



**HAL**  
open science

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

Jingyu Qiu, Neville Pillay, Carsten Schradin, Lindelani Makuya, Heiko G Rödel

► **To cite this version:**

Jingyu Qiu, Neville Pillay, Carsten Schradin, Lindelani Makuya, Heiko G Rödel. Higher proactivity in later-borns: effects of birth date on personality in a small mammal. *Behavioral Ecology and Sociobiology*, 2024, 78 (12), pp.124. 10.1007/s00265-024-03531-x . hal-04833533

**HAL Id: hal-04833533**

**<https://cnrs.hal.science/hal-04833533v1>**

Submitted on 12 Dec 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 Higher proactivity in later-borns: effects of birth date on  
2 personality in a small mammal  
3

4 **Published as:**

5 Qiu, J., N. Pillay, **C. Schradin**, L. Makuya & H. G. Rödel (2024) Higher proactivity in  
6 later-borns: effects of birth date on personality in a small mammal. *Behavioral*  
7 *Ecology and Sociobiology*, **78**, 124.

8

9 Jingyu Qiu<sup>1,2\*</sup>, Neville Pillay<sup>1</sup>, Carsten Schradin<sup>1,2</sup>, Lindelani Makuya<sup>1</sup>, Heiko G.

10 Rödel<sup>3</sup>

11 <sup>1</sup>School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, South Africa

12 <sup>2</sup> Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France

13 <sup>3</sup>Laboratoire d'Ethologie Expérimentale et Comparée UR 4443 (LEEC), Université Sorbonne Paris Nord,  
14 F-93430 Villetaneuse, France

15

16 \*Corresponding author. Jingyu Qiu

17 Email: [jqingyuqiu@gmail.com](mailto:jqingyuqiu@gmail.com)

18 Jingyu Qiu: <https://orcid.org/0000-0002-6993-2549>

19 Neville Pillay: <https://orcid.org/0000-0002-0778-726X>

20 Carsten Schradin: <https://orcid.org/0000-0002-2706-2960>

21 Lindelani Makuya: <https://orcid.org/0000-0002-2986-1627>

22 Heiko G. Rödel: <https://orcid.org/0000-0003-0228-2884>

23

24 **Acknowledgments**

25 This study is made possible by the administrative and technical support of the Succulent  
26 Karoo Research Station (registered South African NPO 122-134). We are thankful to Siya  
27 Sangweni and several research assistants for managing the field site, marking, trapping  
28 and monitoring the bush Karoo rats. We are also grateful to two anonymous reviewers  
29 for their constructive comments.

30 **Significance statement**

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

42

43 **Abstract**

44 In short-lived animals, individuals born earlier in the breeding season frequently  
45 reproduce within the season of birth. Consequently, it has been proposed that those born  
46 early benefit from a more proactive behavioral type to compete for reproductive  
47 opportunities whereas later-borns adopt a more reactive personality to conserve energy to  
48 survive through the non-breeding season and reproduce in the following year. However,  
49 being proactive could also benefit later-borns in acquiring decreasing resources in the late  
50 breeding season. We investigated personality differences depending on the date of birth  
51 in relation to resource variation in a free-living population of the bush Karoo rat (*Otomys*  
52 *unisulcatus*). This species constructs stick lodges, a critical resource protecting the rats  
53 from the harsh semi-desert environments, but the availability of vacant lodges decreases

54 with increasing population density during the breeding season. We predicted an increased  
55 occurrence of proactive phenotypes during the later breeding season, contrasting with the  
56 commonly assumed decrease in proactive phenotypes in late season due to lack of  
57 reproductive opportunity. We behaviorally phenotyped  $n = 99$  individuals through  
58 repeated behavioral tests and found consistent individual differences along a proactive-  
59 reactive gradient. Most importantly, later-borns showed greater activity, boldness and  
60 exploration tendencies, indicating a more proactive personality. In addition, among early-  
61 born females, individuals which reproduced showed no differences in personality  
62 compared to those which did not reproduce. Our results indicate that seasonal differences  
63 in personality types in the bush Karoo rat may be driven by resource constraints in the  
64 late season rather than by differences in reproduction opportunities.

65

66 *Keywords:* behavioral phenotype, consistent individual differences, *Otomys*, pace-of-life  
67 syndrome

68 **Introduction**

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

81 Over the past decade, behavioral studies have gained a deeper understanding of  
82 consistent individual differences (animal personality), how these are maintained and  
83 their association with life history (Réale et al. 2007; Biro and Stamps 2008). The pace-  
84 of-life syndrome proposes that the trade-off between current versus future reproduction  
85 leads to differences in behavioral traits (Réale et al. 2010; Dammhahn et al. 2018): in  
86 seasonal breeding rodents, individuals born early which have an opportunity to  
87 reproduce within the season of birth, should benefit from an active and risk-taking  
88 personality that could be advantageous when acquiring resources needed for  
89 reproduction. In contrast, being less bold and less risk-taking may be more adaptive for  
90 later-borns because such a personality type will contribute to saving energy, increasing  
91 the probability of surviving through the non-breeding season until they can reproduce in

92 the following year (Gracceva et al. 2014). Such an association between personality and  
93 the timing of birth has been reported, for example, in eastern chipmunks (*Tamias*  
94 *striatus*), in which birth cohorts with early reproductive opportunities were faster  
95 explorers than those reproducing at a later age (Montiglio et al. 2014). Similarly, in  
96 European shags (*Phalacrocorax aristotelis*), chicks hatched early in the breeding season  
97 had higher social ranks and showed higher levels of aggression compared to those  
98 hatched later (Velando 2000). However, another study suggests a differential  
99 association between personality and timing of birth: in short-lived common voles  
100 (*Microtus arvalis*); individuals captured in spring (mostly late-born cohorts from the  
101 previous year) were bolder than those captured at other times of the year (Eccard and  
102 Herde 2013). This contradiction among different studies suggests the necessity to  
103 investigate the effect of seasonal environmental factors, which may contribute to  
104 explain the emergence of differences in behavioral types between different seasonal  
105 birth cohorts.

106       Apart from reproductive trade-offs that underly the pace-of-life continuum,  
107 ecological conditions can also be important drivers of personality (Dammhahn et al.  
108 2018; Jablonszky et al. 2018; Montiglio et al. 2018). Individuals with proactive  
109 phenotypes are usually more successful in competing for resources (Sih et al. 2004;  
110 Smith and Blumstein 2008). During the late breeding season, resource availability  
111 typically declines, while population density increases at the same time. Being proactive  
112 can be beneficial for individuals born late in the season in competition for limited  
113 resources. Therefore, two alternative hypotheses exist: (1) early-borns are more  
114 proactive to acquire enough resources for reproduction *versus* (2) late-borns are more  
115 proactive to acquire enough resources for survival. Therefore, to understand the

116 association between personality and the birth timing, further investigations, preferably  
117 under natural conditions are necessary.

