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ORIGINAL ARTICLE

Higher proactivity in later-borns: effects of birth date on personality in a small mammal

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Abstract

In short-lived animals, individuals born earlier in the breeding season frequently reproduce within the season of birth. Consequently, it has been proposed that those born early benefit from a more proactive behavioral type to compete for reproductive opportunities whereas later-borns adopt a more reactive personality to conserve energy to survive through the non-breeding season and reproduce in the following year. However, being proactive could also benefit later-borns in acquiring decreasing resources in the late breeding season. We investigated personality differences depending on the date of birth in relation to resource variation in a free-living population of the bush Karoo rat (*Otomys unisulcatus*). This species constructs stick lodges, a critical resource protecting the rats from the harsh semi-desert environments, but the availability of vacant lodges decreases with increasing population density during the breeding season. We predicted an increased occurrence of proactive phenotypes during the later breeding season, contrasting with the commonly assumed decrease in proactive phenotypes in late season due to lack of reproductive opportunity. We behaviorally phenotyped $n = 99$ individuals through repeated behavioral tests and found consistent individual differences along a proactive-reactive gradient. Most importantly, later-borns showed greater activity, boldness and exploration tendencies, indicating a more proactive personality. In addition, among early-born females, individuals which reproduced showed no differences in personality compared to those which did not reproduce. Our results indicate that seasonal differences in personality types in the bush Karoo rat may be driven by resource constraints in the late season rather than by differences in reproduction opportunities.

Significance statement

In short-lived animals, the birth date during the breeding season can lead to differences in life history and corresponding behavioral traits. We studied the link between birth date and personality in the bush Karoo rat, a seasonally-breeding and short-lived rodent which relies on a limited resource, stick lodges, essential to survive in a harsh semi-desert environment. Individuals born later in the season were more active, bolder and more explorative; these traits likely help them to successfully compete for stick lodges during the late breeding season when population density and thus competition is high. Early-born females, which can potentially start reproducing within their season of birth, showed no personality differences regardless of their reproductive status, suggesting that resource availability rather than reproduction opportunity may underly the emergence of seasonal personality differences in this species.

Keywords Behavioral phenotype · Consistent individual differences · *Otomys* · Pace-of-life syndrome

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Introduction

For animals living in seasonal environments, reproduction typically coincides with periods of high resource abundance (Whittier and Crews 1987). The timing of birth during such highly concentrated reproductive periods can lead to different life history trade-offs and thus to alternative phenotypic developmental trajectories (Roff 1993; Varpe 2017). In many short-lived species, such as rodents, individuals born early during the breeding season can reach sexual maturity and reproduce within the same season (Tkadlec and Zejda 1995; Montiglio et al. 2014). In contrast, individuals born later experience a shorter resource-rich period and are less likely to reproduce within the season of their birth. Thus, they need to survive through the non-productive period to reproduce in the following year (Lambin and Yoccoz 2001). Consequently, the timing of birth within the season may shape distinct behavioral traits in early and late born offspring to adaptively cope with their different survival and reproduction challenges.

Over the past decade, behavioral studies have gained a deeper understanding of consistent individual differences (animal personality), how these are maintained and their association with life history (Réale et al. 2007; Biro and Stamps 2008). The pace-of-life syndrome proposes that the trade-off between current versus future reproduction leads to differences in behavioral traits (Réale et al. 2010; Dammhahn et al. 2018): in seasonal breeding rodents, individuals born early which have an opportunity to reproduce within the season of birth, should benefit from an active and risk-taking personality that could be advantageous when acquiring resources needed for reproduction. In contrast, being less bold and less risk-taking may be more adaptive for later-borns because such a personality type will contribute to saving energy, increasing the probability of surviving through the non-breeding season until they can reproduce in the following year (Gracceva et al. 2014). Such an association between personality and the timing of birth has been reported, for example, in eastern chipmunks (*Tamias striatus*), in which birth cohorts with early reproductive opportunities were faster explorers than those reproducing at a later age (Montiglio et al. 2014). Similarly, in European shags (*Phalacrocorax aristotelis*), chicks hatched early in the breeding season had higher social ranks and showed higher levels of aggression compared to those hatched later (Velando 2000). However, another study suggests a differential association between personality and timing of birth: in short-lived common voles (*Microtus arvalis*); individuals captured in spring (mostly late-born cohorts from the previous year) were bolder than those captured at other times of the year (Eccard and Herde 2013). This contradiction among different studies suggests the necessity to investigate the effect of seasonal environmental factors, which may contribute to explain the emergence of differences in behavioral types between different seasonal birth cohorts.

Apart from reproductive trade-offs that underly the pace-of-life continuum, ecological conditions can also be important drivers of personality (Dammhahn et al. 2018; Jablonszky et al. 2018; Montiglio et al. 2018). Individuals with proactive phenotypes are usually more successful in competing for resources (Sih et al. 2004; Smith and Blumstein 2008). During the late breeding season, resource availability typically declines, while population density increases at the same time. Being proactive can be beneficial for individuals born late in the season in competition for limited resources. Therefore, two alternative hypotheses exist: (1) early-borns are more proactive to acquire enough resources for reproduction *versus* (2) late-borns are more proactive to acquire enough resources for survival. Therefore, to understand the association between personality and the birth timing, further investigations, preferably under natural conditions are necessary.

The seasonal breeding bush Karoo rat (*Otomys unisulcatus*), a short-lived small mammal living in arid environments of South Africa, is an appropriate model to study the association between birth timing and personality. This species shows a distinct ecological feature that can result in intense resource competition during the breeding season. Bush Karoo rats construct "stick lodges" from dry plant material as refugia (Vermeulen 1988; Pillay 2001), providing a favorable micro-climate that protects the rat from the harsh ambient environment (Vermeulen 1988; Brown and Willan 1991; Du Plessis et al. 1992). A stick lodge is costly to build and is commonly used by only one adult individual in this solitary species (Makuya et al. 2024), although it can be reused by others after the builder disappears. Thus, vacant stick lodges represent a limited survival resource, and the availability decreases in the late breeding season when subadult individuals start to occupy stick lodges of their own. As more lodges become occupied, individuals born later face increasing difficulties in finding unoccupied lodges or will even need to build new ones. In this situation, having a proactive personality becomes adaptive as it could lead to finding and competing for unoccupied lodges, or in competing for building materials for constructing new lodges (Vermeulen 1988).

