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1 **Seasonal variation in attention and spatial performance in a wild**
2 **population of the African striped mouse (*Rhabdomys pumilio*).**

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30

31 **Abstract**

32

33 Cognitive flexibility describes the reversible changes of cognition in response to environmental
34 changes. Although various environmental factors such as temperature, photoperiod and rainfall change
35 seasonally, seasonal variation in cognitive performance has been reported in merely a few birds and
36 mammals. We assessed whether cognitive performance in a wild population of African striped mice
37 *Rhabdomys pumilio*, from the Succulent Karoo semi-desert of South Africa, differed between summer
38 and winter. In order to measure cognitive performance, striped mice were trapped in the field, tested
39 under laboratory conditions at our research station, and returned to the field within 5 hours. We
40 measured attention and spatial memory using the standardized orientation response test and the Barnes
41 maze test. Males tested during summer oriented faster toward a predator-stimulus but made more
42 errors and took longer to locate a shelter than males tested during winter. In contrast, females’
43 performance did not differ between the two seasons. We discuss how the faster orientation in males
44 during winter might be the consequence of lower temperatures and/or prolonged food restriction. We
45 suggest that the enhancement of spatial performance during winter might be due to a greater
46 motivation for future dispersal in male striped mice, as spring represents the breeding season.

47

48 **Keywords**

49 Cognitive flexibility, Seasonality, Orientation response, Spatial memory, Sex differences

50

51 **Introduction**

52

53 Reversible changes in cognitive performance are defined as cognitive flexibility, which is a particular
54 type of phenotypic flexibility (Piersma and Drent 2003). One example of cognitive flexibility is
55 seasonal variation in cognitive performance, which has been observed in a few bird and mammal
56 species. For instance, song production and learning are increased during the breeding season in
57 passerine birds (Tramontin & Brenowitz 2000). Moreover, spatial memory of several seasonal
58 breeders is enhanced before the onset of the breeding season, for example in the parasitic birds
59 *Molotrus bonariensis* and *M. rufoaxillaris* (Clayton et al. 1997) and in dispersing rodents such as deer
60 mice *Peromyscus maniculatus* (Galea et al. 1994) and *P. leucopus* (Pyter et al. 2006) and voles
61 *Microtus pennsylvanicus* (Galea et al. 1996) and *Clethrionomys glareolus* (Yaskin 2013). In contrast,
62 spatial memory of food-caching birds improves in winter (Sherry and Hoshooley 2009). Interestingly,
63 in some of these species, there is also evidence of seasonal variation in the volume of the brain
64 structures controlling song production (i.e. song control nuclei: Tramontin & Brenowitz 2000) and
65 spatial memory (i.e. hippocampus: Clayton et al. 1997; Galea and McEwen 1999).

66

67 Cognitive performance might be enhanced under harsh seasonal conditions as an adaptation to meet
68 specific ecological needs (Buchanan et al. 2013). For example, improved cognition might help an
69 individual to face changes in food availability. Food restriction (i.e. low availability and/or
70 predictability) leads to improved learning in cichlid fish *Simochromis pleurospilus* (Kotrschal and
71 Taborsky 2010), mountain chickadees *Poecile gambeli* (Pravosudov and Clayton 2001), rats *Rattus*
72 *rattus* (Aimé et al. 2007) and mouse lemurs *Microcebus murinus* (Dal-Pan et al. 2011). Predation risk
73 is another factor affecting learning. For example, in tadpoles, short exposure to predatory cues induces
74 a stronger defense response (i.e. lower activity level) and longer memory retention to a predator
75 stimulus (Ferrari 2014). Alternatively, cognitive performance might be impaired under harsh seasonal
76 conditions because of a need to reduce energy-demanding physiological processes, including
77 cognition. Cognitive processing is energetically costly because the development of the underlying
78 neuronal structures requires neurogenesis (Isler and van Schaik 2006), synaptic formation (Roth et al.
79 2010), and the generation and propagation of neuronal signals (Gilsenan et al. 2009). The cost of
80 maintaining or even improving cognitive performance is thus expected to be of particular importance
81 for individuals experiencing extreme environmental harshness (Laughlin 2001). In sum, although
82 seasonal environmental changes are expected to influence cognition, to date, few studies have tested
83 whether cognition is maintained, impaired, or improved during the harshest season.