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

134 Our aim was to investigate the effect of the date of birth on personality in adult bush  
135 Karoo rats. First, we studied whether free-living bush Karoo rats show consistent  
136 personality traits in activity, boldness and exploration behavior. Next, considering the  
137 potential effects of increasing population density on the availability of stick lodges, we  
138 predicted that such personality traits would be associated with birth timing, as later-  
139 borns would adopt a more proactive (active, bold and/or explorative) behavioral type.



140 Finally, we studied whether there was a seasonal change in behavior, specifically  
141 whether the proactive response decreased in the food restricted dry season when  
142 compared to the food rich moist season. We conducted a field study over two years  
143 (2022 - 2023) and repeatedly quantified six behavioral parameters related to three  
144 different behavioral personality traits, activity, boldness and exploration (sensu Réale et  
145 al. 2007), which was compared between individuals born earlier and later during the  
146 breeding season.

147 **Materials and Methods**

148 *Study site and study population*

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

161 The study was conducted in the Goegap Nature Reserve, Northern Cape Province,  
162 South Africa. The field site in the semi-arid Succulent Karoo (Cowling et al. 1999) is  
163 characterized by an annual rainfall of 160 mm/year on average, and by temperatures  
164 varying from -1.5 to 24 °C during winter and from 4 to 42 °C during summer (weather  
165 station at the field site). Most of the rainfall occurs in winter, creating abundant  
166 vegetation that supports the onset of reproductive activity in our study population  
167 (Wolhuter et al. 2021). The field site for the study is approximately 4.5 ha.

168

169 *Stick lodge surveys*

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

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

183

#### 184 *Trapping and individual tagging*

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

194 At first capture, bush Karoo rats were individually marked with aluminum band ear  
195 tags in both ears (0.25 g per tag) with a unique individual number (National Band and  
196 Tag Co., Newport, KY, USA). During re-trapping, we always checked for infections at  
197 the ear tags, which would have resulted in the removal of the tag on the affected ear;  
198 such cases never occurred during the study period. Birth date was estimated from the  
199 animals' body mass, based on the linear association between age and body mass in the  
200 bush Karoo rat as published in Pillay (2001). Trapping data used for our study spanned  
201 from 1<sup>st</sup> January 2022 to 14<sup>th</sup> December 2023. When a female born within the season  
202 showed signs of pregnancy/lactation (palpable embryos at late pregnancy stage;  
203 lactation as evident by the developmental stage of the mammary glands), or when a  
204 female had dependent young (as evident by juveniles trapped at the same stick lodge  
205 prior to the next breeding season), this female was considered as having reproduced  
206 during the season of birth ('precocious reproduction').

207

#### 208 *Assessment of changes in population density*

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

218 observations (described in Makuya et al. 2024), enabling us to identify occupied lodges  
219 and unmarked juveniles.

220

### 221 *Experimental procedure*

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

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

238 As was evident from our trapping data, females usually disperse for shorter distances  
239 and therefore were more likely be continually caught using our trapping protocol. Thus,  
240 in the first year, the selection of focal individuals was limited to females and included  
241 four behavioral test replicates. In the second year, both males and females were selected

242 as focal individuals. However, due to time constraints, the rats underwent only the first  
243 and second behavioral tests in the second year. Due to unpredictable field conditions,  
244 trapping of focal individuals was not always successful, which led to delays for repeated  
245 behavioral tests in some cases. The average age for “young” adults (at the 1<sup>st</sup> and 2<sup>nd</sup>  
246 test) was 54 days, and the average age for “older” adults (at the 3<sup>rd</sup> and 4<sup>th</sup> test) was 151  
247 days. Because our study involved individually-marked focal animals, the  
248 experimenter(s) were not naive to individual identities during testing.

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

256 During the first year (2022), we tested a total of 56 individuals, out of which 37  
257 individuals were successfully trapped and underwent the last two (3<sup>rd</sup> and 4<sup>th</sup>) tests as  
258 older adults: 19 of them underwent all four tests (i.e. two times during older adult stage  
259 and two times during young adult stage), eight individuals were tested three times (i.e.  
260 two times during older adult stage and one time during young adult stage), and 10  
261 individuals were only tested two times (i.e. two times during older adult stage). This  
262 was not the case for 19 individuals that had disappeared prior to the last testing during  
263 older adult stage. During the second year (2023), we tested a total of 43 individuals, out  
264 of which 29 underwent all two tests; note that during the second year, we only carried  
265 out two tests during the younger adult stage (see details above). The remaining 14

266 individuals could only be trapped and tested for the 1<sup>st</sup> test. Overall, out of the total of  
267 99 individuals tested in 2022 and 2023, 66 individuals did not disappear prior to the end  
268 of the testing.

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

#### 274 *Behavioral tests*

275 One to a maximum of four individuals were trapped for behavioral tests per day. A  
276 white chamber (100 cm long, 85 cm wide and 65 cm high) made of melamine panels  
277 was used as a test arena (Fig. 1). Before introducing a new individual into the arena, the  
278 arena was always thoroughly cleaned using 95% alcohol and air dried. All tests were  
279 video-recorded and later analyzed using the software BORIS (Friad and Gamba 2016)  
280 and Single Mouse Tracker (Icy software, De Chaumont 2012). Focal individuals  
281 underwent three successive behavioral tests directly after the morning trapping. To  
282 minimize observer bias, blinded methods were used when all behavioral data were  
283 recorded and/or analyzed.

284 *Starting box*– This part of the apparatus (the starting box) consisted of a 10 cm<sup>3</sup> black  
285 acrylic and opaque square box with one side that could be opened (door) and a lid at the  
286 other side. The open side was directly attached to the test arena and separated by a  
287 closed door (Fig. 1a). After individuals were placed into the starting box via the lid,  
288 they were allowed to calm down for 3 min in the closed box. Then the door was opened  
289 and we recorded whether the animal entered the test arena in the following 10 min. If

290 the animal did not enter the arena within this time, it was gently nudged in using a  
291 plastic ruler ( $2 \times 30$  cm) by reaching into the box through the lid. Once the individual  
292 had entered the arena, the door was closed to prevent its return into the starting box.

