuum, reflecting adaptations to environmental predictability or to mortality rates (Stearns 1983; see Reznick *et al.* 2002 and references therein). Chelonian life histories fall at the slow end of the continuum; they display slow growth, delayed sexual maturity, iteroparity and low hatchling/juvenile survivorship (Wilbur & Morin 1988; Shine & Iverson 1995). These traits seem to be related to the protective value of the chelonian shell, which influences size-related mortality because the shell strengthens with growth (Kuchling 1999). Nevertheless, environmental factors affect many aspects of chelonian physiology, behaviour and ecology, and ultimately influence the life history traits of species (Stearns 2000; Tuljapurkar *et al.* 2009 and references therein).

Environmental conditions vary on a temporal and spatial scale. Seasonal changes in temperature and rainfall can influence body condition (Nagy & Medica 1986; Henen 1997; Loehr *et al.* 2007a) and hence fitness parameters such as reproductive output (Hofmeyr *et al.* 2005; Loehr *et al.* 2007a) and survival (Shine *et al.* 2001). Geographic variation in environmental productivity can influence population density, with lower densities in arid than mesic regions (see Branch 1984; Mason *et al.* 2000). Resource availability influences growth rates in chelonians but the outcome is not always the same in different species. In *Gopherus polyphemus*, individuals in regions with poor forage quality grow slower and reach sexual maturity later than they do in more productive regions (Aresco & Guyer 1999). In contrast, *Gopherus agassizii* females, but not males, grow faster and reproduce earlier where resources are limited, which likely compensates for low juvenile survivorship in harsh environments (Curtin *et al.* 2009). Differential growth rates and early maturity in one sex may have wider implications on the population's demography. It leads to sexual size dimorphism (Gibbons & Lovich 1990; Lefebvre *et al.* 2011) and the smaller body size may influence mortality, which in turn can skew the sex ratio of a population (Hellgren *et al.* 2000). Data on species' demography are integral to conservation assessments and hence management strategies, particularly in view of climate change (Heppell 1998; Scott *et al.* 2012). Chelonians have a high extinction risk (Rhodin *et al.* 2011), and climate change will aggravate declines, leading to a reduction in species richness (Ihlow *et al.* 2012). Southern Africa has the most diverse tortoise fauna in the world (Branch *et al.* 1995), and predictions of significant increases in temperature and evapotranspiration over the region (Davis 2011) necessitate conservation assessments of all tortoise species. Yet little information exists on the demography of the region's tortoises. Here we present demographic data of the Kalahari tent tortoise, *Psammobates oculifer*.

Psammobates oculifer inhabits arid savannah and scrub desert in South Africa, Botswana and Namibia (Branch 2008). Annual precipitation over the species' range varies from below 250 mm to approximately 750 mm, with a coefficient of variation between 25% and 40% (Schulze 1997). Although little is known about the species' biology, it has been reported that the species is active during summer and remains relatively dormant during the dry winter months (Boycott & Bourquin 2000; Branch 2008). Furthermore, it is known that females are larger than males and that they lay single-egg clutches in late summer (Boycott & Bourquin 2000). We studied the ecology of a population at the southernmost limit of the species' distribution over 13 months, to assess if life history traits of *P. oculifer* conform to chelonian patterns in arid environments. Based on climatic conditions in the species' habitat, the population's peripheral position in the species' distribution range, and apparent low reproductive potential of females, we predicted that population size and age structure will be indicative of low recruitment, and that population density will be low. Furthermore, we expected differences in growth rates and/or age at maturity of males and females due to their known sexual dimorphism, and that body condition will reflect environmental seasonality.

Materials and methods
We studied population characteristics of *P. oculifer* at Benfontein farm (28853' S; 24851' E), near Kimberley, South Africa, over 13 months, from March 2006 to April 2007. There were 12 field excursions with 182 field days covering five seasons: autumn 2006 (44 days),

winter (23 days), spring (35 days), summer (47 days) and autumn 2007 (33 days). The study area of approximately 2 700 ha was divided into sites E (east) and W (west); site E was typical savannah, consisting of grasses, interspersed thinly with trees, whereas vegetation at site W was more karoid, with a mixture of small shrubs and grasses.

During the first 23 days of autumn 2006, we used structured searches, involving one to five people, to search sites E and W on foot or by driving farm tracks for free- ranging *P. oculifer*. We took measurements of all tortoises encountered and attached radio-transmitters to a subset of 12 males and 13 females, equally distributed between sites, to record their movement patterns over the remaining study period. From mid-April 2006, we no longer used structured searches and the search effort for the population ecology study coincided with the time spent in the field locating telemetered tortoises (usually one person), both on foot and in a vehicle. Our search effort (hours per day) was relatively consistent within seasons, as we typically tracked telemetered tortoises from early morning, before they became active, until late afternoon, after activity finished.