Our aim was to investigate the effect of the date of birth on personality in adult bush Karoo rats. First, we studied whether free-living bush Karoo rats show consistent personality traits in activity, boldness and exploration behavior. Next, considering the potential effects of increasing population density on the availability of stick lodges, we predicted that such personality traits would

be associated with birth timing, as later-borns would adopt a more proactive (active, bold and/or explorative) behavioral type. Finally, we studied whether there was a seasonal change in behavior, specifically whether the proactive response decreased in the food restricted dry season when compared to the food rich moist season. We conducted a field study over two years (2022–2023) and repeatedly quantified six behavioral parameters related to three different behavioral personality traits, activity, boldness and exploration (sensu Réale et al. 2007), which was compared between individuals born earlier and later during the breeding season.

Materials and methods

Study site and study population

Our study population occurred in the arid Succulent Karoo, a biodiversity hotspot in South Africa, characterized by variable climate and low precipitation. Bush Karoo rat breeding activity coincides with season (Wolhuter et al. 2022). Reproduction is concentrated in the moist period from July to November, followed by the hot and dry non-breeding period from December to June. Bush Karoo rats have a relatively short life span (1–2 years). The earliest age at sexual maturity is between 5 and 6 weeks, and the reproductive period spans over 4–5 months per year (Vermeulen 1988; Wolhuter et al. 2022). Offspring born early in the breeding season can reach sexual maturity within the season of their birth (Wolhuter et al. 2022). The competition for reproductive resources mostly concerns individuals born early in the season, while the availability of stick lodges is relevant for the survival of all individuals and may be especially limiting for those born late in the season.

The study was conducted in the Goegap Nature Reserve, Northern Cape Province, South Africa. The field site in the semi-arid Succulent Karoo (Cowling et al. 1999) is characterized by an annual rainfall of 160 mm/year on average, and by temperatures varying from − 1.5 to 24 °C during winter and from 4 to 42 °C during summer (weather station at the field site). Most of the rainfall occurs in winter, creating abundant vegetation that supports the onset of reproductive activity in our study population (Wolhuter et al. 2022). The field site for the study is approximately 4.5 ha.

Stick lodge surveys

Stick lodge surveys were conducted twice a year, at the beginning of the breeding season in July and after the breeding season in January. We classified the stick lodges, which built within shrubs, into three size categories: (i) small: lodges with a height below 20 cm; (ii) medium: lodges with a height from 21 to 50 cm; and (iii) large: lodges that almost covered the entire shrub with a height above 50 cm (Schradin 2005). For every lodge, we recorded whether it was old (several years old) or whether it was newly built within the past few months, based our field records.

For each season, we calculated the total number of stick lodges on the field site as the total of old lodges surveyed in January (e.g. lodge survey in January 2023 for the breeding season that started in July 2022). Because we wanted to have a measure of available old lodges, we recorded these separately from lodges that were built within the prevailing season (the new lodges). More fine-scaled data on changes in the numbers of available stick lodges during 2022 and 2023 were not available for this study.

Trapping and individual tagging

In the field site, trapping was carried out at all occupied stick lodges throughout the year as part of a long-term data collection. The field site was split into 6 trapping areas, with trapping being carried out at two areas simultaneously by two people for three days, before switching to two other areas. Additional trapping was done at lodges with previously unmarked juveniles and focal individuals for behavioral tests. Trapping was done 5 days a week, and occurred before sunrise. The traps were set at lodge entrances and checked every 30 min. All traps were closed within two hours after sunrise to avoid overheating. We used Sherman traps and locally produced metal (Sherman-like) live traps (26 × 9 × 9 cm), which had small holes in the sides to allow circulation of air.

At first capture, bush Karoo rats were individually marked with aluminum band ear tags in both ears (0.25 g per tag) with a unique individual number (National Band and Tag Co., Newport, KY, USA). During re-trapping, we always checked for infections at the ear tags, which would have resulted in the removal of the tag on the affected ear; such cases never occurred during the study period. Birth date was estimated from the animals' body mass, based on the linear association between age and body mass in the bush Karoo rat as published in Pillay (2001). Trapping data used for our study spanned from 1st January 2022 to 14th December 2023. When a female born within the season showed signs of pregnancy/lactation (palpable embryos at late pregnancy stage; lactation as evident by the developmental stage of the mammary

glands), or when a female had dependent young (as evident by juveniles trapped at the same stick lodge prior to the next breeding season), this female was considered as having reproduced during the season of birth ('precocious reproduction').

Assessment of changes in population density

Based on trapping data, we recorded the population density of adult (older than 5 weeks) bush Karoo rats (*n*/ha) at the beginning of the breeding season in July and again after the breeding season in January for both seasons. Therefore, for each month, we counted the total number of trapped adult bush Karoo rats and divided this number by the size of the field site. We were able to mark and monitor the population through observations because the field site is an open terrain (dispersed shrubs with sandy areas in between), the bush Karoo rat is diurnal, and occupied stick lodges showed clear signs of occupancy. At lodges with signs of occupancy where we did not trap an individual within 3 days, we continued with additional trapping. We also conducted behavioral observations (described in Makuya et al. 2024), enabling us to identify occupied lodges and unmarked juveniles.

Experimental procedure

Trapping of focal individuals was conducted using the same method as described above. Individuals were transported to a field laboratory situated next to the field site (less than 10 min walking distance) for behavioral testing. Except when checking ear tags and performing behavioral tests, the rats remained in their traps during the whole time. After the test procedure, individuals were released next to their stick lodge, i.e., at the site where they had been trapped.

Focal individuals underwent up to four repetitions of behavioral tests. Because the field site changed from the moist to dry season with a decrease in food abundance over time, we measured behavioral repeatability at short term (two-week interval) and long term (16-week interval, in the moist and dry seasons) to account for the seasonal variation of food abundance. The test schedule was determined by age; the first and second tests were conducted at early adult stage (age class "young adults"), with the first age at approximately 6 weeks when they reach sexual maturity (Pillay 2001). The second test was scheduled two weeks later. The third and fourth tests were conducted at fully adult stage (age class "older adults"), with the third test scheduled when individuals were approximately 20 weeks old, and the fourth test two weeks later.