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

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

306 After the open field test was completed, the animal remained in the arena and was  
307 confined again by the experimenter using the same black acrylic square box. The box  
308 was attached to a fixed pulley system so it could be lifted to release the individual with  
309 minimum disturbance. The focal individual was first placed in the center of the arena  
310 while covered by the box. Then, four identical hollow metal, egg-shaped sieve balls ( $4.5$   
311  $\times 3.9$  cm, steel) providing the same novel odors were placed inside the arena, 10 cm  
312 away on the extended diagonal of the black box (see Fig. 1b). The source of odor used  
313 in the 1<sup>st</sup> test was orange peel, tomato sauce was in the 2<sup>nd</sup> test (two weeks later), peanut



314 butter was used in the 3<sup>rd</sup> test and strawberry jam in the 4<sup>th</sup> test. After setting up the  
315 arena, the rat was allowed to calm down for 5 min inside the box, then the box was  
316 lifted and the individual was given 5 min to explore the four metal balls. We recorded  
317 two behavioral parameters: (1) the time the animal spent exploring the objects, defined  
318 as the total (summed-up) duration the individual sniffed or touched one of the four tea  
319 balls; and (2) the number of objects explored, defined as the total number of tea balls,  
320 which were sniffed or touched by the individual during the test (range from 0 – 4).

321

### 322 *Quantification of seasonal food abundance*

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

### 332 *Statistical analysis and sample sizes*

333 In total, 99 individuals ( $n_{\text{males}} = 15$ ,  $n_{\text{females}} = 84$ ) were tested in 226 behavioral tests.  
334 We considered potential effect of multiple test replicates per individuals, as such  
335 repeated testing may lead to habituation effects (Salomons et al. 2010). The sample  
336 sizes available during the different test replicates (hereafter referred to as “test

337 sequence”), see more details above, in the last paragraph of section “Experimental  
338 procedure”.

339 Statistical analyses were carried out in R, version 4.3.0 (R Core Team 2023). In the  
340 first step, we checked for repeatabilities of the six behavioral variables quantified in the  
341 starting box test, open field test and in the novel odor test, across the four different test  
342 sessions, as well as for associations between these behavioral variables. All six response  
343 variables (behavioral variables, given in Table 1) were scaled for analysis. This analysis  
344 (with  $n = 99$  individuals) was done using a single, multivariate generalized linear  
345 mixed-effects model GLMM (i.e., with six response variables) based on the R package  
346 *MCMCglmm* (Hadfield 2010). The predictors were year and sex (2 levels each) and test  
347 sequence (number of tests the individual has done before, 4 levels), with random effects  
348 for individual ID. We applied a weakly informative prior, allowing the data to primarily  
349 inform the posterior distributions. One chain was run with 100,000 iterations. The first  
350 5,000 iterations were discarded as burn-in, and every 100<sup>th</sup> iteration was retained  
351 (thinning interval = 100), resulting in 950 samples per chain. The response variables  
352 followed appropriate distributions: a categorical distribution for the latency to enter the  
353 arena, poisson distribution for the number of objects explored (count variable from 0 to  
354 4), and Gaussian distribution (after some transformations, see details below Table 1) for  
355 the remaining four continuous behavioral variables. As the early disappearance of some  
356 animals prior to the completion of the four test sessions in the year 2022 or of the two  
357 test sessions in 2023 may have potentially created a calculation bias, we repeated the  
358 analysis by a multivariate GLMM with a subsample of  $n = 66$  animals (out of the  
359 original  $n = 99$  individuals) which were still present (i.e. trapped and tested) during the  
360 last test sessions of both years of study. See more details above, in the section

361 “Experimental procedure”. However, this more conservative analysis revealed highly  
362 similar findings, as presented in Tables B, C in Suppl. Materials.

363 Repeatabilities across the (up to) four repeated tests per behavioral parameter (see  
364 Table 1) and pair-wise correlation coefficients between the different behaviors (see  
365 Table 3) were calculated based on the within-individual and among-individual variance  
366 matrices provided by this model. Associations between the different behavioral  
367 variables were considered statistically significant ( $P < 0.05$ ) when the 95% Bayesian  
368 credible intervals of the correlation coefficients ( $R$ ) did not overlap zero (Houslay and  
369 Wilson 2017). However, in case of repeatabilities over time, as per definition only non-  
370 negative values can be obtained and thus the 95% credible intervals cannot overlap zero,  
371  $P$ -values could not be calculated based on the above-mentioned method (Houslay and  
372 Wilson 2017). Consequently, our inference on repeatabilities was only based on  
373 interpretation of the 95% credible intervals. We calculated the overall (long-term)  
374 repeatability, based on all (up to) four behavioral tests of our 99 focal individuals over  
375 all age classes (young adult at first and second tests, older adult at third and fourth tests;  
376  $n = 226$  measurements for each behavioral variable), as well as short-term repeatability,  
377 based on the first two behavioral tests for 99 young adults with a total of  $n = 145$   
378 measurements for each behavioral variable.

379 In the second step, we tested the effects of the date of birth (covariate, 1<sup>st</sup> July as  
380 baseline; see the rather consistent distribution of birth dates along the season in Fig. 2)  
381 on the six different behavioral variables (see Table 3). Therefore, using the R package  
382 *lme4* (Bates et al. 2015), we applied separate models - a generalized linear mixed-  
383 effects model (GLMM) for binomial data with a logit link for the probability to enter  
384 the test arena (see Table 3a), and linear mixed-effects models (LMM) for all remaining

385 (continuous) behavioral variables (see Table 3b-f). To obtain a normal distribution of  
386 model residuals (verified by visually checking normal probability plots) and  
387 homogeneity of variances (by plotting residuals versus fitted values) for LMMs, we  
388 square-root transformed the distance travelled and the % time the animals spent  
389 exploring the walls and corners of the arena, and  $\log [x+1]$  transformed the time the  
390 animal spent exploring the object in the novel odor test. Individual identity was always  
391 included as a random (intercept) factor. All models included the age class at testing  
392 (“young adult” at the 1<sup>st</sup> and 2<sup>nd</sup> tests or “older adult” at the 3<sup>rd</sup> and 4<sup>th</sup> tests; 2 levels),  
393 the sex of the focal animals and the year of testing (all factors with 2 levels), the test  
394 sequence (factor with 4 levels) and the food plant abundance at testing (covariate).  
395 Because we were interested in whether possible differences between earlier- and later-  
396 born individuals were only apparent in young adults or in older adult individuals, we  
397 also tested the 2-way interaction between date of birth and age class. When non-  
398 significant, this interaction was removed from the models and these were recalculated  
399 (Engqvist 2005). *P*-values were calculated by type-3 Wald chi-square tests (Bolker et al.  
400 2009).