Upon capture, we immediately weighed animals with a digital balance (9 0.1 g; Ohaus CT6000 portable balance, New Jersey, USA) before urination or defecation could occur. We also weighed (with the exception of winter) each telemetered tortoise on the first and last day of each field excursion. Regular weighing allowed a consistent evaluation of seasonal changes in body condition of telemetered tortoises. We measured straight carapace length (SCL, mm), shell width at the middle (SWM, at the sixth marginal scute; mm) and shell height (SHM, at the apex of the highest dorsal scute; mm) for each tortoise with vernier callipers (9 0.01 mm; Kanon, Tokyo) to calculate shell volume (SV, cm^3) using a modified formula for an ellipsoid: SV =p * SCL * SHM * SW/6000 (Loehr *et al.* 2004; Hofmeyr *et al.* 2005; Loehr *et al.* 2007a). Body mass and SV were used to calculate body condition as a ratio of mass to shell volume (Loehr *et al.* 2004) and as mass scaled to shell volume (Loehr *et al.* 2007a). Because scute ring counts often provide a reliable estimate of age in chelonians (Germano 1994; Germano & Bury 1998; Hellgren *et al.* 2000), we used a hand lens to count scute rings (annuli) on the dorsal and ventral sides of all individuals. We also took digital photographs of dorsal and ventral surfaces, which helped to verify annuli counts made in the field. We classified each tortoise as male, female or juvenile; males were distinguished from females by their flatter shell, longer tail and large, incurved supracaudal scute (Branch 1988; Boycott & Bourquin 2000) whereas small individuals with no sexual dimorphic characteristics were classified as juveniles. Prior to releasing a tortoise, we notched specific marginal scutes of the tortoise (Honegger 1979) for future identification.

We collected rainfall data, using an electronic rain gauge erected in the study area, from 17 April 2006. We obtained rainfall data prior to 17 April 2006 and hourly temperatures throughout the study from the South African Weather Service's (SAWS) weather station approximately 5 km from the study area. Long-term annual

rainfall at Kimberley airport (SAWS) averaged 4159135 mm over 46 years (1960-2005), with a 32% coefficient of variation. Rainfall for April 2006 to March 2007 was lower than the long-term average, at 323 mm and 301 mm at Kimberley airport and the study site, respectively. The difference from the long-term average was due to exceptionally low rainfall in summer (December, January and February). Rains commenced in March, and April 2007 rainfall was higher than the long-term average. Mean maximum temperatures (SAWS) ranged from 19.18C in May 2006 to 34.58C in February 2007, while mean minima temperatures ranged from 0.98C in June 2006 to 18.58C in February 2007. Temperature extremes recorded at the study site were -48C and 408C in the shade.

Data and statistical analyses

To calculate the search time locating non-telemetered tortoises, we took the number of hours spent searching and multiplied it by the number of people involved in each search. We determined search hours per day as the difference between the time of arrival in the field and locating the last tortoise each day. Because our sampling method was not suitable to calculate density per unit area, or probability of capture, we evaluated hours per unit capture (HPUC; similar to capture per unit effort) as a surrogate measure (see Freilich *et al.* 2000; Rodda 2012). This was done within each of the 12 field excursions, thus if no tortoise was located at the end of a field excursion, that time was not 'carried forward' to the next field excursion. The amount of time that passed between arriving in the field and the capture of the first tortoise was the HPUC for that tortoise. Time then accumulated until the capture of the next tortoise, and we repeated this process across days until the end of a field excursion. We calculated HPUC per season and did so for males, females and juveniles separately as well as for cohorts combined. No tortoises were found opportunistically from 17 May to 20 August 2006 (34 days in the field), thus although time was recorded, it was not included in HPUC analyses. We did not analyse HPUC between sites, as it was not feasible to filter out actual time spent per site.

To test that the sex ratio did not differ from 1:1 and for the effect of season on sex ratios, we used goodness of fit tests (x^2). We used contingency table analyses (x^2) to evaluate the effect of site on sex ratios and the differences in frequencies among size and annuli categories, with a Yates correction for continuity where the degrees of freedom equalled one. For analyses of SCL categories, the lowest category chosen was less than 70 mm and the highest more than 120 mm, with categories increasing in 10 mm increments between the two. Similarly, mass and volume increments started at B150 g or cm^3 and increased in 50 g or cm^3 increments up to >400 g or cm^3. In each case, categories were chosen to give a relatively even spread of the data. In all instances where contingency table analyses were used, mean expected frequencies (n/ rc, where n =total count, r =the total for each row and c =the total for each column) were more than or equal to six (Zar 2001).

