



Life history traits of free-living bush Karoo rats (*Otomys unisulcatus*) in the semi-arid Succulent Karoo

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Abstract

Life history traits are adaptations to specific environmental conditions but are also phylogenetically constrained. We studied life history traits of free-living bush Karoo rats (*Otomys unisulcatus*) that are endemic to the semi-arid regions of South Africa. They show behavioural, rather than physiological, adaptations to arid environments, which might affect life history traits compared to their mesophylllic otomyine relatives. We studied the reproduction and lifespan of bush Karoo rats over 2 and a half years. The mean litter size was 1.7 and was not dependent on the month of birth. Males were larger and had higher disappearance rates than females. Age and mass at reproductive maturity did not differ between the sexes. Individuals born earlier (May to July) in the breeding season reached reproductive maturity in the year of their birth, whereas those born later (August to November) reached maturity in the following year. Mass at maturity was dependent on timing of birth; individuals born earlier were lighter than those born later. The growth rate of all males was double that of all females, and male post-weaning growth rates were greater than that of females but not affected by the timing of birth. Lifespan, which was shorter in males than females, was not dependent on timing of birth. Compared to other members of the tribe Otomyini, bush Karoo rats had a slow pace of life, possibly because of the energy constraints in their arid habitat. Litter size, mass at maturity and lifespan are assumed to be phylogenetically constrained in the tribe Otomyini.

Keywords Bush Karoo rat · Life history · *Otomys unisulcatus* · Development · Environment

Introduction

Life history traits are behavioural, physiological, anatomical and genetic adaptations that directly influence reproduction and survival (Ricklefs and Wikelski 2002). Therefore, studies of life history traits, such as litter size, age and mass at maturity, growth rate and lifespan, are needed to understand how a species is adapted to its environment and how it can cope with environmental change. The exhibition of such traits are the result of trade-offs in energy allocation for survival (Ricklefs and Wikelski 2002; Dunkel et al.

2010) and are influenced by gene × environment interactions (Dunkel et al. 2010). Thus, variation in life history traits can be sensitive to environmental conditions (Ricklefs and Wikelski 2002). For example, life history traits in field voles (*Microtus agrestis*, body mass and timing of maturity) (Ergon et al. 2001), blue tits (*Parus caeruleus*, laying dates and clutch size) (Lambrechts et al. 1997) and red-bellied piranha (*Pygocentrus nattereri*, size at maturity, fecundity, female growth rate and condition) (Duponchelle et al. 2007) were responsive to environmental factors (i.e. food availability). However, some life history traits have limited reaction norms (i.e. phylogenetic constraints). Reaction norms are the range of phenotypes of the same genotype that may be expressed under different environmental conditions (Murren et al. 2014). This range may be limited by phylogenetic constraints which are defined as ancient characters in a taxon's phylogeny that limit the range of life history traits and behaviours that can evolve (Price 1994). Stearns (1983) reported that, in a sample of 65 and 162 mammal species, life history was strongly phylogenetically constrained even after accounting for mass effects. Phylogenetic constraints

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of life history traits have also been reported in passerine birds for egg mass, time to independence and, incubation and fledgling period (Pienaar et al. 2013). Thus, life history traits explain how species can cope with their environment, and they can vary depending on the environment but only within a specific set of reaction norms driven by phylogenetic constraints (Stearns 1983).

The suite of life history traits may be described in terms of pace of life that describes the co-variation in life history traits as a result of the trade-offs in energy allocation into growth and reproduction (Stearns 1983). Organisms fall along a fast–slow life history continuum in which those with a slow pace of life produce smaller litters, display delayed maturation and have slower growth rates and longer life spans than those with a fast pace of life (Promislow and Harvey 1990). For example, limited resource availability is typically associated with a slower paces of life (Dammhahn et al. 2018). Reduced or increased resource availability may delay or speed up certain life history traits such as maturation and growth rate (Altmann and Alberts 2005; Rimbach et al. 2021), thus modifying an individual's pace of life within the restricted reaction norm. This may result in different paces of life within a single population. Since life history traits have evolved in response to environmental conditions, a species pace of life may reflect environmental influences (Dammhahn et al. 2018).