84

85 There are a number of factors, such as food availability and photoperiod, that are associated with the
86 change of seasons and may serve as environmental cues leading to changes in cognitive functions. One
87 important factor that changes seasonally in most environments is ambient temperature. Maintaining a

88 constant body temperature is energetically highly expensive for endotherms, especially for smaller
89 bodied species, such as rodents (Canals et al. 1989). Numerous studies have demonstrated that the
90 basal metabolic rate increases as the ambient temperature drops (e.g. Geiser 2004). In addition,
91 endotherms face the necessity to invest more energy into thermoregulation in environments where
92 ambient temperatures fall clearly below their thermoneutral zone (i.e. range of ambient temperatures at
93 which the metabolic cost of maintaining body temperature is minimal). Individuals living in energy
94 restricted environments are expected to trade-off between investing energy either into cognition or into
95 other life sustaining processes, such as thermoregulation (Maille and Schradin, submitted). Increased
96 thermoregulatory costs could thus affect the energy available for cognitive processing, especially in
97 animals with a high surface : volume ratio, such as rodents. In the current study, we aimed to establish
98 whether a seasonal decrease in ambient temperature would lead to lower cognitive performance in a
99 free-living population of rodents. In the northern hemisphere, the cold season is also a season of low
100 food availability which leads to the difficulty of disentangling the influence of seasonal changes in
101 food availability *versus* ambient temperature on cognitive performance. To study the effect of ambient
102 temperature independent of food availability, one would need a study system where the ambient
103 temperature changes seasonally but food availability does not.

104

105 We assessed cognitive performance in a wild population of African striped mice *Rhabdomys pumilio*,
106 living in a semi-desert characterized by pronounced seasonal changes in ambient temperature. This
107 rodent species is a good model to study cognitive flexibility in free ranging mammals because sample
108 sizes are large, it is diurnal, which enables behavioural testing during the day, and it can be tested
109 using standardized cognitive procedures for laboratory rodents, offering a high degree of control (e.g.
110 Rymer et al. 2008; Pillay and Rymer 2015). We focused on cognitive traits important for a small
111 diurnal rodent living in an open environment to avoid predators (Abrams 1994). First, we assessed
112 attention in a simulated predation event (appearance of an image of a bird of prey). Second, we studied
113 spatial memory because learning the locations of safe shelters is crucial for prey to escape predators.
114 We compared the cognitive performance of striped mice tested either during summer (hot ambient
115 temperature) or during winter (cold ambient temperature), using two standardized laboratory tests, the
116 orientation response test (i.e. measurement of attention: Rodriguiz and Wetsel 2006) and the Barnes
117 maze test (i.e. measurement of spatial learning and memory: Barnes 1979).

118

119 The environmental conditions occurring during the study enabled us to assess the influence of seasonal
120 changes in temperature on cognitive performance of striped mice, while food availability remained
121 relatively stable. In the year of the study, temperatures dropped from 9 °C at night in the austral
122 summer to 1 °C at night in the austral winter, in both cases being clearly below the striped mouse
123 thermoneutral zone of 31 °C (Scantlebury et al. 2006). However, food plant density remained low
124 during both seasons because winter precipitation, characteristic of our study site in the Succulent

125 Karoo, arrived very late (in June that is 2 months later than usual). The striped mice that were tested
126 thus experienced a 6-month period of low food availability. We assumed that striped mice faced a
127 greater need to trade-off energy allocation for cognition in winter, because of the prolonged period of
128 low food availability coupled with the increased energetic costs of thermoregulation. We therefore
129 predicted a reduction in cognitive performance of striped mice from summer to winter.

130

131 **Material and methods**

132

133 **Study species**

134 We studied a population of African striped mice *Rhabdomys pumilio* living in the Succulent Karoo of
135 South Africa. Social groups of striped mice (2-30 adult individuals of both sexes) share one nest and
136 territory but forage solitarily (Schradin 2006). Striped mice do not usually breed in the year of their
137 birth but do so in the following year when they are 10-12 months old (Schradin and Pillay 2005). All
138 individuals tested were born during the previous breeding season (i.e. that takes place in austral spring:
139 September to November; Schradin and Pillay 2005).