After testing if data were parametric, before or after transformation ($\log_{10}$), we used multifactor ANOVAs (F or H statistic), followed by Student-Newman-Keuls (SNK) or Dunn's post hoc tests, to compare HPUC among cohorts and seasons, and growth increments among cohorts. We used simple regressions (r^2) to evaluate the dependency of SCL and SV on the number of scute annuli. If data were parametric and regressions significant (before or after $\log_{10}$ transformation), we used analysis of covariance (ANCOVA) to compare regression slopes and elevations of (a) SV (cm^3) and (b) SCL (mm) on annuli counts among cohorts, and (c) regression slopes and elevations of body mass (BM, g) on SV among seasons and between sexes.

Regressions of BM on SV provide the best surrogate measure of body condition (BC) in chelonians (Hofmeyr *et al.* 2005; Loehr *et al.* 2007a). We used the mean BM per season for the relevant individual when doing seasonal analyses because we measured tortoises' BM more than once per season for radio-tracked and recaptured animals. Seven radio-tracked tortoises died during the course of the study (see Keswick 2012) from unknown causes. Hence, before calculating seasonal mean BM for these seven tortoises, we first plotted the body condition indices (BCI; BM/SV) of all tortoises against time. After scrutinising the plots, we identified the point at which the BCI for each of the seven tortoises deviated from the general pattern and then excluded this BM and all subsequent BMs from the calculation of that tortoise's mean seasonal BM.

In all analyses, whenever we used multiple tests, we adjusted alpha with a sequential Bonferroni procedure (Holm 1979). Statistical analyses were performed using SigmaStat 2.03 and PASW 18 (SPSS Inc., Chicago, USA), and in the case of ANCOVA, both PASW 18 and Microsoft Excel. For simplicity and ease of comparison, we reported means (9 standard deviations), even when using non-parametric tests, except for growth increments.

Results
Population composition and capture effort
The 188 *P. oculifer* captured at Benfontein included fewer juveniles than adults (goodness of fit test, $x^2_1 = 124:5$, $P<0.0001$, Table 1). The male to female ratio was 1.00:0.90, not significantly different from a 1:1 sex ratio (goodness of fit test, $P= 0.54$). The proportional representation of cohorts did not differ between sites (contingency table analysis, $P=0.29$), but more tortoises were captured in site W than in site E (goodness of fit test, v^2 ¼ 9:8, $P=0.0017$, Table 1).

Seasonal comparisons included recaptured tortoises, and the number of tortoises caught differed among seasons (goodness of fit test, $x^2_4 > 133:0$, $P<0.0001$). Proportionately more tortoises were captured in spring than in any other season and catches in autumn 2006 were higher than they were in autumn 2007 (goodness of fit test, $x^2_1 \geq 5:96$, $P<0.015$), but summer catches did not differ from autumn 2006 and 2007 ($P >0.10$). We caught no tortoises in winter (Fig. 1A). Captures of juveniles did not differ among seasons, but female captures were higher in spring than in summer and autumn 2007 (goodness of fit tests, $x^2_1 = 8:48$, $P=0.004$).

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Table 1. Seasonal summary for number of field days, person-hours (hours per day multiplied by the number of searchers), and the number of *Psammobates oculifer* captured at Benfontein. Total captures for females, males, juveniles and all cohorts combined are indicated as the numbers captured + recaptures = total. Tortoise captures include the first capture of telemetered tortoises (13 females and 12 males in autumn 2006 and 2 females in summer).

Season	Days	Hours	Females	Males	Juveniles	All
Autumn-06	44	386.6	31 + 0 = 31	14 + 0 = 14	3 + 0 = 3	48 + 0 = 48
Winter	23	174.7	0 + 0 = 0	0 + 0 = 0	0 + 0 = 0	0 + 0 = 0
Spring	35	324.8	29 + 8 = 37	50 + 8 = 58	8 + 0 = 8	87 + 16 = 103
Summer	47	321.0	9 + 6 = 15	20 + 2 = 22	2 + 1 = 3	31 + 9 = 40
Autumn-07	33	255.7	12 + 3 = 15	6 + 0 = 6	4 + 1 = 5	22 + 4 = 26
Total	182	1462.6	81 + 17 = 98	90 + 10 = 100	17 + 2 = 19	188 + 29 = 217

Similarly, male captures peaked in spring and were higher in summer than in autumn 2007 ($x^2_1 \geq 8:04$, $P < 0.005$, Fig. 1A). Season also influenced the cohort composition of tortoises captured (contingency table analysis, $x^2_6 = 20.2$, $P = 0.0026$). The proportion of juveniles relative to either gender did not differ among seasons (Fisher's exact test $P > 0.065$; Fig. 1A) but male to female ratios for spring and autumn 2006 differed ($x^2_1 = 0.98$, $P = 0.0018$). More males than females were captured in spring, whereas more females than males were captured in autumn 2006. Although male to female ratios did not differ among remaining seasons, the difference in sex ratio between spring and autumn 2007 approached significance ($P = 0.014 >$ adjusted a = 0.010; Fig. 1A).