The relationship between life history traits and the environment has been shown in several mammals. For example, striped mice (*Rhabdomys pumilio*) from an arid habitat showed faster growth rates during increased food availability (Rimbach et al. 2021). Additionally, individual striped mice born during the hot dry summer grew slower than those born in spring, when conditions were more favourable (Rimbach et al. 2021). This example also emphasises the existence of different paces of life within the same population. Age at reproductive maturity is also impacted by resource availability. For example, savannah baboons (*Papio cynocephalus*) experiencing greater food availability showed faster rates of sexual maturity (Altmann and Alberts 2005). Resource availability also impacted litter size and lifespan in yellow-bellied marmots (*Marmota flaviventris*): females inhabiting localities in which snow cover persisted for longer (reduced food availability) had smaller litter sizes, and offspring born late in the season showed reduced survivorship, apparently due to insufficient time to accumulate enough fat stores to survive hibernation (Van Vuuren and Armitage 1991). Thus, resource availability significantly influences mammalian life history traits.

The bush Karoo rat (*Otomys unisulcatus*) is a medium-sized (70–135 g) strictly herbivorous rodent (Pillay 2001) endemic to the Succulent Karoo and the Karoo of South Africa (Kerley and Erasmus 1992). The Succulent Karoo is characterised by a moist and cold winter and spring (May to November, frost

being common) and a long summer dry season (December to April) when temperatures often reach 40 °C. Food availability increases in winter, reaches its maximum in spring and can be very low in summer for several months. The bush Karoo rat is physiologically poorly adapted to the arid habitats it occupies (Du Plessis et al. 1989; Kerley and Erasmus 1992; Jackson and Spinks 1998): it has a higher basal metabolic rate than predicted for its mass, a low thermal neutral zone with a lower critical temperature of 22.5 °C (Du Plessis et al. 1992), and it displays symptoms of heat stress at 31 °C (Du Plessis et al. 1989; Kerley and Erasmus 1992; Jackson and Spinks 1998). However, it has especially well-developed kidneys for water conservation (Pillay et al. 1994; Jackson and Spinks 1998). It is also behaviourally adapted to arid conditions, building extensive stick lodges that provide protection against low humidity and temperature extremes (lodge temperatures are 10–25 °C) (Du Plessis et al. 1992).

Studies in captivity indicate that bush Karoo rats have a mean litter size of 2.1, a growth rate of 0.052 g.day⁻¹, are weaned by 14 days and reach sexual maturity at an age of 5–6 weeks at a body mass of around 60 g, with no differences between the sexes (Pillay 2001). These studies in captivity demonstrate the phenotypic expression under optimal environmental conditions without heat stress or food restriction. Field studies are needed to understand the influence of environmental conditions on life history characteristics under natural conditions. Our aims were to document the life history traits of bush Karoo rats under natural conditions throughout different seasons, focussing on litter size, age and mass at reproductive maturity, growth rate, tenure on the field site (lifespan) and sexual dimorphism. Since the species occupies a highly seasonal habitat, with a long dry season, which individuals must survive to reach the next breeding season, we expected a slow pace of life. Thus, due to low energy intake as a result of the long dry season, we predicted a comparatively small litter size, slow growth rate and late maturity. Based on the captive study, we also predicted that the age at maturity would differ between the sexes but not mass at maturity, and the growth rate would not differ between the sexes. Finally, due to the seasonality of the environment, we predicted early born individuals, which experienced a longer moist period with high food availability, to grow faster, reach maturity at an earlier age and have longer lifespans than individuals born at the end of the moist season.

Materials and methods

Study species

The bush Karoo rat is one of the 29 species in the *Otomys* genus (Wilson et al. 2017). Some workers placed it into a

separate genus *Myotomys*, together with the ice rat *M. sloggetti* (Edwards et al. 2011; Agnani et al. 2020), but we follow the IUCN categorisation that has both species in the genus *Otomys*. Together, the 29 *Otomys* species with 2 species in the genus *Parotomys* form the tribe Otomyini (Wilson et al. 2017) that falls under the subfamily Murinae in the family Muridae (Lecompte et al. 2008; Wilson et al. 2017). The sample size for our study consisted of a total of 224 individuals, 133 females and 91 males and a total of 58 litters.