140

141 **Study area and period**

142 The study was conducted in Goegap Nature Reserve, near Springbok in the Northern Cape Province,
143 South Africa (S 29 41.56, E 18 1.60; for pictures of the field site see www.stripedmouse.com). The
144 area is semi-arid, with an average annual rainfall of 160 mm p.a. (Rosch 2001). The vegetation type is
145 classified as Succulent Karoo (Cowling et al. 1999). The study area of 5 ha was occupied by 14 groups
146 of striped mice. Group association of individual mice was determined by trapping, radio-tracking and
147 behavioural observations of nesting sites during mornings and afternoons (Schradin and Pillay 2005).

148 The study took place from 17th January to 8th July 2014. The weather was hot and dry during the
149 austral summer months of the study (17th January to 8th April: average temperature \pm SE = 25.1 \pm 2.0
150 °C, total rainfall = 35 mm p.a.) whereas a drop in temperature occurred during the austral winter
151 months (15th May to 8th July: average temperature \pm SE = 14.6 \pm 1.4 °C, total rainfall = 46 mm p.a.,

152 **Table 1).**

153 Striped mice mainly feed on plants (> 99%) and plant surveys were conducted on the 1st and on the
154 15th of each month at our field site, using the Braun-Blanquet Method. The number of food plants
155 species (palatability known from behavioural observations; Schradin & Pillay 2006) was recorded in
156 each of eight monitoring plots of 2 x 2 m. Food availability for the striped mice remained relatively
157 stable within the study period and population size only decreased slightly from summer to winter
158 **(Table 1).**

159

160

161 **Study animals**

162 Cognitive tests were performed on 105 adult mice from nine different groups: 59 mice (30 males, 29
163 females) were tested in summer from 17th January to 8th April and 46 mice (26 males, 20 females)
164 were tested in winter from 15th May to 8th July. None of the individuals was tested in both seasons to
165 avoid any learning effect.

166

167 *Trapping and marking*

168 Striped mice were trapped directly at their nests by using metal live traps similar to Sherman traps (26
169 x 9 x 9 cm) baited with a mixture of bran flakes, raisins, oil and sea salt. Traps were placed in the
170 shade under bushes where the mice had been nesting the night before. Individuals were permanently
171 marked using numbered metal ear tags (National Band and Tag Co., Newport, KY, USA).
172 Additionally, each individual was marked on the pelage for visual identification by using commercial
173 hair dye (Rapido, Pinetown, South Africa). All methods followed standard protocol and have been
174 used successfully on striped mice since 2001 (Schradin and Pillay 2005).

175

176 *Body mass and metabolism*

177 We measured body mass and performed blood sampling 5 to 20 days before cognitive testing to be
178 able to measure metabolic indicators (glucose, ketone and corticosterone) while at the same time
179 giving the mice enough time to rest between blood sampling and cognitive testing. Striped mice were
180 trapped early in the morning before they left their nest to forage in order to obtain measurements after
181 the overnight fast and before onset of foraging and pronounced physical activity. As soon as a mouse
182 entered a trap it was anaesthetized with diethyl ether and approximately 400µL of blood was obtained
183 from a sub-lingual vein. Blood glucose and ketone bodies were directly measured using the One
184 Touch Ultra glucometer (Lifescan, Inc., Milpitas, CA, USA) and the Freestyle Optium Blood β-
185 Ketone meter (Abbott Laboratories, Australia). Samples were collected within a 3 minutes delay and
186 were transported to the research station where they were centrifuged twice for 10 minutes in order to
187 obtain serum. Alliquots were stored at – 20°C and later analysed at the Institut Pluridisciplinaire
188 Hubert Curien using a validated commercial kit from IBL Hamburg.