Including the first capture of tortoises for a telemetry study and all opportunistic captures (including recaptures), 98 females, 100 males and 19 juveniles ($n = 217$) were captured during the study (Table 1). We recaptured one female three times, four females and one male twice, and 189 tortoises (98 males and 91 females) once. Days and person-hours spent in the field were 182 and 1 463, respectively (Table 1). Hours per unit capture (HPUC) were 10.189 11.08 for females, 10.699 15.83 for males, 34.949 34.56 for juveniles and 5.139 6.55 for all cohorts combined. There was a significant difference in HPUC among cohorts (two-way ANOVA, data $\log_{10}$ transformed, $F_{2,205} = 7.63$, $P = 0.0005$) with juveniles being harder to catch than either adult, but no difference between males and females. The HPUC also varied among seasons (winter excluded; data $\log_{10}$ transformed, $F_{3,205} = 6.20$, $P = 0.0006$) with an interaction between cohort and season ($F_{6,205} = 2.94$, $P = 0.009$). We found it easier to locate tortoises in spring than in the other seasons (Fig. 1B). This was due to males being easier to find in spring because season did not affect HPUC of females and juveniles (Fig. 1B). In spring, we found males easier to capture than females, and juveniles were the hardest to locate. In autumn 2007, HPUC was higher for juveniles than females, whereas HPUC did not differ among cohorts in autumn 2006 or in summer (Fig. 1B).
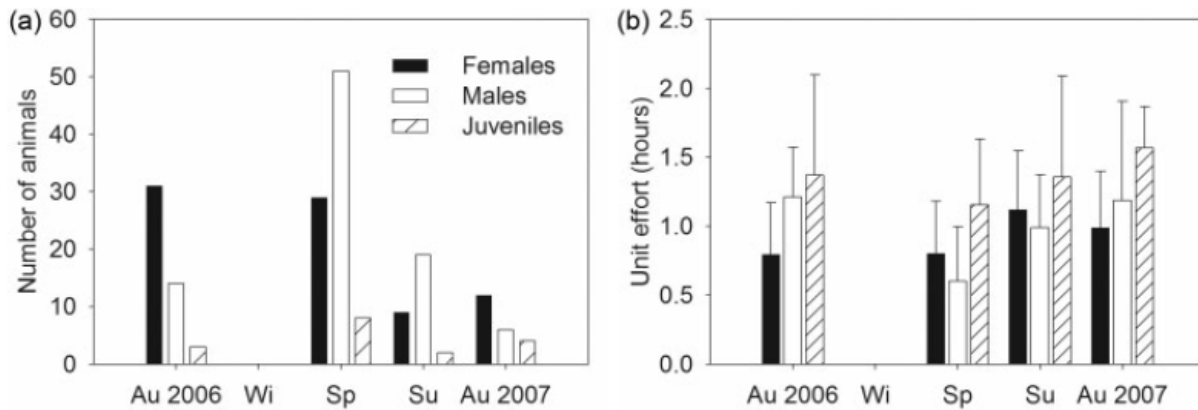
Figure 1. (A) Number of *Psammobates oculifer* captured per season at Benfontein, including first capture of telemetered tortoises and recaptured individuals; (B) Seasonal changes in hours per unit capture ($\log_{10}$ hours, $\pm$SD) for *P. oculifer* cohorts. No tortoises were caught during winter. Hours per unit capture was based on the cumulative number of hours between a capture of each cohort.

Body size, growth ring distributions and size at maturity

Psammobates oculifer females were larger and heavier than males, and juveniles had the lowest SCL, SV and body mass (one-way ANOVAs, $F \geq 189$, df1 $=2$, df2 ≥ 168, $P\text{B}0.00001$). Frequency distributions of SCL size categories showed that large juveniles and small males overlapped in the 80 to 89 mm range (Fig. 2A). This range may represent the transition to maturity for males, because the smallest male found in courtship behaviour (12 males and 10 females; see Keswick 2012) had an SCL of 87.4 mm (SV $=157.4$ cm^3; annuli $=12$). Female and juvenile SCL did not overlap but a few females overlapped with males in the 90 to 99 mm range (Fig. 2A). The smallest female found in a refuge with a male during mating time was 92.9 mm (SV $=184.9$ cm^3; annuli $=14$) whereas the smallest of five gravid females encoun- tered was 109.5 mm (SV $=329.1$ cm^3; annuli $=19$). The frequency distributions for body mass and shell volume were similar. All juveniles had a shell volume of less than 150 cm^3 and most weighed less than 150 g (Fig. 2B). Males' mass (and shell volume) were predominately between 150 and 249 g or cm^3 whereas female shell volume and mass were more evenly spread over size categories between 250 and 399 g or cm^3 (Fig. 2B).