401 We also tested whether the behavioral responses of early-born females (i.e., females  
402 born until/including the 5<sup>th</sup> week of the breeding season, when the last reproducing  
403 female was born) in the different tests were associated with their actual reproductive  
404 activity during their season of birth. Using the R package *lme4* (Bates et al. 2015), we  
405 applied GLMMs for binomial data with a logit link using the same transformations for  
406 some of the behavioral variables (now used as predictors in our model) as described  
407 above. Each model included one behavioral variable, and all included year of testing (2

408 levels) as fixed variance. Individual identity was always included as a random  
409 (intercept) factor. Also, *P*-values were calculated by type-3 Wald chi-square tests.

410 **Results**

411 *Seasonal differences in population density and stick lodge availability*

412 In both years of the study, the adult population density showed dramatic variation  
413 between the breeding/non-breeding seasons. Population density increased during the  
414 breeding season from July to January by 120.7% on average. Specifically, during the  
415 first year of study (Jul 2022 – Jan 2023), the adult density increased by 81.4% from 12.6  
416 to 23.4 individuals/ha, and during the second year (Jul 2023 – Jan 2024), it increased by  
417 160% from 6.5 to 16.9 individuals/ha. However, the population also dramatically  
418 decreased during the non-breeding season by 72.0% between January to July 2023.

419 In the breeding season starting in July 2022, 172 old lodges (i.e. existing ones) were  
420 available and 26 new lodges were built. The availability of old lodges decreased during  
421 the breeding season, from 3.1 to 1.6 lodges/adults from July 2022 to January 2023. In  
422 the breeding season starting in July 2023, 194 old lodges were available and 9 new  
423 lodges were built. The availability of old lodges decreased from 6.9 to 1.8 lodges/adults  
424 from July 2023 to January 2024. When only considering the large lodges with a height  
425 above 50 cm, which can be assumed to be the most valuable resource, this seasonal  
426 difference was more pronounced. The availability of such large lodges decreased from  
427 0.8 per adult individual to 0.4 in 2022/2023, and from 1.7 to 0.4 in 2023/2024.

428

429 *Pattern of seasonal reproduction*

430 We quantified the temporal distribution of reproductive events during the breeding  
431 season using the estimated dates of birth of the juveniles trapped, based on a sample of  
432  $n = 226$  juveniles (129 born in 2022 and 97 born in 2023, Fig. 2). The annual start of the  
433 reproductive season was determined by the occurrence of at least three juveniles born

434 on different dates within a week (i.e., apparently from different litters), revealing a  
435 highly similar onset of the reproductive season between the two years of study (2022:  
436 19<sup>th</sup> July; 2023: 14<sup>th</sup> July). In 2022, the mean date of birth was on 29<sup>th</sup> August, and  
437 during the reproductive season in 2023, it was on 8<sup>th</sup> September.

438

#### 439 *Consistent individual differences in behavior*

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

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

454 We also found significant associations among the parameters recorded in the starting  
455 box test and open field test. Specifically, the probability to enter the arena, the distance  
456 travelled, the % time the animals showed activity and the % time the animals spent

457 exploring the walls and corners of the open field arena were positively and significantly  
458 correlated at the between-individual level (Table 2).

459 *Effects of birth date on personality traits*

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

473 In two parameters measured in the open field, we found significant sex differences;  
474 males travelled a longer distance in the arena (Table 3b) and spent a higher % time  
475 being active (Table 3c). We also found highly significant effects of the test sequence  
476 (number of tests the individuals had experienced, range from 0 - 3) regarding the  
477 distance travelled, the % time active, and the % time of exploring walls and corners in  
478 the open field arena (Table 3b-d). Post hoc comparisons revealed that for these three  
479 parameters, the values were significantly higher during the first test compared to all  
480 subsequent test sessions (post-hoc statistics in Fig. A in Suppl. Material).



481 *Personality-specific reproduction of early-born females*

482       Out of 84 females tested, 9 (10.7%) had already reproduced in the breeding season of  
483 their birth. All reproducing females were born early in the breeding season, during in  
484 the first 3 weeks of the season in 2022 and during the first 5 weeks of the season in  
485 2023.

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

490

491

492 **Discussion**

493 We studied whether the date of birth during the breeding season affects personality in  
494 a seasonally breeding rodent, the bush Karoo rat. We hypothesized that individuals born  
495 later in the season should adopt a more proactive personality because such a behavioral  
496 type would be advantageous for finding/building their own stick lodges. This was  
497 confirmed by our findings: later-born individuals were bolder and more active and  
498 explorative in behavioral tests, suggesting a more proactive personality in these rats  
499 than in those born earlier. We did not find support that proactivity has evolved to  
500 support reproduction in early-born females because females that reproduced within the  
501 season of their birth did not show higher proactivity compared to females that did not  
502 reproduce within the same season. Finally, while food abundance decreased from the  
503 moist breeding season to dry non-breeding season, this did not affect the proactive  
504 responses.

505 Individuals displayed higher levels of some behaviors during the first test compared  
506 to all subsequent tests (Suppl. Material, Fig. A), even in three behavioral parameters  
507 which were notably repeatable over time. Such decreases in the expression of behaviors  
508 related to activity and exploration is frequently explained by the animals' habituation to  
509 the test arena, i.e. learning about its structural elements, thus leading to a loss of  
510 motivation to explore (Bolivar et al. 2000; Salomons et al. 2010). Accordingly, a study  
511 in laboratory mice showed that the introduction of novel, tactile cues during repeated  
512 open-field testing could prevent such decreases in behaviors indicative of exploration  
513 (Chen et al. 2023). In contrast, in our setting, the open field arena constituted a novel  
514 environment only during the first trial, triggering comparatively higher levels of  
515 exploration-related behaviors. Nevertheless, as shown in our study, such an initial

516 change in population-level test responses over the first two test sessions does not call  
517 into question the existence of consistent individual rank differences in personality.  
518 Similar findings have been reported in other studies conducting behavioral phenotyping  
519 in small mammals, frequently showing notably higher or lower responses (dependent on  
520 the kind of test) during the first test repeat compared to subsequent ones (Võikar et al.  
521 2004; Matsunaga and Watanabe 2010; Lewejohann et al. 2011).