As was evident from our trapping data, females usually disperse for shorter distances and therefore were more likely be continually caught using our trapping protocol. Thus, in the first year, the selection of focal individuals was limited to females and included four behavioral test replicates. In the second year, both males and females were selected as focal individuals. However, due to time constraints, the rats underwent only the first and second behavioral tests in the second year. Due to unpredictable field conditions, trapping of focal individuals was not always successful, which led to delays for repeated behavioral tests in some cases. The average age for "young" adults (at the 1st and 2nd test) was 54 days, and the average age for "older" adults (at the 3rd and 4th test) was 151 days. Because our study involved individually-marked focal animals, the experimenter(s) were not naive to individual identities during testing.

Population density of small mammals in our field site typically decreases dramatically during the dry season to the onset of the next breeding season, when it is only approximately a quarter of the density at the end of the breeding season (Nater et al. 2018). As expected, many individuals disappeared from the field site throughout the study, mainly due to predation. We could not predict which individuals would disappear, so we tested as many individuals as possible at the onset of the breeding season.

During the first year (2022), we tested a total of 56 individuals, out of which 37 individuals were successfully trapped and underwent the last two (3rd and 4th) tests as older adults: 19 of them underwent all four tests (i.e. two times during older adult stage and two times during young adult stage), eight individuals were tested three times (i.e. two times during older adult stage and one time during young adult stage), and 10 individuals were only tested two times (i.e. two times during older adult stage). This was not the case for 19 individuals that had disappeared prior to the last testing during older adult stage. During the second year (2023), we tested a total of 43 individuals, out of which 29 underwent all two tests; note that during the second year, we only carried out two tests during the younger adult stage (see details above). The remaining 14 individuals could only be trapped and tested for the 1st test. Overall, out of the total of 99 individuals tested in 2022 and 2023, 66 individuals did not disappear prior to the end of the testing.

As a consequence of the disappearance of some animals in combination with the differences in (re-)trapping success, the individuals had different experiences when undergoing the different tests. All 99 individuals of our sample were tested at least one time, $n = 78$ individuals underwent at least a 2nd test, $n = 30$ individuals underwent at least a 3rd test and only $n = 19$ individuals underwent all four tests.

Behavioral tests

One to a maximum of four individuals were trapped for behavioral tests per day. A white chamber (100 cm long,

85 cm wide and 65 cm high) made of melamine panels was used as a test arena (Fig. 1). Before introducing a new individual into the arena, the arena was always thoroughly cleaned using 95% alcohol and air dried. All tests were video-recorded and later analyzed using the software BORIS (Friad and Gamba 2016) and Single Mouse Tracker (Icy software, De Chaumont 2012). Focal individuals underwent three successive behavioral tests directly after the morning trapping. To minimize observer bias, blinded methods were used when all behavioral data were recorded and/or analyzed.

Starting box

This part of the apparatus (the starting box) consisted of a 10 cm^3 black acrylic and opaque square box with one side that could be opened (door) and a lid at the other side. The open side was directly attached to the test arena and separated by a closed door (Fig. 1a). After individuals were placed into the starting box via the lid, they were allowed to calm down for 3 min in the closed box. Then the door was opened and we recorded whether the animal entered the test arena in the following 10 min. If the animal did not enter the arena within this time, it was gently nudged in using a plastic ruler (2 × 30 cm) by reaching into the box through the lid. Once the individual had entered the arena, the door was closed to prevent its return into the starting box.

Open field test

Once the rat had entered the arena, the open field test began (Fig. 1a). During the following 5 min, the individual could freely explore the arena. We recorded three behavioral parameters: (1) the distance travelled, defined as the total distance of locomotion measured in cm; (2) the % time the individual was active in the arena, defined as the total time minus the time being immobile (i.e. no obvious movements for more than 10 s); and (3) the % time the animal spent exploring the walls and corners of the arena, defined as sniffing or putting the front paws against the walls.

Novel odor test

During our preliminary tests, bush Karoo rats did not show notable interactions with plastic toys presented as visual novel objects. However, interactions were observed when objects were applied with novel odors (e.g., orange peel). We therefore did not apply classical novel object tests (Denninger et al. 2018) but instead measured the animals' exploration behavior towards objects carrying novel odors in a standardized setting.

After the open field test was completed, the animal remained in the arena and was confined again by the experimenter using the same black acrylic square box. The box was attached to a fixed pulley system so it could be lifted to release the individual with minimum disturbance. The focal individual was first placed in the center of the arena while covered by the box. Then, four identical hollow metal, egg-shaped sieve balls (4.5 × 3.9 cm, steel) providing the same novel odors were placed inside the arena, 10 cm away on the extended diagonal of the black box (see Fig. 1b). The source of odor used in the 1st test was orange peel, tomato sauce was in the 2nd test (two weeks later), peanut butter was used in the 3rd test and strawberry jam in the 4th test. After setting up the arena, the rat was allowed to calm down for 5 min inside the box, then the box was lifted and the individual was given 5 min to explore the four metal balls. We recorded two behavioral parameters: (1) the time the animal spent exploring the objects, defined as the total (summed-up) duration the individual sniffed or touched one of the four tea balls; and (2) the number of objects explored, defined as the total number of tea balls, which were sniffed or touched by the individual during the test (range from 0 – 4).