Annuli counts differed significantly among cohorts (one-way ANOVA, $F_{2,149} = 61.7$, $P <0.00001$) and were lowest in juveniles (9.2±2.6, range 2-13), intermediate in males (15.0±3.1, range 10-24) and highest in females (17.7±2.8, range 12-23; Fig. 3). The frequency distributions for annuli differed among cohorts (contingency table analysis, $x^2_{12} = 134.6$, $P <0.0001$) with juveniles dominating the lower annuli counts and females the higher annuli counts. Sex ratios were biased in favour of males in adults with fewer than 16 annuli (goodness of fit test, $x^2_1 = 13.28$, $P = 0.0003$) but the bias switched to females in adults with more than 16 annuli (goodness of fit test, $x^2_1 = 18.02$, $P <0.0001$; Fig. 3).

Regressions of both SCL and SV on annuli counts (all parameters $\log_{10}$ transformed) were significant for males ($F_{1,61} > 29.36$, P B0.0001, $r^2 > 0.32$), females ($F_{1,70} > 23.75$, $P < 0.0001$, $r^2 > 0.25$) and juveniles ($F_{1,15} > 36.55$, P B0.0001, $r^2 > 0.70$; Fig. 4). For SCL on annuli counts, juveniles had a steeper slope than adults had ($F_{2,146} = 6.28$, $P = 0.0024$; Fig. 4A). Regression slopes for adults did not differ but the elevation for females was higher than that of males ($F_{1,132} = 69.8$, $P < 0.0001$; Fig. 4A).
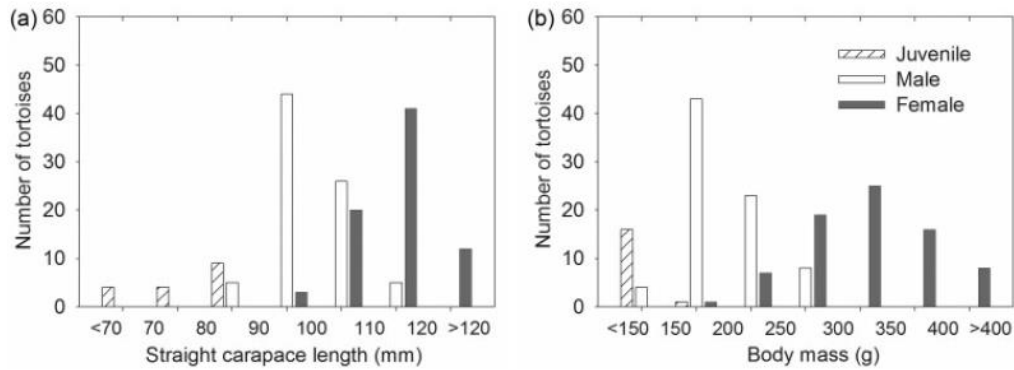

Figure 2. Size distributions of juvenile, male and female *Psammobates oculifer* at Benfontein by (A) straight carapace length and (B) body mass.
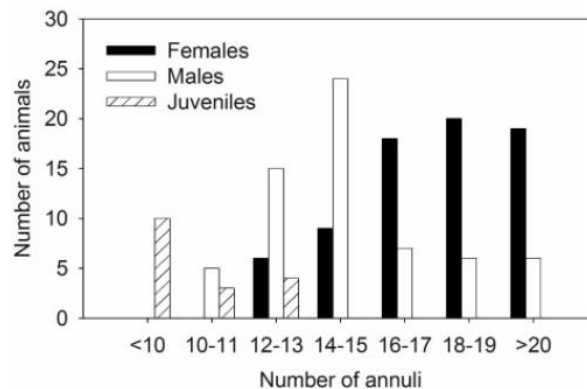

Figure 3. Frequencies for the number of annuli counted for male, female and juvenile *Psammobates oculifer* at Benfontein.

Similarly, when SV was used as the dependent variable, the slope for juveniles was steeper than the slopes of the adults ($F_{2,146} = 6.62$, $P < 0.0018$), and females had a higher elevation than males had ($F_{1,132} = 200.0$, $P < 0.0001$; Fig. 4B).