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

535 The main hypothesis of our study, that later-borns are more proactive, was based on  
536 the assumption that such individuals face more intense competition for stick lodges, a  
537 critical and limiting resource for survival in their harsh ambient environment. As it is  
538 typical for a short-lived seasonal breeder, population density of bush Karoo rat peaks  
539 during the late breeding season, and such a high population density has the potential to

540 negatively affect resource availability (White 2008). Accordingly, in our study, we  
541 found a sharp rise in population density during the course of the breeding season and an  
542 associated and notable decrease in stick lodge availability. Although there was always  
543 more than one lodge available per adult, lodges differed in their quality, such that the  
544 availability of large high-quality lodges decreased to below one lodge per adult by the  
545 end of the breeding season. The availability of smaller lodges was higher but they were  
546 usually less steady and in poor condition, thus needing a higher investment in building  
547 and repairing. The emergence of new lodges during both seasons suggests that the  
548 existing lodges were not able to meet the demand of the increasing population. Thus,  
549 stick lodges clearly represented a limited resource at the end but not at the start of the  
550 breeding season.

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

563 materials. Thus, being more proactive could be beneficial in later-born individuals in  
564 response to the increasing difficulty of acquiring stick lodges.

565 The life history of bush Karoo rats allows individuals born early to have the chance  
566 for precocious reproduction within the same season. In our study, precocious  
567 reproduction occurred in 10.7% ( $n = 9$ ) of the females, which is lower than in some  
568 other seasonally breeding rodents or lagomorphs (greater Guinea pig *Cavia magna*:  
569 18.8%, Kraus et al. 2005; European rabbits in a Mediterranean habitat: 18.6%, Soriguer  
570 1981). In our study, females reproducing during their season of birth were born  
571 relatively early, all before the middle of the breeding season. However, when only  
572 considering early born females, we did not find support for a higher proactivity  
573 associated with precocious reproduction. In addition, females born early, i.e. the ones  
574 that had an opportunity to reproduce, were generally less proactive than those born later  
575 during the season (see Fig. 3).

576 We suggest that the emergence of a lower proactivity in earlier-born bush Karoo rats  
577 has possibly evolved due to ecological constraints. Our study population experiences a  
578 short breeding season and individuals have to survive a long dry season thereafter. Such  
579 a harsh environment could limit the benefits of precocious reproduction. Reproducing at  
580 young age can even have negative fitness consequences on both the first litters and the  
581 mothers (Lambin and Yoccoz 2001; Rödel et al. 2023), and furthermore a more  
582 proactive personality has negative consequences on survival (Smith and Blumstein  
583 2008; Cole and Quinn 2011; Luna et al. 2020), for example through increased predation  
584 risk (Rödel et al. 2015; Denoël et al. 2019). Even though earlier-born females may  
585 benefit from being proactive in competition for reproductive resources, the survival  
586 impact might decrease the general fitness of both the young females and their litters to

587 below the threshold for surviving the extremely harsh non-productive period. As a  
588 result, the benefit of being proactive may depend on the time of birth during the  
589 breeding season: for earlier-born individuals, being a proactive breeder may not be  
590 adaptive due to the harsh ecological environments, while for later-borns, the scarcity of  
591 life-critical resources (stick lodges) makes the risk of being proactive worthwhile in  
592 exchange of better chances in acquiring stick lodges.

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

603

#### 604 **Declarations**

##### 605 *Ethics approval*

606 The study was conducted according to accepted international standards regarding the  
607 guidelines for the use of animals in behavioral research (Vitale et al. 2018), and the legal  
608 requirements (section 20 permit) of South Africa, where the study was carried out. Ethical  
609 clearance (2022/05/02B) was provided by the Animal Research and Ethics Committee of  
610 the University of the Witwatersrand, Johannesburg, South Africa. No injuries or

611 mortalities occurred in any study animals; all individuals were successfully released at  
612 the exact sites from where they were trapped.

613 *Funding*

614 This study was supported by a Wits-CNRS joint PhD fellowship and is part of the long-  
615 term Studies in Ecology and Evolution (SEE-Life) program of the CNRS.

616 *Competing interests*

617 The authors declare no conflicts of interest.

618 *Author contributions*

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

623 *Data availability*

624 All data generated or analysed during this study are included in this article and the  
625 supplementary information files “ESM\_2.zip”.

626

627 **References**

- 628 Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models  
629 using lme4. *J Stat Softw* 67:1–48
- 630 Biro PA, Stamps JA (2008) Are animal personality traits linked to life-history  
631 productivity? *Trends Ecol Evol* 23:361–368
- 632 Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS  
633 (2009) Generalized linear mixed models: a practical guide for ecology and evolution.  
634 *Trends Ecol Evol* 24:127–135
- 635 Boon AK, Réale D, Boutin S (2008) Personality, habitat use, and their consequences for  
636 survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos* 117:1321–  
637 1328
- 638 Bolivar VJ, Caldarone BJ, Reilly AA, Flaherty L (2000) Habituation of activity in an  
639 open field: a survey of inbred strains and F1 hybrids. *Behav Genet* 30:285–293
- 640 Brown E, Willan K (1991) Microhabitat selection and use by the bush Karoo rat *Otomys*  
641 *unisulcatus* in the Eastern Cape Province. *S Afr J Wildl Res* 21:69–75
- 642 Chen W, Wang Z, Ma C, Ma X, Meng W, Yin F, Yang Y (2023) Tactile cues are  
643 important to environmental novelty during repeated open field tests. *Behav Process*  
644 204:104796
- 645 Cole EF, Quinn JL (2011) Personality and problem-solving performance explain  
646 competitive ability in the wild. *Proc R Soc Lond B* 279:1168–1175
- 647 Cowling RM, Esler KJ, Rundel PW (1999). Namaqualand, South Africa – an overview  
648 of a unique winter-rainfall desert ecosystem. *Plant Ecol* 142:3–21



649 Dammhahn M, Dingemanse NJ, Niemelä PT, Réale D (2018) Pace-of-life syndromes: a  
650 framework for the adaptive integration of behaviour, physiology and life history.  
651 Behav Ecol Sociobiol 72:62

652 De Chaumont F, Dallongeville S, Chenouard N, Hervé N, Pop S, Provoost T, Meas-  
653 Yedid V, Pankajakshan P, Lecomte T, Le Montagner Y (2012) Icy: an open  
654 bioimage informatics platform for extended reproducible research. Nat Methods  
655 9:690–696

656 Denninger JK., Smith BM., Kirby ED (2018) Novel object recognition and object  
657 location behavioral testing in mice on a budget. J Vis Exp (141):e58593