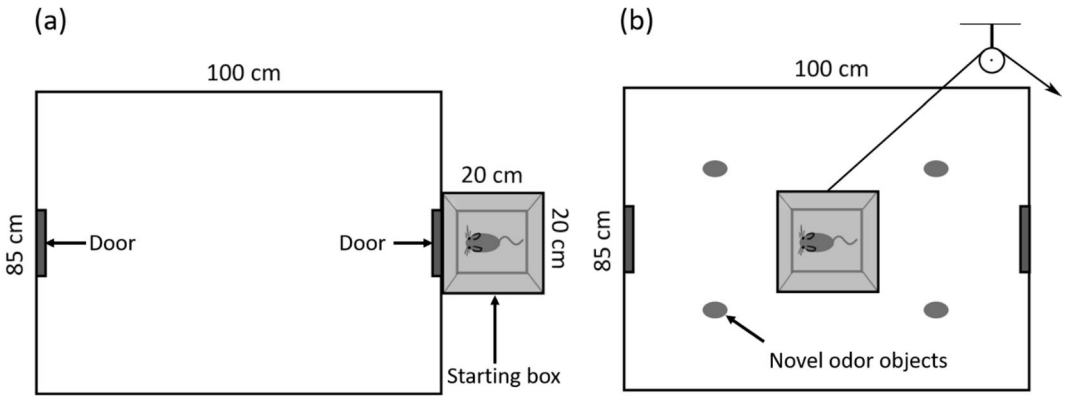

Fig. 1 Experimental setting used for (**a**) starting box/open field tests and (**b**) novel odor tests, either orange skin, tomato sauce, peanut butter or strawberry jam (for the 4 replicates) were used to provide novel odors carried in the identical sieve balls. Note that the starting box inside the arena in (**b**) was lifted by a pulley system once the experiment started

Quantification of seasonal food abundance

Because the repeated behavioral tests were conducted in two seasons with variable food availability, we quantified seasonal changes in the abundance of food plants and considered the potential effects on individual behavioral performance during testing. Food plant abundance was measured monthly using the Braun-Blanquet method as part of the long-term data collection on the field site, assessed by the average number of food plants from eight 2 m × 2 m plots randomly located in the field site (Werger 1974; Schradin and Pillay 2006). The resulting index was used in the statistical analysis (see details below) as an estimate of the food plant availability at the time of the different test sessions.

Statistical analysis and sample sizes

In total, 99 individuals (n_{males} = 15, $n_{females}$ = 84) were tested in 226 behavioral tests. We considered potential effect of multiple test replicates per individuals, as such repeated testing may lead to habituation effects (Salomons et al. 2010). The sample sizes available during the different test replicates (hereafter referred to as "test sequence"), see more details above, in the last paragraph of section "Experimental procedure".

Statistical analyses were carried out in R, version 4.3.0 (R Core Team 2023). In the first step, we checked for repeatabilities of the six behavioral variables quantified in the starting box test, open field test and in the novel odor test, across the four different test sessions, as well as for associations between these behavioral variables. All six response variables (behavioral variables, given in Table 1) were scaled for analysis. This analysis (with $n = 99$ individuals) was done using a single, multivariate generalized linear mixed-effects model GLMM (i.e., with six response variables) based on the R package *MCMCglmm* (Hadfield 2010). The predictors were year and sex (2 levels each) and test sequence (number of tests the individual has done before, 4 levels), with random effects for individual ID. We applied a weakly informative prior, allowing the data to primarily inform the posterior distributions. One chain was run with 100,000 iterations. The first 5,000 iterations were discarded as burn-in, and every 100th iteration was retained (thinning interval = 100), resulting in 950 samples per chain. The response variables followed appropriate distributions: a categorical distribution for the latency to enter the arena, poisson distribution for the number of objects explored (count variable from 0 to 4), and Gaussian distribution (after some transformations, see details below Table 1) for the remaining four continuous behavioral variables. As the early disappearance of some animals prior to the completion of the four test sessions in the year 2022 or of the two test sessions in 2023 may have potentially created a calculation bias, we repeated the analysis by a multivariate GLMM with a subsample of $n = 66$ animals (out of the original $n = 99$ individuals) which were still present (i.e. trapped and tested) during the last test sessions of both years of study. See more details above, in the section "Experimental procedure". However, this more conservative analysis revealed highly similar findings, as presented in Tables B, C in Suppl. Materials.

Repeatabilities across the (up to) four repeated tests per behavioral parameter (see Table 1) and pair-wise correlation coefficients between the different behaviors (see Table 2) were calculated based on the within-individual and among-individual variance matrices provided by this model. Associations between the different behavioral variables were considered statistically significant ($P < 0.05$) when the 95% Bayesian credible intervals of the correlation coefficients (R) did not overlap zero (Houslay and Wilson 2017). However, in case of repeatabilities over time, as per definition only non-negative values can be obtained and thus the 95% credible intervals cannot overlap zero, P-values could not be calculated based on the above-mentioned method (Houslay and Wilson 2017).

Table 1 Repeatability (R, including its 95% credible interval CI) of behavior parameters measured in repeated starting box (SB), open field (OF) and novel odor (NO) tests of 99 individuals. Analysis by a multivariate GLMM including individual identity as a random factor, year, sex and test sequence (4 levels) as fixed variance. (a) long-term repeatability was based on all (up to) four behavioral tests of all age classes ($n = 226$ measurements for each behavioral variable), (b) short-term repeatability was based on (up to) two behavioral tests during young adult stage ($n = 145$ measurements for each behavioral variable)

	(a) Long-term repeatability		(b) Short-term repeatability	
	R	$CI_{95\%}$	R	$CI_{95\%}$
SB - Probability to enter arena	0.699	[0.483, 0.872]	0.477	[0.050, 0.860]
OF - Distance travelled[1]	0.364	[0.204, 0.521]	0.384	[0.141, 0.610]
OF - % Time active	0.167	[0.025, 0.308]	0.219	[< 0.001, 0.417]
OF - % Time exploring **walls and corners of arena**[1]	0.253	[0.093, 0.427]	0.317	[0.039, 0.536]
NO - Time exploring object[2]	0.119	[< 0.001, 0.325]	0.038	[< 0.001, 0.158]
NO - Number of objects explored	0.127	[< 0.001, 0.364]	0.051	[< 0.001, 0.244]

[1] square-root transformation of dependent variable

[2] log [x + 1] transformation of dependent variable

Table 2 Associations between the different behavioral parameters, based on measurements taken from 99 individuals of different age classes. Analysis by a multivariate GLMM including individual identity as a random factor, and year, sex and test sequence (4 levels) as fixed variance. Correlation coefficients (among individual-level) are given, values given in bold indicate that the 95% credible intervals do not overlap zero, otherwise they are given in brackets. Note that results stem from the same model as used for the calculation of Table 1a, more details, including the credible intervals, are given in table A in suppl. Materials

	PEA	DT	%TA	%TEA	TEO	NOE
PEA		**0.763**	**0.840**	**0.780**	(0.549)	(0.454)
DT			**0.786**	**0.620**	(0.484)	(0.429)
%TA				**0.848**	(0.605)	(0.470)
%TEA					(0.494)	(0.372)
TEO						(0.614)
NOE						