The regression for juveniles was $\log_{10}$ SCL $= 0.3892$ $\log_{10}$ annuli$+1.4975$, relating to a change in growth increments from 9.74 mm/annulus (between growth rings one and two) to 2.62 mm/annulus (between growth rings 12 and 13; the upper limit recorded for juveniles; Fig. 4A). The median growth increment between annuli 1 and 13 was 3.74 mm (25-75%: 3.00-5.30 mm) for juveniles.
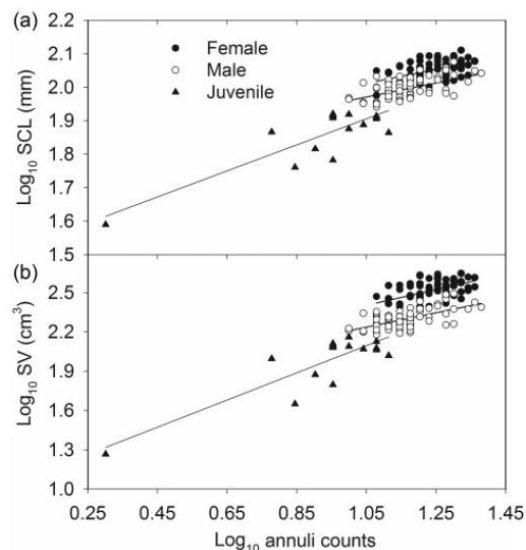
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Figure 4. Linear regressions of (A) straight carapace length (SCL) and (B) shell volume (SV) on the number of annuli for female, male and juvenile *Psammobates oculifer* at Benfontein.

The lowest number of annuli recorded for males and females, respectively, was 12 and 14, with the highest number being 24. The median for SCL growth increments of females was 1.32 mm (25-75%: 1.17-1.53 mm; range: 1.76-1.07 mm between annuli 12 and 24) whereas for males it was 1.27 mm (25-75%: 1.09-1.52 mm; range: 1.85-0.98 mm between annuli 10 and 24) per annulus. SCL growth increments per annulus were higher for juveniles than adults, with no difference between sexes ($H_2 = 24.15$, P B0.0001). When SV was considered, the regression for juveniles was $\log_{10}$ SV $= 1.0381 \log_{10}$ annuli+1.0057, corresponding to a median increment of 11.33 cm^3 (25-75%: 11.08-11.48 cm^3; range: 10.67-11.58 cm^3 between annuli 1 and 13) per annulus formed (Fig. 4B). Corresponding SV increases per annulus formed were 11.28 cm^3 (25-75%: 10.61-12.13 cm^3; range: 13.04-10.15 cm^3 between annuli 12 and 24) for females and 7.01 cm^3 (25-75%: 6.44-7.77 cm^3; range: 8.70-6.05 cm^3 between annuli 10 and 24) for males. With regard to SV, the growth increments of females and juveniles did not differ, but exceeded those of males ($H_2 = 25.85$, P B0.0001).

At the end of the study, we recounted the number of growth rings of 10 males and 6 females that we had used for a telemetry study. At least one year had passed since the first capture of each tortoise. We counted one additional annulus for five of the 10 males, two additional annuli on one male, whereas no new growth rings formed on the remaining four males. Three of the females had one extra growth ring but no additional annuli developed on the other three females.

Seasonal changes in body condition (BC)
The regression slopes of BM on SV between sites, sexes and among seasons did not differ (data $\log_{10}$ transformed, three factor ANCOVA, $P = 0.538$) but regression elevations differed for all three factors ($F \geq 6.81$, df 1 $\geq$1, df 2 $=248$, $P < 0.003$); there was no interaction among factors ($P > 0.079$). Female BC was higher than that of males, and the tortoises in site E had a higher BC than

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tortoises in site W. Among seasons, regression elevations of BM on SV (BC) were lowest in summer but did not differ among other seasons.

Discussion
Life history traits
The population of *P. oculifer* at Benfontein was skewed towards adults, which is similar to that recorded for many other testudinid populations (for example see Van Heezik *et al.* 1994; Hellgren *et al.* 2000; Lagarde *et al.* 2001). A high predation rate of juveniles and a low probability of finding them were both considered plausible reasons for low juvenile catches of *Stigmochelys pardalis* and *Chersina angulata* in the Eastern Cape (Mason *et al.* 2000). Mathematical modelling showed that survival rates in juvenile reptiles are often higher than surmised, promoting detection difficulties over predation as an explanation for low catch rates (Pike *et al.* 2008). Nevertheless, high predation rates of small size classes can be real, as was indicated for *Gopherus polyphemus* where all hatchlings (n =85) fitted with radio-transmitters were predated within 335 days of hatching (Pike & Seigel 2006).

Potential predators of tortoises such as the jackal (*Canis mesomelas*), yellow mongoose (*Cynictis penicillata*), secretary bird (*Sagittarius serpentarius*) and a variety of snakes were all present at Benfontein, and the presence of tortoise scutes in jackal scats at Benfontein (Klare *et al.* 2010) indicates that predation occurs. We do not have data to confirm that predation rates differed among size classes, but similar to other chelonians, mortality is probably higher in juvenile than in adult *P. oculifer* because the protective value of the shell increases with age (Wilbur & Morin 1988; Kuchling 1999). Other contributing factors to the skewed population size structure at Benfontein probably included detection difficulties in finding small-sized individuals, as well as an apparent low reproductive potential. Female *P. oculifer* produces only one egg per clutch over a restricted reproductive season (Boycott & Bourquin 2000), but multiple opportunities to reproduce over a long lifespan should counter the threat of extinction. Despite a low presence of small size classes in the population, it is clear that recruitment occurred, although it is low, as predicted.