Study site

The study was conducted in Goegap Nature Reserve in the Northern Cape, South Africa ($S 29.68139^{\circ}$, $E 17.96917^{\circ}$). The area is arid, consisting of Succulent Karoo vegetation (Jackson et al. 2002; Keller and Schradin 2008). The dominant shrubs are *Zygophyllum retrofractum* and *Lycium cinereum* (Schradin 2005). The area is characterised by winter rainfall, averaging 160 mm a year (Jackson et al. 2002; Schradin 2005) and temperatures ranging from -5°C in winter to 42°C in summer (Schradin 2005). Our study took place from September 2017 to February 2020, with monthly trapping in all months except April, September, November and December of 2018. During the study, temperatures ranged from -2.6 to 41.4°C , and the area experienced a severe drought with an average rainfall of 50 mm.

Trapping and tagging

Trapping took place 5 days a week. Two metal Sherman-like traps ($26 \times 9 \times 9$ cm) were placed at the entrances to each occupied lodge, which were identified by the observation of faeces, active runways or direct sightings of bush Karoo rats. The traps were placed in the sun on cold days and in the shade on hot days to avoid hypo- and hyperthermia, respectively. A mixture of crushed bran flakes, raisins, sea salt and sunflower oil were used as bait (Schradin 2005). Trapping took place in two sessions each day (one in the morning and one in the afternoon). The morning trapping session started 20 min before sunrise (06h00–08h00) and the afternoon session began 45 min before sunset (17h00–19h30). Traps were checked after 40 min. Individuals were tagged using uniquely numbered metal ear tags (National Band and Tag Company Newport, USA) attached to each ear, and marked with non-toxic hair dyes for identification during observations.

Trapping and life history data

Data for each individual were collected during trapping sessions, including (i) date of capture; (ii) assigned lodge number; (iii) weight (to the nearest 0.4 g); (iv) sex; and (v) reproductive status. Lodges were numbered using iron rods

and assigned a unique number. Individuals were sexed by using the ano-genital distance: 2–3 cm in adult males, 1 cm in adult females, and 8 mm and 2.5 mm in male and female dependent (unweaned) young, respectively. Other sexually defining characteristics were: males have an oval of dark fur proximal to the anus, an external marker of the cauda epididymis; and adult females have two pairs of inguinal nipples (Pillay 2001). Juvenile females also had a non-perforate vaginal scar. Reproductive activity was recorded as follows: males were scrotal (testes distinctly visible in the scrotal sac); and females had prominent nipples, an open vagina (i.e. perforate) and sometimes with a sperm plug after mating. Thereafter, the individual was released at the lodge where it was trapped, 2 to 5 min after being removed from the trap, albeit longer if the individual was not already tagged.

The potential mothers of each pup were determined based on the adult female occupants of the lodges where pups were trapped and from direct lodge observations of mother and offspring. Date of birth (DOB) was determined for individuals weighing less than 60 g using a formula based on date and weight $\ln a t \left(\frac{ss}{weight} \right)^f i r s t c a p u t e D O B = date - T; T = \left[\frac{\ln a t \left(\frac{ss}{weight} \right)^f i r s t c a p u t e D O B + 15}{-0.052} \right]$ obtained from Pillay (2001). The date of birth was then rounded to the 1st (1st to 7th and 23rd to 31st) or 15th (8th to 22nd) of that month. The operational sex ratio was determined each month based on the number of adults (individuals weighing 70 g or more and/or showing signs of reproductive activity). Sexual dimorphism was determined by comparing the masses of adult males and females trapped between February and April 2019 (the non-breeding season). Litter size at emergence from a lodge was determined by counting the number of known offspring of each female with the same DOB. The minimum age at reaching sexual maturity was determined for each sex separately by recording the age of the youngest individual showing signs of reproductive activity (open vagina for females and descended testes for males) (Pillay 2001). Furthermore, the influence of timing of birth (early or late during the breeding season) on age and mass at sexual maturity was tested. Timing of birth was determined as the number of days from the 14th of May (the earliest date of birth observed) to the individual's DOB. Growth rates were calculated at the population level for each sex (44 females and 28 males) over 2 years using the Richards growth equation (Karkach 2006; Teleken et al. 2017) that provided the best fit in CurveExpert Professional 2.6.5 (Hyams 2019). The number of measurements per individual ranged from 1 to 71. This variation was due to some individuals being more inclined to enter traps than others and may have affected growth rate calculations. We accounted for these differences by analysing individual as well as a population growth rates. For female growth rate, the masses of pregnant females were omitted from the dataset. On the individual level, post-weaning (after 14 days of age) growth rates were calculated for