PEA: Probability to enter arena; DT: Distance travelled (square-root transformed); %TA: % Time active; %TEA: % Time exploring walls and corners of arena (square-root transformed); TEO: Time exploring object (log [x + 1] transformed); NOE: Number of objects explored

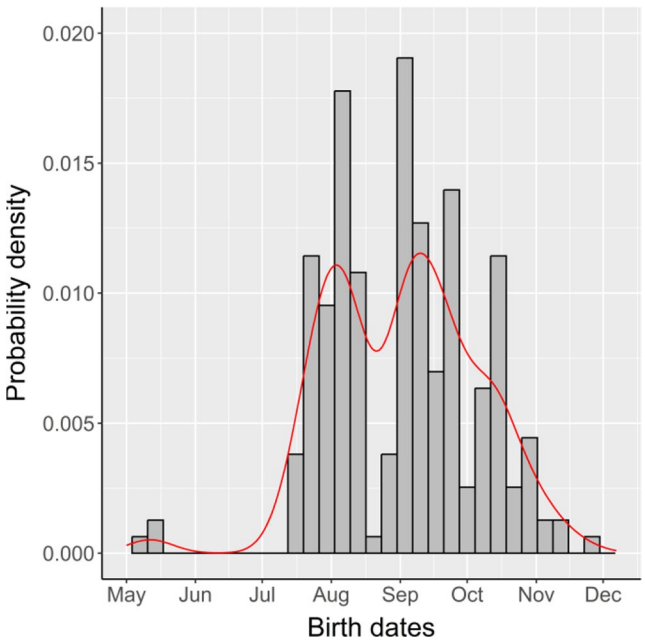

Fig. 2 Distribution of reproductive activity (assessed by the frequency of birth events) during the breeding season in the bush Karoo rat, given as density probability (red line). Data from $n = 226$ individuals captured during the years 2022 and 2023, including the 99 focal individuals which underwent behavioral tests

Consequently, our inference on repeatabilities was only based on interpretation of the 95% credible intervals. We calculated the overall (long-term) repeatability, based on all (up to) four behavioral tests of our 99 focal individuals over all age classes (young adult at first and second tests, older adult at third and fourth tests; $n = 226$ measurements for each behavioral variable), as well as short-term repeatability, based on the first two behavioral tests for 99 young adults with a total of $n = 145$ measurements for each behavioral variable.

In the second step, we tested the effects of the date of birth (covariate, 1st July as baseline; see the rather consistent distribution of birth dates along the season in Fig. 2) on the six different behavioral variables (see Table 2). Therefore, using the R package *lme4* (Bates et al. 2015), we applied separate models - a generalized linear mixed-effects model (GLMM) for binomial data with a logit link for the probability to enter the test arena (see Table 2a), and linear mixed-effects models (LMM) for all remaining (continuous) behavioral variables (see Table 2b-f). To obtain a normal distribution of model residuals (verified by visually checking normal probability plots) and homogeneity of variances (by plotting residuals versus fitted values) for LMMs, we square-root transformed the distance travelled and the % time the animals spent exploring the walls and corners of the arena, and log [x + 1] transformed the time the animal spent exploring the object in the novel odor test. Individual identity was always included as a random (intercept) factor. All models included the age class at testing ("young adult" at the 1st and 2nd tests or "older adult" at the 3rd and 4th tests; 2 levels), the sex of the focal animals and the year of testing (all factors with 2 levels), the test sequence (factor with 4 levels) and the food plant abundance at testing (covariate). Because we were interested in whether possible differences between earlier- and later-born individuals were only apparent in young adults or in older adult individuals, we also tested the 2-way interaction between date of birth and age class. When non-significant, this interaction was removed from the models and these were recalculated (Engqvist 2005). *P*-values were calculated by type-3 Wald chi-square tests (Bolker et al. 2009).

We also tested whether the behavioral responses of early-born females (i.e., females born until/including the 5th week of the breeding season, when the last reproducing female was born) in the different tests were associated with their actual reproductive activity during their season of birth. Using the R package *lme4* (Bates et al. 2015), we applied GLMMs for binomial data with a logit link using the same transformations for some of the behavioral variables (now used as predictors in our model) as described above. Each model included one behavioral variable,

and all included year of testing (2 levels) as fixed variance. Individual identity was always included as a random (intercept) factor. Also, *P*-values were calculated by type-3 Wald chi-square tests.

Results

Seasonal differences in population density and stick lodge availability

In both years of the study, the adult population density showed dramatic variation between the breeding/non-breeding seasons. Population density increased during the breeding season from July to January by 120.7% on average. Specifically, during the first year of study (Jul 2022– Jan 2023), the adult density increased by 81.4% from 12.6 to 23.4 individuals/ha, and during the second year (Jul 2023– Jan 2024), it increased by 160% from 6.5 to 16.9 individuals/ha. However, the population also dramatically decreased during the non-breeding season by 72.0% between January to July 2023.

In the breeding season starting in July 2022, 172 old lodges (i.e. existing ones) were available and 26 new lodges were built. The availability of old lodges decreased during the breeding season, from 3.1 to 1.6 lodges/adults from July 2022 to January 2023. In the breeding season starting in July 2023, 194 old lodges were available and 9 new lodges were built. The availability of old lodges decreased from 6.9 to 1.8 lodges/adults from July 2023 to January 2024. When only considering the large lodges with a height above 50 cm, which can be assumed to be the most valuable resource, this seasonal difference was more pronounced. The availability of such large lodges decreased from 0.8 per adult individual to 0.4 in 2022/2023, and from 1.7 to 0.4 in 2023/2024.

Pattern of seasonal reproduction

We quantified the temporal distribution of reproductive events during the breeding season using the estimated dates of birth of the juveniles trapped, based on a sample of $n = 226$ juveniles (129 born in 2022 and 97 born in 2023, Fig. 2). The annual start of the reproductive season was determined by the occurrence of at least three juveniles born on different dates within a week (i.e., apparently from different litters), revealing a highly similar onset of the reproductive season between the two years of study (2022: 19th July; 2023: 14th July). In 2022, the mean date of birth was on 29th August, and during the reproductive season in 2023, it was on 8th September.