As well as looking at size distributions, we attempted to gain insight into the age of the population by counting scute growth rings, or annuli. There was evidence from recaptured individuals that *P. oculifer* added one annulus per year but that some individuals failed to deposit an annual growth ring. The latter may be due to the extended summer drought, as has been reported for species such as *Pseudemydura umbrina* (Burbidge 1981) and *Gopherus agassizii* (Germano & Fritts 1994). Generally, counting annuli becomes more difficult after the onset of sexual maturity, as growth rings become compacted (Germano 1992; this study). Furthermore, the carapace, and to a lesser degree the plastron, often became worn in older *P. oculifer*, which made it difficult to count annuli. A possible reason for a worn carapace is sand abrasion over time, which may be worse in older individuals. In a few individuals (fewer than 10 animals), the scute boss appeared to have been shed, a phenomenon that also should be considered when evaluating age-size relationships in *P. oculifer* (see Zug 1991). The strong correlation between body size and annuli counts of juvenile *P. oculifer* indicates that annuli counts represent the age of juveniles. Adult

tortoises, however, may be older than their annuli suggest, particularly since the high coefficient of variation for rainfall indicates that drought may occur relatively often in this area.

Although it was not possible to ascertain longevity for *P. oculifer*, body size regressed on annuli counts showed that juveniles grew quicker than adults did. The shell of chelonians hardens and thickens with age to provide better protection against predation (Wilbur & Morin 1988; Kuchling 1999). Consequently, a fast growth rate in juveniles should lower predation rates quickly. The difference between the lower limit of annuli counts for males and females suggests that *P. oculifer* females matured later than males did, whereas higher regression elevations of females compared to males indicate that females matured at a larger size than their male counterparts did. Thus, our prediction for differential maturing of the sexes was confirmed. Sexual size dimorphism in *P. oculifer* was thus attained through differences in the age and size at maturity and not through differential growth rates. Nevertheless, because females mature at a larger size, their growth increment per annulus was larger than that of males, particularly when considering a three-dimensional estimate of body size (SV). Size at maturity relative to maximum body size (73% for males and 76% for females) corresponded closely to the value for reptiles (ca. 70%; Shine & Iverson 1995). Early maturity in males may be advantageous in that they start reproducing sooner and can leave offspring before death may occur (reviewed in Stearns 1992). Late maturity in females may be linked to selection for fecundity through larger body sizes, as in females of the arid zone tortoise *Testudo horsfieldi* (Lagarde *et al.* 2001).

Apart from maturing later than males, *P. oculifer* females mature at a later age (ca. 14 years) than would be expected for a chelonian of its size (mean mass of 319 g), which should be at 7.8 years according to an equation derived from 35 chelonian species (Iverson 1992). Similar results were obtained for another small-bodied tortoise (*Homopus signatus*) from South Africa that matures at 11-12 years instead of the projected 5.5 years (Loehr *et al.* 2007b). These authors ascribed the protracted growth period of *H. signatus* to limited resource availability in the Succulent Karoo habitat of the species. The five-year study of Loehr *et al.* (2007b) indicated that *H. signatus* experiences negative growth rates in drought years, but growth rates of *P. oculifer* and *H. signatus* are nevertheless quite similar (2.62-9.74 mm/annulus for juvenile and 0.98-1.85 for adult *P. oculifer* versus 2.5-9.5 mm/year for juvenile and -0.4-2.3 mm/year for adult *H. signatus*). These growth rates tend to be lower than growth rates described for some other chelonians: 0-5.1 mm/year for adult *Cuora flavomarginata* (Chen & Lue 2002) and 7.03-7.49 mm/year for *G. agassizii* up to 23-25 years old (Medica *et al.* 2012).

The sex ratio for *P. oculifer* did not differ from 1:1, similar to other South African testudinids (Branch 1984; Van Heezik *et al.* 1994; Loehr 2002; McMaster & Downs 2006). Nevertheless, tortoises with fewer annuli were predominately males, but this switched to a female bias in older tortoises. Early sexual maturation in males explains why males dominated the younger adult age classes. The dearth of males in older cohorts may indicate that the smaller body size of males makes them more predation prone. In a population of *Gopherus berlandieri*, Hellgren *et al.* (2000) found that females, which mature earlier and are smaller than males, predominate in younger cohorts with the bias switching to males in older generations. The authors gave differential predation rates as one of the possible causes of fewer females in older generations.