each individual (39 females and 34 males) separately using the formula ($\frac{\text{mass}_2 - \text{mass}_1}{t_2 - t_1}$). This was done to test for statistical significance between the sexes and because there were not enough comparative data to run a Richards growth equation for each individual. Tenure on the field site was determined from date of birth and the date of last capture.

Statistical analysis

All statistical analyses were carried out using R (R Core Team 2018). Normality tests were carried out using Shapiro–Wilk tests. A *t* test was used to analyse litter size at emergence early and late in the breeding season. Chi-squared tests were used to analyse the bias in operational sex ratios. A Mann–Whitney *U* test was used to analyse sexual dimorphism in mass and post-weaning growth rates and to compare growth rates of females and males born early and late in the breeding season. Regression analyses were used to assess the influence of timing of birth and sex on the age and mass at sexual maturity and of year of birth on all life history traits. ANOVAs were used to analyse the influence of timing of birth (early vs late) and sex on age at reproductive maturity and lifespan. A regression between the predicted Richards growth and the observed growth was used to analyse the significance of the Richards fit. Lastly, a Cox proportional hazard model (survival package) (Therneau 2015) was used to test for sex-specific differences in tenure and used to assess longevity. Data are presented as mean \pm SD.

Results

The average (\pm SD) litter size at emergence (when offspring were old enough to leave the lodges and enter traps) was 1.67 ± 0.86 individuals ($n=58$ litters). The sex ratio of the offspring was 53/42 in favour of females. Sizes of litters born earlier (1.5 ± 0.9 individuals) vs later (1.7 ± 0.9 individuals) in the breeding season did not differ significantly ($t = -0.66$, $df = 19.92$, $p = 0.519$). Additionally, there was no difference in litter size between years ($\chi^2 = 5.24$, $df = 2$, $p = 0.073$). The mean (\pm SD) mass at emergence was 24.3 ± 3.1 g, ranging from 17 to 28.9 g. The operational sex ratio of the population (Online Resource 1a) was significantly female-biased for most of the year ($p < 0.05$) except for January ($\chi^2 = 1.08$, $df = 1$, $p = 0.297$), May ($\chi^2 = 2.88$, $df = 1$, $p = 0.090$) and July ($\chi^2 = 3.52$, $df = 1$, $p = 0.061$) of 2019 and February ($\chi^2 = 3.2$, $df = 1$, $p = 0.074$) of 2020, when the number of males did not differ significantly from the number of females. Adult males (101.56 ± 19.16 g) were significantly heavier than adult females (85.9 ± 13.55 g; $U = 401.5$, $n = 33.16$, $p = 0.003$) in the non-breeding season (breeding season data excluded to avoid bias of pregnancy).