Consistent individual differences in behavior

We analyzed the consistency of six behavioral variables recorded in up to four repeated starting box tests, open field tests and novel odor tests. Overall, we found notable long-term consistencies across time (i.e., repeatability) and thus across different age classes (young to older adults), with respect to three of the four behavioral variables recorded in the starting box and open field tests. These variables were the probability to enter the arena within 10 min, the distance travelled, and the % time the individual spent exploring the walls and corners of the arena (Table 1a). In contrast, the % time the rats were active in the open field arena as well as both behavioral variables measured during the novel odor tests showed very low repeatabilities with large credible interval closely approaching zero (Table 1a).

Regarding short-term consistency, when only considering the first two tests during which individuals could be considered as young adults, we found repeatabilities similar to long-term consistency in the starting box and open field test, but again no noticeable repeatability in the novel odor test (Table 1b).

We also found significant associations among the parameters recorded in the starting box test and open field test. Specifically, the probability to enter the arena, the distance travelled, the % time the animals showed activity and the % time the animals spent exploring the walls and corners of the open field arena were positively and significantly correlated at the between-individual level (Table 3).

Effects of birth date on personality traits

All behavioral parameters recorded in the starting box and open field tests were significantly associated with the individual date of birth (Table 2). The probability to enter the arena (Table 2a, Fig. 3a), the distance travelled (Table 2b, Fig. 3b), the % time active (Table 2c, Fig. 3c) and the % time exploring the walls and corners of the arena (Table 2d, Fig. 3d) were all significantly higher in individuals born later in the season. The interaction between the date of birth and age class at testing was never statistically significant, indicating that the significant effects of date of birth on behavior (Table 2a-d) were independent of age class. In contrast, the two parameters recorded during the novel odor test were not significantly associated with date of birth (Table 2e, f). We found a significant and positive effect of the current food plant abundance only for the total time spent exploring the objects carrying the novel odors (Table 2e). Specifically, the higher the food availability around the time of testing, the longer the individuals explored the novel odor.

In two parameters measured in the open field, we found significant sex differences; males travelled a longer distance

Table 3 Effects of different predictor variables on behavioral traits (a-g) of 99 individuals, repeatedly measured up to 4 times in starting box (SB), open field (OF) and novel odor (NO) tests. Analysis by a multifactorial GLMM including individual identity as a random factor. The 2-way interaction between age class at testing and the date of birth during the reproductive season was tested in all models but was never statistically significant ($P > 0.05$). Significant effects are given in bold

Dependent variable	Predictors	χ^2	df	β ± SE	*P*
(a) SB - Probability to enter arena	Date of birth within seaso	6.065	1	0.043 ± 0.017	**0.014**
	Age class at testing [old]	0.002	1	–0.041 ± 1.003	0.967
	Sex [m]	3.493	1	2.446 ± 1.309	0.062
	Food plant abundance at testing	0.630	1	0.383 ± 0.483	0.427
	Test sequence [2nd]	2.623	3	–0.806 ± 0.525	0.454
	[3rd]			–0.529 ± 0.993	
	[4th]			–0.092 ± 1.116	
	Year [2nd]	3.258	1	–1.554 ± 0.861	0.071
(b) OF - Distance travelled [1]	Date of birth within season	4.000	1	3.017 ± 1.508	**0.045**
	Age class at testing [old]	0.885	1	–3.189 ± 3.389	0.347
	Sex [m]	5.541	1	9.151 ± 3.888	**0.019**
	Food plant abundance at testing	0.822	1	1.459 ± 1.610	0.365
	Test sequence [2nd]	91.163	3	–15.774 ± 1.706	**<0.001**
	[3rd]			–16.216 ± 3.461	
	[4th]			–21.940 ± 3.934	
	Year [2nd]	0.063	1	0.728 ± 2.898	0.802
(c) OF: % Time active	Date of birth within season	8.608	1	0.306 ± 0.105	**0.003**
	Age class at testing [old]	1.110	1	–7.531 ± 7.149	0.292
	Sex [m]	3.266	1	13.183 ± 7.295	0.071
	Food plant abundance at testing	0.931	1	3.414 ± 3.539	0.335
	Test sequence [2nd]	51.848	3	–25.279 ± 3.932	**<0.001**
	[3rd]			–22.149 ± 7.226	
	[4th]			–40.905 ± 8.195	
	Year [2nd]	1.345	1	–6.245 ± 5.386	0.246
(d) OF: % Time exploring walls and corners of arena [1]	Date of birth within season	10.610	1	0.021 ± 0.006	**0.001**
	Age class at testing [old]	4.524	1	–0.875 ± 0.412	**0.033**
	Sex [m]	0.479	1	0.308 ± 0.445	0.489
	Food plant abundance at testing	1.968	1	0.280 ± 0.199	0.161
	Test sequence [2nd]	41.058	3	–1.197 ± 0.215	**<0.001**
	[3rd]			–1.359 ± 0.418	
	[4th]			–2.274 ± 0.475	
	Year [2nd]	0.695	1	0.276 ± 0.331	0.405
(e) NO: Time exploring object [2]	Date of birth within season	2.497	1	0.204 ± 0.129	0.114
	Age class at testing [old]	3.007	1	–0.518 ± 0.299	0.083
	Sex [m]	0.025	1	0.052 ± 0.328	0.873
	Food plant abundance at testing	6.700	1	0.373 ± 0.144	**0.010**
	Test sequence [2nd]	6.810	3	–0.319 ± 0.155	0.078
	[3rd]			0.013 ± 0.304	
	[4th]			0.284 ± 0.345	
	Year [2nd]	4.806	1	–0.535 ± 0.244	**0.028**
(f) NO: Number of objects explored	Date of birth within season	1.264	1	0.091 ± 0.081	0.261
	Age class at testing [old]	3.199	1	–0.351 ± 0.196	0.074
	Sex [m]	0.445	1	0.141 ± 0.211	0.505
	Food plant abundance at testing	3.252	1	0.170 ± 0.094	0.071
	Test sequence [2nd]	1.894	3	–0.146 ± 0.111	0.595
	[3rd]			–0.135 ± 0.195	
	[4th]			–0.062 ± 0.217	
	Year [2nd]	2.164	1	–0.232 ± 0.158	0.141