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Effect of the environment on population characteristics Environmental differences between sites E and W had no effect on life history traits such as sex ratios and cohort structures of *P. oculifer*. However, tortoise captures in site W exceeded those in site E. Possible reasons for this are higher tortoise densities in site W and/or that tortoises were easier to capture in site W. To have higher tortoise densities in site W seems unlikely given that site E was more similar to the species' typical savannah habitat where grasses dominate (Boycott & Bourquin 2000). Additionally, the higher body condition of tortoises in site E indicates that this habitat was generally more suitable. The more plausible suggestion for high capture rates in site W is that tortoises were easier to locate because vegetation cover was sparser than it was in site E (Keswick 2012). We did not separate search effort between sites, which may also affect capture rates.

Differences in body condition between sites probably relate to vegetation differences that affected food and refuge availability, as well as the thermal profiles of sites (see Keswick 2012). The lower body condition of males compared to females is difficult to explain, particularly since it was not limited to a specific season. Despite using denser refuges than females did, the smaller males still had a higher mean body temperature than females (Keswick 2012). Thus low body condition in males could be associated with the effects of a high body temperature on metabolic rate and/or water loss (Loehr *et al.* 2007a and references therein). Alternatively, the formula used to calculate SV might have overestimated male body size, which would have resulted in an apparent lower body condition for males relative to females.

Season affected tortoise body condition, as predicted, and was lowest in summer. Poor summer body condition may have been due to the delay in summer rainfall. December, January and February are the hottest months at Benfontein, and rainfall usually peaks in mid- to late summer (46 year mean to 2006: 63, 67 and 70 mm for January to March respectively), which would mitigate body condition as food availability would increase after rain, and tortoises can rehydrate. Although March 2007 rainfall was close to the long-term mean (64 mm at the study site), January (26.8 mm) and February (6.2 mm) were much drier than usual, and it is likely that this negatively affected tortoise body condition at Benfontein in summer 2007. Low seasonal rainfall is a probable cause of poor body condition in other arid zone testudinids (Nagy & Medica 1986; Henen 1997; Loehr *et al.* 2007a) due to depleted energy and protein reserves (Loehr *et al.* 2007a) or dehydration (Henen 1997).

Although the overall sex ratio was 1:1, catches of tortoises at Benfontein differed seasonally; more males than females were captured in spring, whereas more females than males were captured in autumn. These differential capture rates obviously influenced seasonal sex ratios. The difficulty of locating inactive animals meant that tortoise captures relied upon bouts of seasonal activity. Males were most active in spring and early summer, probably related to males' mate searching, and females were most active in autumn (see Keswick 2012 and references therein). These results show the pitfalls of estimating population life history traits, such as sex ratios, from

data obtained over a short period, or from long-term studies where data collection is limited to a particular season.

Sampling design did not allow us to estimate population size or density, but HPUC was used as a surrogate measure of density. The HPUC in this study (5.13 hours/tortoise) was slightly higher than the mean recorded in a six-year study of *G. agassizii* (4.03 hours/tortoise on average; Freilich *et al.* 2000), where the estimate for population density was 42 adults/km^2 or 0.42 adults/ha (Freilich *et al.* 2000). Assuming that catchability for *P. oculifer* is similar to that of *G. agassizii*, HPUC indicate that *P. oculifer* at Benfontein had a density of approximately 0.33 tortoises/ ha. Low population densities were also recorded for the Savanna tortoise *Kinixys spekii* in Zimbabwe (0.16 adults/ha; Coulson & Hailey 2001), the dry forest species *Pyxis arachnoides* in Madagascar (2.08-4.63 tortoises/ha; Walker *et al.* 2007) and the large-bodied *S. pardalis* in the arid Nama-Karoo of South Africa (0.017 tortoises/ha; McMaster & Downs 2006). In contrast, *C. angulata* attains a density of 38.3 individuals/ha in a mesic region of its range (Branch 1984). Apart from low productivity of the environment, other contributing factors to the low population density of *P. oculifer* in this study may be the location of the study site at the fringes of the species' distribution (Brown *et al.* 1995), and the low reproductive potential of females (Boycott & Bourquin 2000). It would be interesting to compare this population to one more centrally located within its range to quantify environmental effects on population dynamics of *P. oculifer*.

In summary, *P. oculifer* at Benfontein displayed slow growth, delayed sexual maturity, sexual size dimorphism and a population size structure indicative of higher mortality for juveniles than for adults. The effects of environmental aridity and variability were seen in the low population density and exceptionally long time, relative to body size, individuals take to mature. These life history traits make *P. oculifer* particularly vulnerable to factors that may increase adult mortality because iteroparity over a long lifespan offsets costs of delayed maturity (Shine & Iverson 1995; Kuchling 1999). Drought had a negative effect on body condition and increased frequencies of drought through climate change may affect adult physiology and survivorship. Since population declines may remain unnoticed for long periods due to the long maturation time of chelonians (Scott *et al.* 2012), the life history traits of *P. oculifer* should be considered in the management strategies for the species.

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