Age at sexual maturity ranged from 5.43 to 45.57 weeks in females and from 4.14 to 43.29 weeks in males. Mass at sexual maturity ranged from 54.2 to 112.5 g in females and 66.5 to 108.3 g in males. Overall, there was no significant sex effect on either age ($F = 0.24$, $df = 1,17$, $p = 0.631$) or mass ($F = 0.35$, $df = 1,17$, $p = 0.564$) at sexual maturity. Due to differences in the timing of birth, we conducted separate analyses for individuals born early in the breeding season (May, June and July) and those born later in the breeding season (August, September, October and November). Age at sexual maturity was positively correlated with the timing of birth ($R^2 = 0.31$; $F = 6.83$, $df = 1,17$, $p = 0.018$), with individuals born earlier in the year reaching reproductive maturity at younger ages than those born later in the year (Fig. 1a). Specifically, individuals born earlier in the year reached reproductive maturity around 4–13 weeks of age, which was significantly sooner than those born later in the year (i.e. 20–46 weeks of age; $F = 8.77$, $df = 1,16$, $p = 0.009$) (Fig. 1a). Mass at sexual maturity correlated with the timing of birth but failed to reach significance ($R^2 = 0.23$; $F = 4.15$, $df = 1,17$, $p = 0.057$) (Fig. 1b). In females, year of birth had an effect on both age ($\chi^2 = 12.02$, $df = 2$, $p = 0.002$) and mass ($F = 7.75$, $df = 2,14$, $p = 0.005$) at maturity with individuals born in 2017 being both older (38.3 ± 4.5 weeks) and heavier (110.6 ± 13.8 g) at the time of maturation than those born in 2018 (age, 10.1 ± 3.9 weeks; mass, 87.9 ± 6.6 g) and 2019 (age, 7.6 ± 3.0 weeks; mass, 60.4 ± 8.8 g). There were no differences for males by year. Males in 2017 (age, 22.4 ± 3.3 weeks; mass, 101 ± 11.5 g) had similar ages and masses to those in 2018 (age, 18.6 ± 18.4 weeks; mass, 84.7 ± 23.1 g) and 2019 (age, 20.8 ± 0.9 weeks; mass, 81.3 ± 4.4 g).

The Richards growth equation for male bush Karoo rats from 4 to 317 days of age yielded the following equation, $y = \frac{104.205}{(1+e^{-6.8-0.016x})^{1/0.0009}}$, with a growth rate of 0.016 g/day (Fig. 2) and the asymptote (obtained from the Richards growth equation) reached at 104 days; model fit was significant ($R^2 = 0.838$, $p < 0.001$). The Richards equation for female bush Karoo rats was $y = \frac{98.48}{(1+e^{-6.83-0.008x})^{1/0.001}}$, with a growth rate of 0.008 g/day (Fig. 2) and the asymptote (obtained from the Richards growth equation) at 98 days; model fit was significant ($R^2 = 0.653$, $p < 0.001$). Males had a post-weaning growth rate of 0.57 ± 0.87 g/day, which was significantly faster than the 0.34 ± 0.65 g/day of females ($W = 417$, $n = 39, 34$, $p = 0.006$). Timing of birth (early vs late) did not have a significant influence on growth rate ($W = 293$, $n = 10, 62$, $p = 0.788$). Year of birth did not have a significant effect on growth rate ($F = 0.06$, $df = 2,65$, $p = 0.936$).

Most individuals of both sexes disappeared around 0–10 weeks of age (Online Resource 1b). The proportion of males that disappeared in the first 10 weeks compared to after

Fig. 1 Relationship between **a** age and **b** mass at reproductive maturity and timing of birth in male (open circles and solid line) and female (open triangles and dotted line) free-living bush Karoo rats

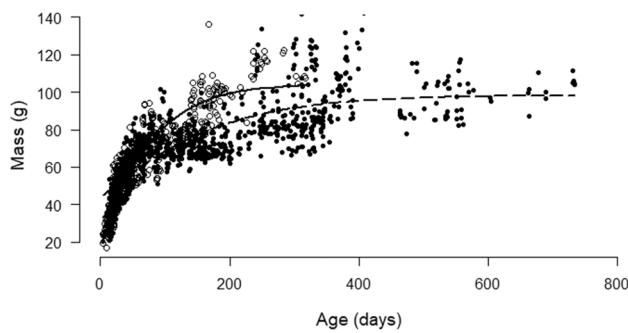
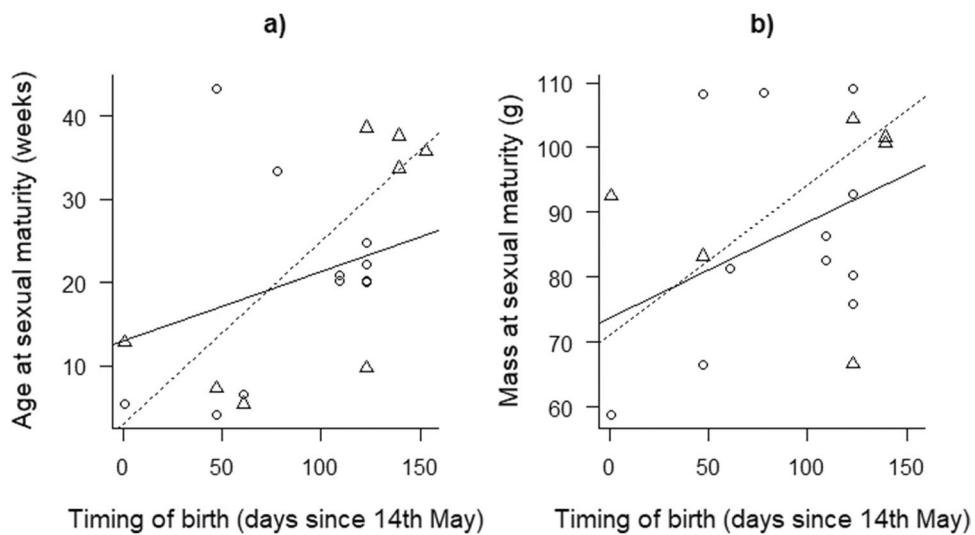