658 Denoël M, Drapeau L, Winandy L (2019) Reproductive fitness consequences of  
659 progenesis: Sex-specific pay-offs in safe and risky environments. J Evol Biol  
660 32:629–637

661 Du Plessis A, Kerley GI, Winter PD (1992) Refuge microclimates of rodents: a surface  
662 nesting *Otomys unisulcatus* and a burrowing *Parotomys brantsii*. Acta Theriol  
663 37:351–358

664 Eccard JA, Herde A (2013) Seasonal variation in the behaviour of a short-lived rodent.  
665 BMC Ecol 13:43

666 Engqvist L (2005) The mistreatment of covariate interaction terms in linear model  
667 analyses of behavioural and evolutionary ecology studies. Anim Behav 70:967-971

668 Friard O, Gamba M (2016) BORIS: a free, versatile open-source event-logging software  
669 for video/audio coding and live observations. Methods Ecol Evol 7:1325-1330

670 Gracevea G, Herde A, Groothuis TGG, Koolhaas JM, Palme R, Eccard JA (2014)  
671 Turning shy on a winter's day: effects of season on personality and stress response in  
672 *Microtus arvalis*. *Ethology* 120:753–767

673 Hadfield JD (2010) MCMC Methods for multi-response generalized linear mixed  
674 models: the MCMCglmm R package. *J Stat Softw* 33:1–22

675 Herde A, Eccard JA (2013) Consistency in boldness, activity and exploration at  
676 different stages of life. *BMC Ecol* 13:49

677 Houslay TM, Wilson AJ (2017) Avoiding the misuse of BLUP in behavioral ecology.  
678 *Behav Ecol* 28:948-952

679 Jablonszky M, Szász E, Krenhardt K et al (2018) Unravelling the relationships between  
680 life history, behaviour and condition under the pace-of-life syndromes hypothesis  
681 using long-term data from a wild bird. *Behav Ecol Sociobiol* 72:52

682 Koolhaas JM, Korte SM, de Boer SF, van der Vegt BJ, van Reenen CG, Hopster H, de  
683 Jong IC, Ruis MAW, Blokhuis HJ (1999) Coping styles in animals: Current status in  
684 behavior and stress-physiology. *Neurosci Biobehav Rev* 23:925–935

685 Kraus C, Trillmich F, Künkele J (2005) Reproduction and growth in a precocial small  
686 mammal, *Cavia magna*. *J Mammal* 86:763–772

687 Kuo YJ, Lee YF, Kuo YM, Tai YL (2024) Sex and state-dependent effects on proactive  
688 behaviors of bent-wing bats across contexts. *Integr Org Biol* 6:obad041

689 Lambin X, Yoccoz NG (2001) Adaptive precocial reproduction in voles: reproductive  
690 costs and multivoltine life-history strategies in seasonal environments. *J Anim Ecol*  
691 70:191–200

- 692 Lantová P, Šíchová K, Sedláček F, Lanta V (2011) Determining behavioural syndromes  
693 in voles – the effects of social environment. *Ethology* 117:124–132
- 694 Lewejohann L, Zipser B, Sachser N (2011) “Personality” in laboratory mice used for  
695 biomedical research: A way of understanding variability? *Dev Psychobiol* 53:624–  
696 630
- 697 Makuya, L, Pillay N, Schradin C (2024) Kin based spatial structure in a solitary small  
698 mammal as indicated by GPS dataloggers. *Anim Behav* 215:45–54
- 699 Matsunaga W, Watanabe E (2010) Habituation of medaka (*Oryzias latipes*)  
700 demonstrated by open-field testing. *Behav Process* 85:142–150
- 701 Montiglio PO, Dammhahn M, Dubuc Messier G, Réale D (2018) The pace-of-life  
702 syndrome revisited: the role of ecological conditions and natural history on the slow-  
703 fast continuum. *Behav Ecol Sociobiol* 72:116
- 704 Montiglio PO, Garant D, Bergeron P, Messier GD, Réale D (2014) Pulsed resources and  
705 the coupling between life-history strategies and exploration patterns in eastern  
706 chipmunks (*Tamias striatus*). *J Anim Ecol* 83:720–728
- 707 Nater CR, Benthem KJ, Canale CI, Schradin C, Ozgul A (2018) Density feedbacks  
708 mediate effects of environmental change on population dynamics of a semidesert  
709 rodent. *J Anim Ecol* 87:1534-1546
- 710 Perals D, Griffin AS, Bartomeus I, Sol D (2017) Revisiting the open-field test: what  
711 does it really tell us about animal personality? *Anim Behav* 123:69–79
- 712 Pillay N (2001) Reproduction and postnatal development in the bush Karoo rat *Otomys*  
713 *unisulcatus* (Muridae, Otomyinae). *J Zool* 254:515–520

714 R Core Team (2023) R: A language and environment for statistical computing. R  
715 foundation for statistical computing, Vienna, Austria, <http://www.R-project.org>

716 Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal  
717 temperament within ecology and evolution. *Biol Rev* 82:291–318

718 Rödel HG, Ibler B, Ozogány K, Kerekes V (2023) Age-specific effects of density and  
719 weather on body condition and birth rates in a large herbivore, the Przewalski's  
720 horse. *Oecologia* 203:435–451

721 Rödel HG, Zapka M, Talke S, Kornatz T, Bruchner B, Geier C (2015) Survival costs of  
722 fast exploration during juvenile life in a small mammal. *Behav Ecol Sociobiol*  
723 69:205–217

724 Roff D (1993) *Evolution of life histories: theory and analysis*. Chapman and Hall, New  
725 York

726 Salomons AR, van Luijk JAKR, Reinders NR, Kirchhoff S, Arndt SS, Ohl F (2010)  
727 Identifying emotional adaptation: behavioural habituation to novelty and immediate  
728 early gene expression in two inbred mouse strains. *Genes Brain Behav* 9:1–10

729 Schradin C (2005) Nest-site competition in two diurnal rodents from the Succulent  
730 Karoo of South Africa. *J Mammal* 86:757–762

731 Schradin C, Pillay N (2006) Female striped mice (*Rhabdomys pumilio*) change their  
732 home ranges in response to seasonal variation in food availability. *Behav Ecol*  
733 17:452–458

734 Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and  
735 evolutionary overview. *Trends Ecol Evol* 19:372–378

