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23

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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 1st January 2022 to 14th 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 1st and 2nd
246 test) was 54 days, and the average age for “older” adults (at the 3rd and 4th 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 (3rd and 4th) 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 1st 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 2nd test, n = 30 individuals underwent at
273 least a 3rd 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 cm³ 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 (2×30 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 1st test was orange peel, tomato sauce was in the 2nd test (two weeks later), peanut

314 butter was used in the 3rd test and strawberry jam in the 4th 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 100th 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, 1st 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 1st and 2nd tests or “older adult” at the 3rd and 4th 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 5th 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 19th July; 2023: 14th July). In 2022, the mean date of birth was on 29th August, and
437 during the reproductive season in 2023, it was on 8th 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.

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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

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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> _{95%}	<i>R</i>	<i>CI</i> _{95%}
SB - Probability to enter arena	0.699	[0.483, 0.872]	0.477	[0.050, 0.860]
OF - Distance travelled¹	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 arena¹	0.253	[0.093, 0.427]	0.317	[0.039, 0.536]
NO - Time exploring object²	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]

772 ¹ square-root transformation of dependent variable

773 ² 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

	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						

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	χ^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	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 [2 nd]	2.623	3	-0.806 ± 0.525	0.454
	[3 rd]			-0.529 ± 0.993	
	[4 th]			-0.092 ± 1.116	
	Year [2 nd]	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 [2 nd]	91.163	3	-15.774 ± 1.706	< 0.001
	[3 rd]			-16.216 ± 3.461	
	[4 th]			-21.940 ± 3.934	
	Year [2 nd]	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 [2 nd]	51.848	3	-25.279 ± 3.932	< 0.001
	[3 rd]			-22.149 ± 7.226	
	[4 th]			-40.905 ± 8.195	
	Year [2 nd]	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 [2 nd]	41.058	3	-1.197 ± 0.215	< 0.001

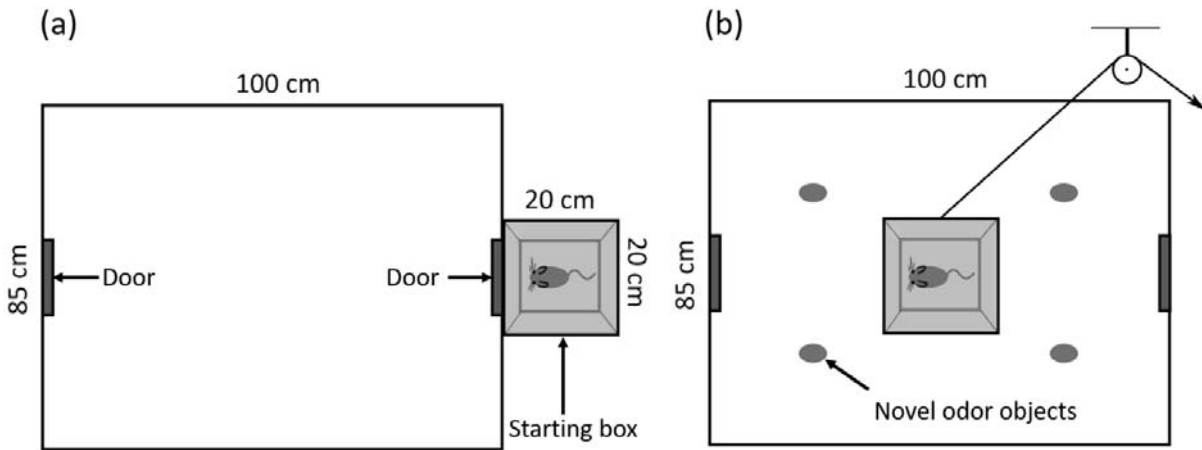
				[3 rd]	-1.359 ± 0.418	
				[4 th]	-2.274 ± 0.475	
		Year [2 nd]	0.695	1	0.276 ± 0.331	0.405
(e) NO: Time exploring object ²	Date of birth within season		2.497	1	0.204 ± 0.129	0.114
	Age class at testing [old]		3.007	1	-0.518 ± 0.299	0.083
	Sex [m]		0.025	1	0.052 ± 0.328	0.873
	Food plant abundance at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