Fig. 2 The mass of male and female bush Karoo rats sampled up to 317 and 734 days of age, respectively. The circles (open for male and shaded for female) represent the actual data, and the line (solid for male and dashed for female) represents the calculated Richards growth curve

10 weeks (17:7) was not significantly higher than in females (14:18; Fisher's test, $p=0.059$). Females showed another spike in disappearance around 40–50 weeks of age. Females had a significantly longer tenure on the field site than males (Cox proportional hazard model, Likelihood ratio = 6.12, $df=1$, $p=0.013$). There was no significant effect of timing of birth (early; 24 ± 21.9 weeks vs late; 18.3 ± 21.3 weeks) on lifespan (i.e. occurrence on the study site; $F=0.626$, $df=1,52$, $p=0.4324$). Year of birth had a significant impact on lifespan ($\chi^2=36.52$, $df=2$, $p<0.001$). Individuals born in 2019 (6.6 ± 4.8 weeks) had a shorter tenure on the field site than those born in 2017 (31.3 ± 28.9 weeks) and 2018 (29.5 ± 20.1 weeks).

Discussion

Bush Karoo rats in the Succulent Karoo inhabit an arid, highly seasonal environment characterised by a long food-restricted dry season with very high temperatures. They had small litters, slow growth rates and slow sexual maturation, especially in individuals born late during the breeding season. These results indicate a relatively slow pace of life for a small mammal, which might be an adaptation to its seasonal environment.

Male bush Karoo rats were larger and grew faster than females, but the sexes did not reach sexual maturity at a different age or body mass. Male tenure at the field site was significantly shorter than female tenure, possibly due to male-biased dispersal and/or increased mortality. In many sexually dimorphic mammals, males grow faster and have delayed maturation and higher mortality (Glucksmann 1974; Moses et al. 1998), such as in spiny rats (*Niviventer coxingi*) (Yu and Lin 1998) and elephant seals (*Mirounga angustirostris*) (Stewart 1997). However, male and female bush Karoo rats reached maturity at similar ages. This indicates that the trade-off between growth and sexual maturity is not skewed towards growth, as in most other mammals (Stamps and Krishnan 1997), maybe because the operational sex ratio at our field site was strongly female-biased, reducing male–male competition and as such favouring early sexual maturity over growth. Another sexually dimorphic mammal species that shows equal rates of maturation in the sexes are fin whales (*Balaenoptera physalus*), where females are longer than males (Aguilar and Lockyer 1987), but both sexes reach sexual maturity around 6–7 years of age (Lockyer 1972). Overall, we found sexual dimorphism in body mass and growth rate but not age at sexual maturity under a female-biased operational sex ratio, and it would be interesting to

study whether this pattern changes when/if the operational sex ratio reaches parity or is male-biased.