[1] square-root transformation of dependent variable

[2] log [x + 1] transformation of dependent variable

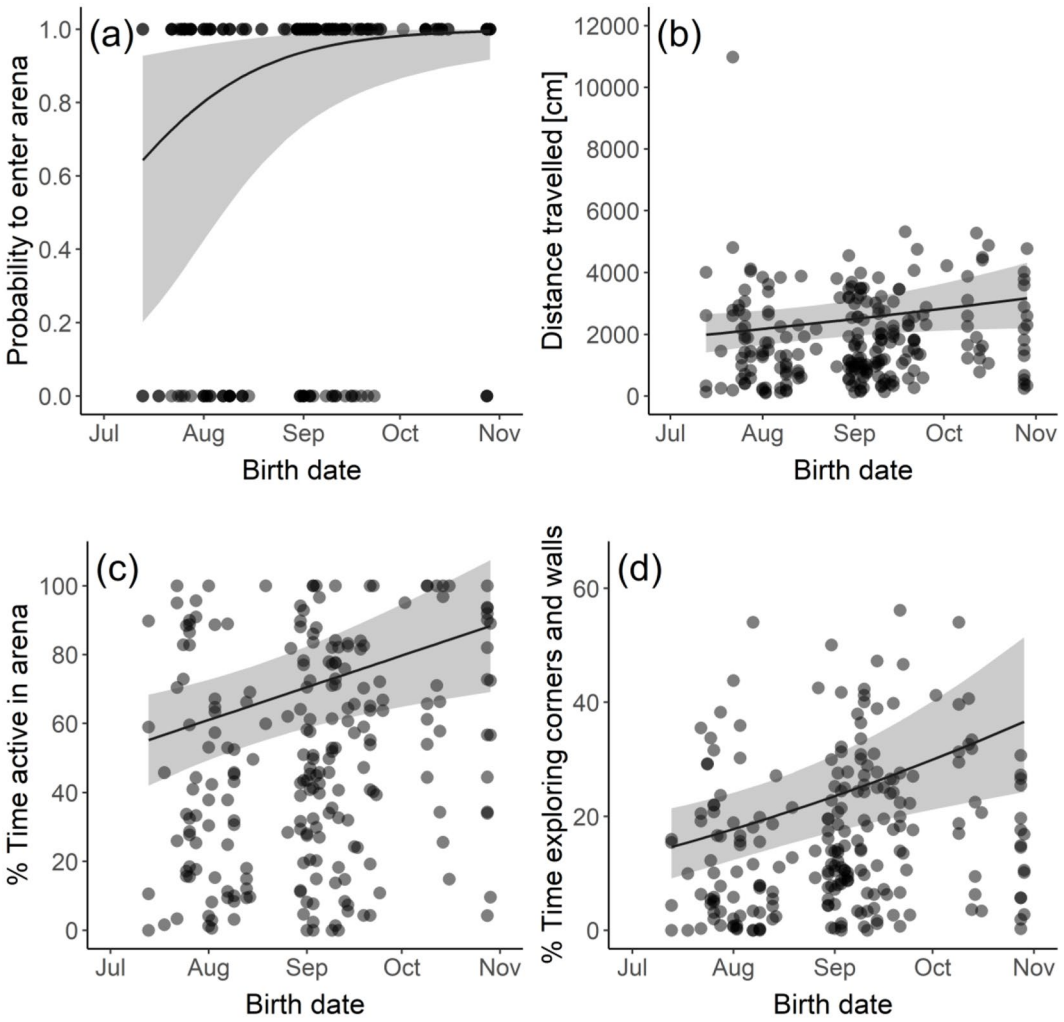

Fig. 3 Effects of birth date within the breeding season on different behavioral traits in the bush Karoo rat. All effects presented here are statistically significant. Regression lines (including 95% confidence intervals given as grey shadings) are based on parameter estimates as given in Table 3

in the arena (Table 2b) and spent a higher % time being active (Table 2c). We also found highly significant effects of the test sequence (number of tests the individuals had experienced, range from 0 to 3) regarding the distance travelled, the % time active, and the % time of exploring walls and corners in the open field arena (Table 2b-d). Post hoc comparisons revealed that for these three parameters, the values were significantly higher during the first test compared to all subsequent test sessions (post-hoc statistics in Fig. A in Suppl. Material).

Personality-specific reproduction of early-born females

Out of 84 females tested, 9 (10.7%) had already reproduced in the breeding season of their birth. All reproducing females were born early in the breeding season, during in the first 3 weeks of the season in 2022 and during the first 5 weeks of the season in 2023.

There were no significant associations between any of the six behavioral variables in early-born females (birth dates during the first 5 weeks of the breeding season, $n = 27$), and the probability of reproduction during the same season (GLMM for binomial data, all $P > 0.50$; see details in Table B in Suppl. Materials).

Discussion

We studied whether the date of birth during the breeding season affects personality in a seasonally breeding rodent, the bush Karoo rat. We hypothesized that individuals born later in the season should adopt a more proactive personality because such a behavioral type would be advantageous for finding/building their own stick lodges. This was confirmed

by our findings: later-born individuals were bolder and more active and explorative in behavioral tests, suggesting a more proactive personality in these rats than in those born earlier. We did not find support that proactivity has evolved to support reproduction in early-born females because females that reproduced within the season of their birth did not show higher proactivity compared to females that did not reproduce within the same season. Finally, while food abundance decreased from the moist breeding season to dry non-breeding season, this did not affect the proactive responses.

Individuals displayed higher levels of some behaviors during the first test compared to all subsequent tests (Suppl. Material, Fig. A), even in three behavioral parameters which were notably repeatable over time. Such decreases in the expression of behaviors related to activity and exploration is frequently explained by the animals' habituation to the test arena, i.e. learning about its structural elements, thus leading to a loss of motivation to explore (Bolivar et al. 2000; Salomons et al. 2010). Accordingly, a study in laboratory mice showed that the introduction of novel, tactile cues during repeated open-field testing could prevent such decreases in behaviors indicative of exploration (Chen et al. 2023). In contrast, in our setting, the open field arena constituted a novel environment only during the first trial, triggering comparatively higher levels of exploration-related behaviors. Nevertheless, as shown in our study, such an initial change in population-level test responses over the first two test sessions does not call into question the existence of consistent individual rank differences in personality. Similar findings have been reported in other studies conducting behavioral phenotyping in small mammals, frequently showing notably higher or lower responses (dependent on the kind of test) during the first test repeat compared to subsequent ones (Võikar et al. 2004; Matsunaga and Watanabe 2010; Lewejohann et al. 2011).