793 ¹ square-root transformation of dependent variable

794 ² 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

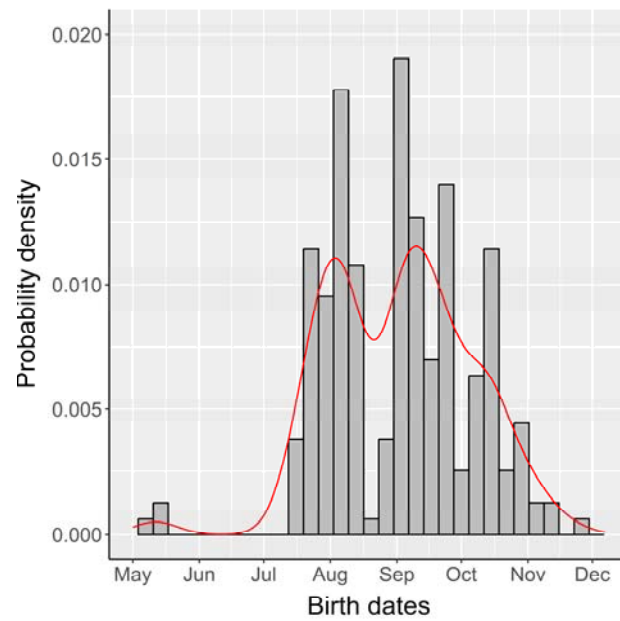
800 replicates) were used to provide novel odors carried in the identical sieve balls. Note

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

802 experiment started

803

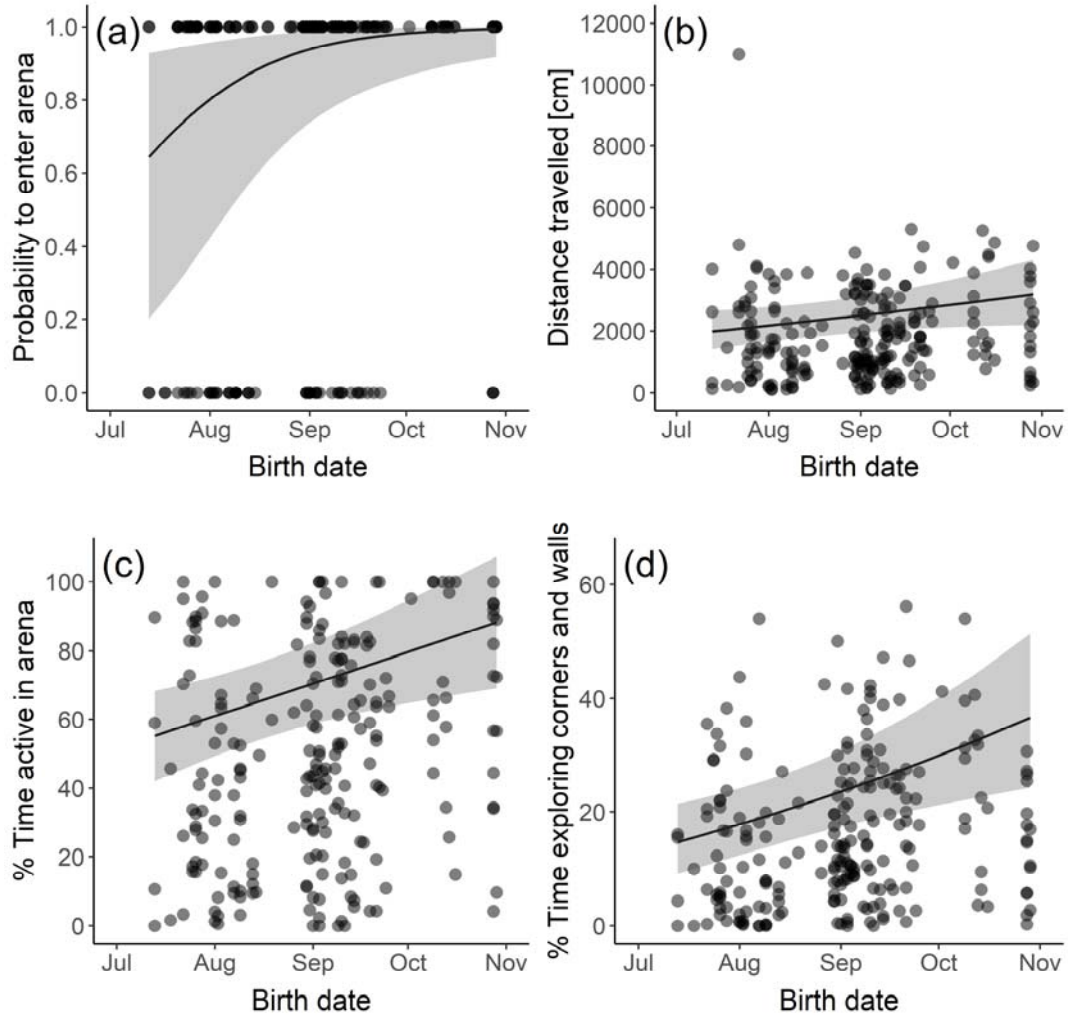
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807 **Fig. 2** Distribution of reproductive activity (assessed by the frequency of birth events)
808 during the breeding season in the bush Karoo rat, given as density probability (red line).
809 Data from $n = 226$ individuals captured during the 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