- 736 Smith BR, Blumstein DT (2008) Fitness consequences of personality: a meta-analysis.  
737 Behav Ecol 19:448–455
- 738 Soriguer RC (1981) Biología y dinámica de una población de conejos (*Oryctolagus*  
739 *cuniculus* L.) en Andalucía Occidental. Doñana Acta Vertebr 8:1–379
- 740 Tkadlec E, Zejda J (1995) Precocious breeding in female common voles and its  
741 relevance to rodent fluctuations. Oikos 73:231–236
- 742 Varpe Ø (2017) Life history adaptations to seasonality. Integr Comp Biol 57:943–960
- 743 Velando A (2000) The importance of hatching date for dominance in young shags.  
744 Anim Behav 60:181–185
- 745 Vermeulen HC, Nell JAJ (1988) The bush Karoo rat *Otomys unisulcatus* on the Cape  
746 West coast. Afr Zool 23:103–111
- 747 Vitale A, Calisi R, Carere C et al (2018) Guidelines for the treatment of animals in  
748 behavioural research and teaching. Anim Behav 135:I–X
- 749 Võikar V, Vasar E, Rauvala H (2004) Behavioral alterations induced by repeated testing  
750 in C57BL/6J and 129S2/Sv mice: implications for phenotyping screens. Genes Brain  
751 Behav 3:27–38
- 752 Werger MJA (1974) On concepts and techniques applied in the Ziirich-Montpellier  
753 method of vegetation survey. Bothalia 11:309–323
- 754 White TCR (2008) The role of food, weather and climate in limiting the abundance of  
755 animals. Biol Rev 83:227–248
- 756 Whittier JM, Crews D (1987) Seasonal reproduction: patterns and control. In: Norris  
757 DO, Jones RE (eds) Hormones and reproduction in fishes, amphibians, and reptiles.  
758 Springer US, Boston, MA, pp 385–409

759 Wolhuter L, Thomson J, Schradin C, Pillay N (2022) Life history traits of free-living  
760 bush Karoo rats (*Otomys unisulcatus*) in the semi-arid Succulent Karoo. Mammal  
761 Res 67:73–81  
762

763 **Tables**

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

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

772 <sup>1</sup> square-root transformation of dependent variable

773 <sup>2</sup> log [x+1] transformation of dependent variable

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

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

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

785

786



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

Dependent variable	Predictors	$\chi^2$	df	$\beta \pm SE$	<i>P</i>
(a) SB - Probability to enter arena	Date of birth within season	6.065	1	0.043 ± 0.017	<b>0.014</b>
	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 [2 <sup>nd</sup> ]	2.623	3	-0.806 ± 0.525	0.454
	[3 <sup>rd</sup> ]			-0.529 ± 0.993	
	[4 <sup>th</sup> ]			-0.092 ± 1.116	
	Year [2 <sup>nd</sup> ]	3.258	1	-1.554 ± 0.861	0.071
(b) OF - Distance travelled <sup>1</sup>	Date of birth within season	4.000	1	3.017 ± 1.508	<b>0.045</b>
	Age class at testing [old]	0.885	1	-3.189 ± 3.389	0.347
	Sex [m]	5.541	1	9.151 ± 3.888	<b>0.019</b>
	Food plant abundance at testing	0.822	1	1.459 ± 1.610	0.365
	Test sequence [2 <sup>nd</sup> ]	91.163	3	-15.774 ± 1.706	<b>&lt; 0.001</b>
	[3 <sup>rd</sup> ]			-16.216 ± 3.461	
	[4 <sup>th</sup> ]			-21.940 ± 3.934	
	Year [2 <sup>nd</sup> ]	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	<b>0.003</b>
	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 [2 <sup>nd</sup> ]	51.848	3	-25.279 ± 3.932	<b>&lt; 0.001</b>
	[3 <sup>rd</sup> ]			-22.149 ± 7.226	
	[4 <sup>th</sup> ]			-40.905 ± 8.195	
	Year [2 <sup>nd</sup> ]	1.345	1	-6.245 ± 5.386	0.246
(d) OF: % Time exploring walls and corners of arena <sup>1</sup>	Date of birth within season	10.610	1	0.021 ± 0.006	<b>0.001</b>
	Age class at testing [old]	4.524	1	-0.875 ± 0.412	<b>0.033</b>
	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 [2 <sup>nd</sup> ]	41.058	3	-1.197 ± 0.215	<b>&lt; 0.001</b>

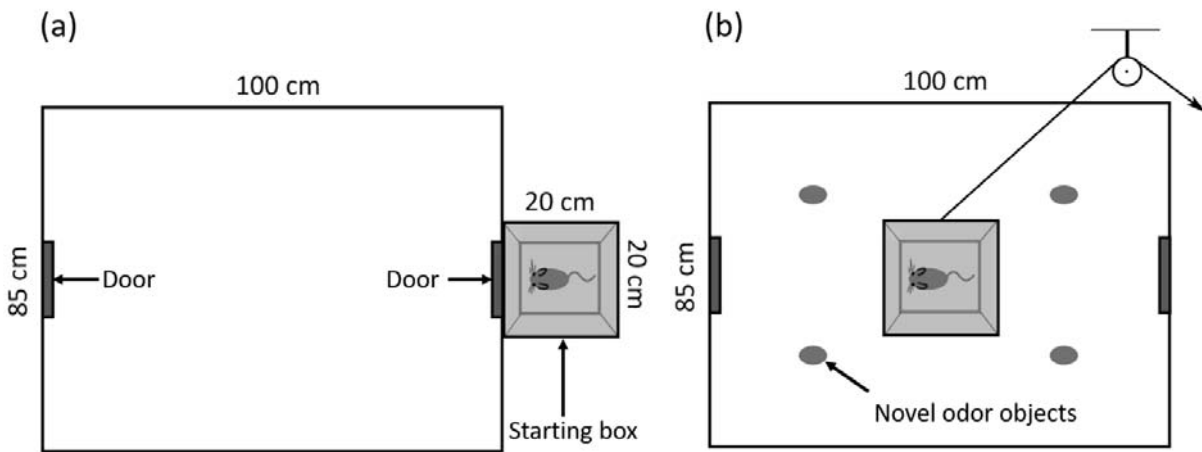
				[3 <sup>rd</sup> ]	-1.359 ± 0.418	
				[4 <sup>th</sup> ]	-2.274 ± 0.475	
	Year [2 <sup>nd</sup> ]	0.695	1	0.276 ± 0.331	0.405	
(e) NO: Time exploring object <sup>2</sup>	Date of birth within season	2.497	1	0.204 ± 0.129	0.114	
	Age class at testing [old]	3.007	1	-0.518 ± 0.299	0.083	
	Sex [m]	0.025	1	0.052 ± 0.328	0.873	
	Food plant abundance at testing	6.700	1	0.373 ± 0.144	<b>0.010</b>	
	Test sequence [2 <sup>nd</sup> ]	6.810	3	-0.319 ± 0.155	0.078	
				[3 <sup>rd</sup> ]	0.013 ± 0.304	
				[4 <sup>th</sup> ]	0.284 ± 0.345	
	Year [2 <sup>nd</sup> ]	4.806	1	-0.535 ± 0.244	<b>0.028</b>	
(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 [2 <sup>nd</sup> ]	1.894	3	-0.146 ± 0.111	0.595	
				[3 <sup>rd</sup> ]	-0.135 ± 0.195	
				[4 <sup>th</sup> ]	-0.062 ± 0.217	
	Year [2 <sup>nd</sup> ]	2.164	1	-0.232 ± 0.158	0.141	