Bush Karoo rats live in a highly seasonal environment. Therefore, we tested whether seasonality (timing of birth) influences bush Karoo rat life history traits. Age at maturity was significantly impacted by seasonality with body mass following the same trend. Individuals born earlier in the year reached maturity sooner and at younger ages. A similar effect has been observed in other rodents, including species with long breeding seasons (Davis and Meester 1981). Female voles (*Lagurus* and *Microtus* genera) and vlei rats (*Otomys irroratus*) born in spring may reproduce within their first year of life, whereas those born in autumn are unable to reach sexual maturity before winter and delay reproduction until the next spring (Pokrovskij 1971; Davis and Meester 1981). Only bush Karoo rats born early in the breeding season reached reproductive maturity within the season of their birth, whereas those born later only matured the following year. Those born earlier in the breeding season experience a longer moist period with high food availability, which may promote early maturation. Litter size, mass at maturity, growth rate and lifespan did not appear to be influenced by timing of birth, and this may instead reflect phylogenetically constrained traits. Comparisons within the tribe Otomyini reveals similar results in these life history traits (Table 1). For example, litter size in the Otomyini

appears to be limited to a maximum of 4 offspring. This is likely due to a morphological constraint since all members have 2 pairs of inguinal nipples (Pillay 2001) and can thus only support a maximum of 4 offspring. Mass at maturity also appears to be consistent within the tribe with both males and females reaching maturity at around 65% of their adult body mass. Lastly, maximum lifespan is around 2 years in many members of the tribe. The consistency of these life history traits among different members of the Otomyini as well as bush Karoo rats studied under different contexts (captive vs free-living), suggests that these traits may be phylogenetically constrained. Conversely, age at maturity and growth rate appear to vary considerably within the tribe. Age at maturity ranges from 4 to 14 weeks, with the ice rat (*Otomys sloggetti robertsi*) having the most delayed age at maturity. The ice rat occurs in the harsh alpine habitat which could explain the delay. Thus, this variation within the tribe (mainly between species occupying vastly different habitats) and the variation by the month of birth in the bush Karoo rat in the current study may suggest that this trait is influenced by environmental factors. Such variation appears to be an adaptation to changing conditions. Growth rate also varies considerably within the tribe, and although no seasonal affects were recorded in the bush Karoo rat, growth rate may still be impacted by environmental conditions as is evident from comparing the data from captive bush Karoo rats kept

Table 1 Ranking of life history traits for free-living Otomyini for which comparative data were available

	Bush Karoo rat (<i>Otomys unisulcatus</i>)	Ice rat (<i>Otomys sloggetti robertsi</i>)	Vlei rat (<i>Otomys irroratus</i>)	Brants' whistling rat (<i>Parotomys brantsii</i>)	Pace of life (arranged from slow to fast)
Habitat type	Succulent Karoo, semi-arid	Alpine, high altitude (cold) ⁴	Grassland–savanna, mesic ¹	Succulent Karoo, semi-arid ³	
Gestation	[37, captivity] ⁴	39–47 (37) ⁵	35–40 ²	30–47 (38) ³	Similar
Litter size, range (mean)	1–4 (1.67)	1–3 (2.14) ⁵	1–4 (2.77) ²	3–4 (3.4) ³	Bush Karoo rat < ice rat < vlei rat < Brants' whistling rat
Age at maturity (weeks)	Males, 4.14 Females, 5.43	Males, 14 ⁵ Females, 9 ⁵	Males, 8 Females, 4 ²	- Females, 5 ³	Males, ice rat < vlei rat < bush Karoo rat Females, ice rat < bush Karoo rat/Brants' whistling rat < vlei rat
Mass at maturity (% of adult body size)	Males, 65.5 Females, 63.1	Males, 66.1 ⁵ Females, 65.7 ⁵	Male, 68.4 Female, 64.3 ²	- Males (0–70 days), 1.21 ³	Similar Similar
Growth rate (g.day ⁻¹)	Males (4–317 days), 0.016 Females (4–734 days), 0.008	-	-	Females (0–70 days), 1.14 ³	-
Maximum lifespan (months)	26.2	12–24 ⁵	22 ²	-	Bush Karoo rat < ice rat < vlei rat
Sexual dimorphism in body mass (males % heavier)	18.2	17.8 ⁵	-	-	-

Dashes indicate data unavailable. Data for captive bush Karoo rats are shown in square brackets (¹Davis 1973; ²Davis and Meester 1981; ³Jackson 2000; ⁴Pillay 2001; ⁵Hinze 2005)

under optimal conditions, which had a faster growth rate from birth to 98 days of age, of $0.052 \text{ g} \cdot \text{day}^{-1}$ compared to that of free-living bush Karoo rats, suggesting flexibility in this trait.