Despite such changes over time in the absolute levels of some of the behaviors considered, we found consistent individual differences in measurements of activity, boldness and exploration as well as significant associations between these different variables, confirming findings obtained in other small mammals under field conditions (e.g., Lantová et al. 2011; Eccard and Herde 2013). Individuals in our study that were more active were also bolder and more explorative, suggesting a behavioral syndrome which we describe as "proactivity" (Koolhaas et al. 1999). Similar associations have been reported in other small mammals under field conditions; for example, more exploratory European rabbits (*Oryctolagus cuniculus*) were bolder during early age, and were less sociable and tended to be more aggressive as subadults (Rödel et al. 2015). Furthermore, bent-wing bats (*Miniopterus fuliginosus*) showed positive associations between traits reflecting boldness, activity and exploration, described by the authors as 'proactiveness' (Kuo et al. 2024).

The main hypothesis of our study, that later-borns are more proactive, was based on the assumption that such individuals face more intense competition for stick lodges, a critical and limiting resource for survival in their harsh ambient environment. As it is typical for a short-lived seasonal breeder, population density of bush Karoo rat peaks during the late breeding season, and such a high population density has the potential to negatively affect resource availability (White 2008). Accordingly, in our study, we found a sharp rise in population density during the course of the breeding season and an associated and notable decrease in stick lodge availability. Although there was always more than one lodge available per adult, lodges differed in their quality, such that the availability of large high-quality lodges decreased to below one lodge per adult by the end of the breeding season. The availability of smaller lodges was higher but they were usually less steady and in poor condition, thus needing a higher investment in building and repairing. The emergence of new lodges during both seasons suggests that the existing lodges were not able to meet the demand of the increasing population. Thus, stick lodges clearly represented a limited resource at the end but not at the start of the breeding season.

Individuals born at high population density during the late breeding season can be expected to be at a disadvantage at locating and occupying vacant stick lodges. Due to their young age and relatively small body size, they can be expected to be less competitive than older and larger individuals born earlier. As a result, they would need to invest in either finding unoccupied lodges or building their own ones, and both would require travelling and exploring a broader range of their habitat. In support, a link between increased space use and a more proactive personality has been found in North American red squirrels (*Tamiasciurus hudsonicus*) in which individuals with higher activity levels in standardized tests were re-trapped over a larger range of the study site (Boon et al. 2008). Under field conditions, the trait combination of being more exploratory and more active, as found in our study (see also Perals et al. 2017), could contribute to an increased efficiency in searching for stick lodges or of building materials. Thus, being more proactive could be beneficial in later-born individuals in response to the increasing difficulty of acquiring stick lodges.

The life history of bush Karoo rats allows individuals born early to have the chance for precocious reproduction within the same season. In our study, precocious reproduction occurred in 10.7% ($n = 9$) of the females, which is lower than in some other seasonally breeding rodents or lagomorphs (greater Guinea pig *Cavia magna*: 18.8%, Kraus

et al. 2005; European rabbits in a Mediterranean habitat: 18.6%, Soriguer 1981). In our study, females reproducing during their season of birth were born relatively early, all before the middle of the breeding season. However, when only considering early born females, we did not find support for a higher proactivity associated with precocious reproduction. In addition, females born early, i.e. the ones that had an opportunity to reproduce, were generally less proactive than those born later during the season (see Fig. 3).

We suggest that the emergence of a lower proactivity in earlier-born bush Karoo rats has possibly evolved due to ecological constraints. Our study population experiences a short breeding season and individuals have to survive a long dry season thereafter. Such a harsh environment could limit the benefits of precocious reproduction. Reproducing at young age can even have negative fitness consequences on both the first litters and the mothers (Lambin and Yoccoz 2001; Rödel et al. 2023), and furthermore a more proactive personality has negative consequences on survival (Smith and Blumstein 2008; Cole and Quinn 2011), for example through increased predation risk (Rödel et al. 2015; Denoël et al. 2019). Even though earlier-born females may benefit from being proactive in competition for reproductive resources, the survival impact might decrease the general fitness of both the young females and their litters to below the threshold for surviving the extremely harsh non-productive period. As a result, the benefit of being proactive may depend on the time of birth during the breeding season: for earlier-born individuals, being a proactive breeder may not be adaptive due to the harsh ecological environments, while for later-borns, the scarcity of life-critical resources (stick lodges) makes the risk of being proactive worthwhile in exchange of better chances in acquiring stick lodges.

In conclusion, our study presents an example of personality differences in association with a key life history trait, the timing of birth within the season. Bush Karoo rats born later in the season showed higher proactivity and we suggest that such an association has evolved in response to the availability of survival resources, particularly the reduced availability of vacant stick lodges. Being more active, bolder, and more exploratory could be adaptive under such conditions because it could help later-borns explore more habitat to find unoccupied lodges or building materials. Our study highlights the importance of investigating not only reproduction opportunity, but also potential survival challenges to better understand the diverse mechanisms underlying the integration between life history and behavioral traits.

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Author contributions JQ, HGR and CS conceived the study. Data collection was performed by JQ and LM, data analysis was performed by JQ and HGR. The first draft of the manuscript was written by JQ and HGR, all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability All data generated or analysed during this study are included in this article and the electronic supplementary material.

Declarations

Ethics approval The study was conducted according to accepted international standards regarding the guidelines for the use of animals in behavioral research (Vitale et al. 2018), and the legal requirements (Sect. 20 permit) of South Africa, where the study was carried out. Ethical clearance (2022/05/02B) was provided by the Animal Research and Ethics Committee of the University of the Witwatersrand, Johannesburg, South Africa. No injuries or mortalities occurred in any study animals; all individuals were successfully released at the exact sites from where they were trapped.

Competing interests The authors declare no conflicts of interest.

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