793 <sup>1</sup> square-root transformation of dependent variable

794 <sup>2</sup> log [x+1] transformation of dependent variable

795

796 **Figures**



797

798 **Fig. 1** Experimental setting used for (a) starting box/open field tests and (b) novel odor

799 tests, either orange skin, tomato sauce, peanut butter or strawberry jam (for the 4

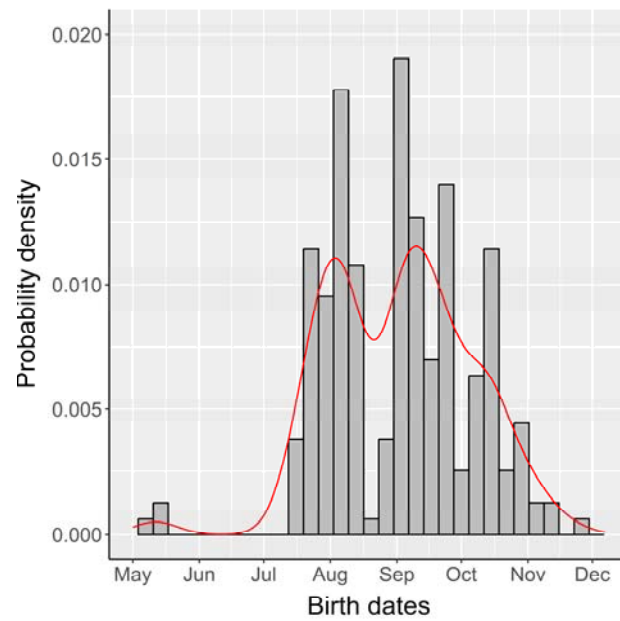
800 replicates) were used to provide novel odors carried in the identical sieve balls. Note

801 that the starting box inside the arena in (b) was lifted by a pulley system once the

802 experiment started

803

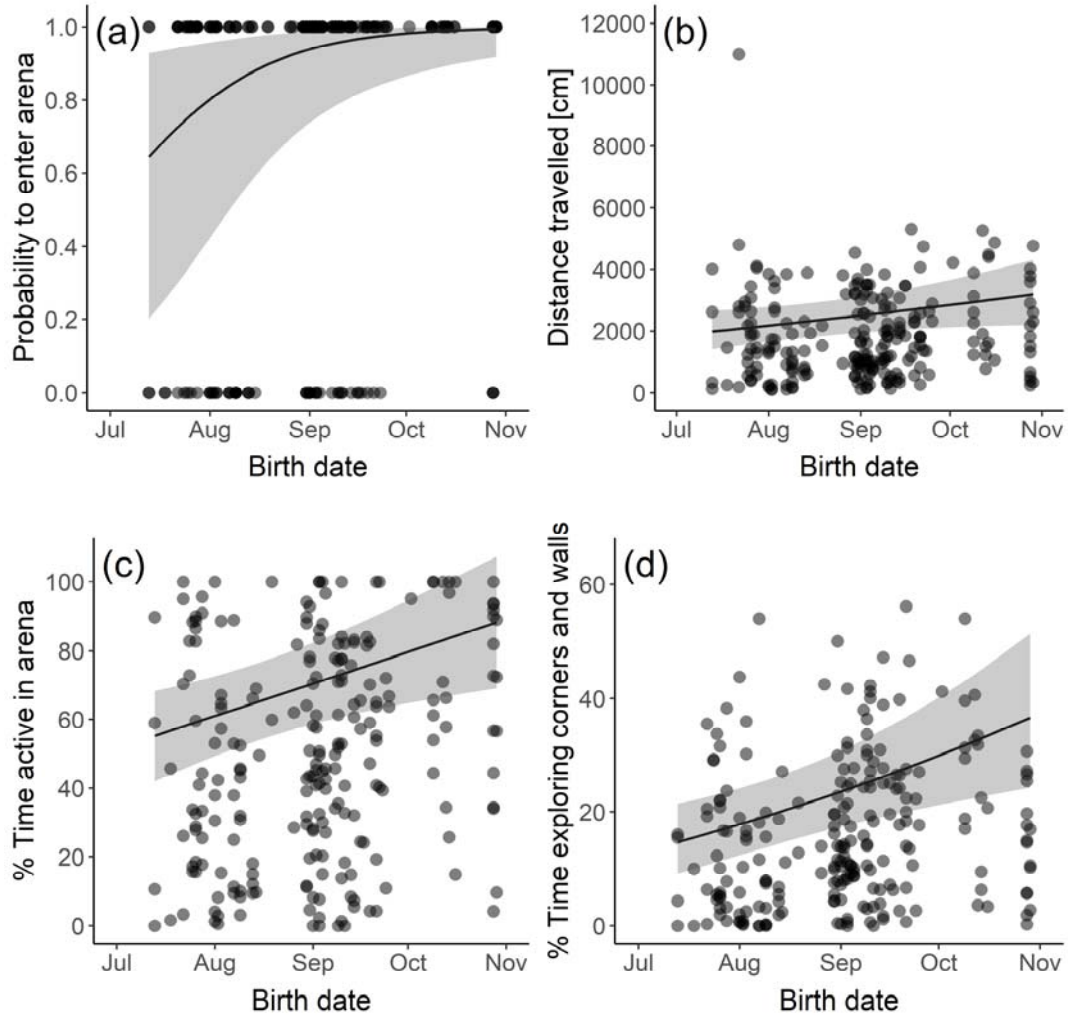
804



805

806

807 **Fig. 2** Distribution of reproductive activity (assessed by the frequency of birth events)  
808 during the breeding season in the bush Karoo rat, given as density probability (red line).  
809 Data from  $n = 226$  individuals captured during the years 2022 and 2023, including the  
810 99 focal individuals which underwent behavioral tests



811  
812

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

817