Pace of life

The energy contained within an environment is limited. Therefore, organisms trade off energy allocation between growth, survival and reproduction. These trade-offs result in co-variation of life history traits (Dammhahn et al. 2018). Free-living ice rats and bush Karoo rats have a comparatively slow pace of life and Brants' whistling rats and the vlei rats a relatively faster pace of life (Table 1) (Promislow and Harvey 1990). The ice rats occupy alpine habitats, characterised by extreme temperatures, high solar radiation and a short growing season (Hinze 2005). Due to the extreme cold, thermoregulation is critical for ice rats, and they balance foraging activities with thermoregulatory activities, such as huddling (Hinze 2005). This trade-off in methods of energy acquisition might reduce energy available for key life history traits, such as growth and maturation, thus resulting in a slow pace of life. The bush Karoo rat also has a slow pace of life and also inhabits a harsh, though very different, environment. The arid Succulent Karoo is characterised by extreme temperatures and reduced food availability during the long dry season. Thus, it appears that the extreme environments of ice rats and bush Karoo rats selected for a slower pace of life. However, Brants' whistling rat occurs syntopically with the bush Karoo rat and has a comparatively fast pace of life. Life history traits have evolved in response to environmental conditions (Dammhahn et al. 2018), and our study indicates that the seasonal changes in the Succulent Karoo environment result in flexibility in some life history parameters, changing the pace of life. Bush Karoo rats born in winter reached sexual maturity sooner and might have reproduced in the upcoming spring (fast pace of life), whereas bush Karoo rats born in spring delayed sexual maturity for several months (slow pace of life), surviving the dry season, to breed one year later. Similarly, female voles (*Lagurus* and *Microtus* genera) (Pokrovskij 1971) and vlei rats (*Otomys irroratus*) (Davis and Meester 1981) born in spring may reproduce within their first year, whereas those born in autumn delay reproduction until the following spring. The occurrence of different paces of life within the same population has also been observed in other traits. For example, striped mice (*Rhabdomys pumilio*) in the Succulent Karoo displayed faster growth rates during periods of increased food availability (Rimbach et al. 2021). Additionally, individual striped mice born during the hot dry summer grew slower (slow pace of life) than those born in spring (fast pace of life), when conditions were more favourable (Rimbach et al. 2021).

Conclusion

Free-living bush Karoo rats show a variable pace of life, being able to reach sexual maturity at a very early age of 4–5 weeks or at a very late age of more than 40 weeks. This is in response to their seasonal environment, with a slow pace of life (late sexual maturity) during the food-restricted dry season and a fast pace (early maturation) during the food-rich moist season. It is apparent that the life history traits of bush Karoo rats show an interplay of environmental influences and phylogenetic constraints, with many traits showing similarities to Otomyini occurring in mesic habitats. Consequently, bush Karoo rats may use behavioural adaptations rather than life history traits to cope with aridity. Although our study suggests important phylogenetic constraints for life history traits such as litter size, it also emphasises how life history can respond flexibly to seasonal changes in resource availability.

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Author contribution All authors contributed to the study conception and design. Material preparation and data collection were performed by Lindy Wolhuter and Jennifer Thomson. Data analysis was performed by Lindy Wolhuter. The first draft of the manuscript was written by Lindy Wolhuter, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available in the figshare repository, https://figshare.com/projects/Life_history_traits_of_free-living_bush_Karoo_rats_Otomys_unisulcatus_in_the_semi-arid_Succulent_Karoo/115491.

Code availability The RStudio codes used for statistical analyses are available in the figshare repository, https://figshare.com/projects/Life_history_traits_of_free-living_bush_Karoo_rats_Otomys_unisulcatus_in_the_semi-arid_Succulent_Karoo/115491.

Declarations

Ethics approval This study was approved by the Animal Research and Ethics Committee of the University of the Witwatersrand (2019/04/28/B).

Consent to participate NA.

Consent for publication The authors consent to publishing.

Competing interests The authors declare no competing interests.

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