189

190 **Cognitive testing**

191 Each morning, 2 to 3 striped mice were trapped at their nest within the first hour after sunrise and
192 brought to a research room located a 5-minute walking distance from the field site. Tests were
193 performed in a specific laboratory room (3.70 x 3.10 x 2.40 m) constructed for this project. The
194 laboratory room was split into two areas with a black non-translucent curtain hanging from the ceiling,
195 one area being used for testing the mice (testing area: 1.60 x 3.10 x 2.40 m) and the other area to serve
196 as a hide for the experimenter. The temperature inside the laboratory room was not controlled and
197 tracked the ambient outdoor temperatures (no heater used in winter). Individuals were first tested for

198 the orientation response test (description below), lasting 10 minutes. Following an interval of 1 to 2
199 hours during which mice were placed individually in a quiet room in a plastic cage (22 x 16.5 x 14
200 cm) with sand for bedding and an egg box as shelter, mice were brought back to the laboratory and
201 tested in the Barnes maze test (description below), lasting 60 to 90 minutes. After testing, mice were
202 given 10 sunflower seeds to compensate for missed foraging opportunities, and were then released at
203 their nest in the field site.

204

205 *Orientation response test*

206 The Orientation response test uses the natural propensity of rodents to orient their head or whole body
207 toward a salient stimulus (Rodríguez and Wetsel 2006). A mouse was placed in a perspex box (18.5 x
208 13 x 11.5 cm) that was centered in a black plastic chamber (57 x 38 x 25 cm). The lid and one lateral
209 side of the box were transparent whereas the other sides had been made opaque using black tape. The
210 transparent lateral side of the box faced a computer screen (7 inches = 15 x 9.5 cm; distance box to
211 screen: 17 cm) connected to a laptop (**Online Resource 1**). After a 5 minute familiarization to the set-
212 up during which the mouse was exposed to a white screen, a raptor-stimulus was projected onto the
213 screen. The raptor-stimulus was a photo of flying jackal buzzard *Buteo rufofuscus*, a natural predator
214 of the striped mouse, presented in a horizontal sliding motion (**Online Resource 1**). The raptor-
215 stimulus presentation was repeated 10 times, once every 25 seconds, each presentation lasting 5
216 seconds. To reduce habituation to the raptor-stimulus, a different starting location on the screen was
217 used for each presentation. In addition, the raptor-stimulus moved either leftward or rightward (5
218 presentations each). Mice were videotaped using a high speed Casio camera EX-ZR200 recording at
219 120 frames/second. Light for videotaping was provided by a 11W lamp mounted above the set-up. For
220 each presentation, we recorded whether the mouse showed an orientation response toward the raptor-
221 stimulus and the time for the mouse to start orienting toward the raptor-stimulus. We considered that a
222 mouse showed an orientation response when it turned its head towards the raptor-stimulus.

223

224 *Barnes maze test*

225 The Barnes maze test (Barnes 1979) measures spatial learning and memory by assessing the ability of
226 rodents to relocate a hole giving access to a shelter among numerous available holes. The maze
227 consisted of a circular platform 110 cm in diameter raised 60 cm from the ground (**Online Resource**
228 **2**). The maze was surrounded by a 30 cm high transparent perspex cylinder because striped mice,
229 unlike laboratory mice and rats, would otherwise have jumped off the platform. The platform was
230 made of white perspex bored with 12 equidistant circular holes 5 cm in diameter and 7 cm from the
231 outer edge (**Online Resource 2**). One hole provided access to a dark escape box underneath (15 x 13 x
232 9 cm) but the 11 remaining holes were closed with black PVC panels made of the same perspex as the
233 escape box (15 x 13 x 0.1 cm, placed under the holes). To provide visual landmarks for the mice, we
234 placed 6 pictures of rocks or plants from the field site on the walls and curtains surrounding the set-up,

235 50 cm above the platform of the Barnes maze (mice could see the landmarks whatever their location in
236 the maze; **Online Resource 2**).

237
238 Individuals were tested for 2 sessions, the second session (i.e. long-term memory session) occurring 8
239 \pm 3 days after the first session (i.e. short-term memory session). The mice were released into the field
240 after the first session and were re-trapped before the second session. Each session consisted of 9 trials
241 separated by a 5-minute delay during which the maze and escape box were cleaned using 70% alcohol
242 and the mouse was transferred from the escape box to the starting box. Trials were always conducted
243 in the same order: 6 neutral trials N1 to N6 (i.e. with the escape box) that were followed by 2 bat trials
244 B1 and B2 (i.e. with the escape box and a bat toy hanging above the maze) and finally a control trial C
245 (i.e. no escape box and no bat toy). During the bat trials, an automated flapping battery run bat-like toy
246 (Out of the Blue KG, Germany) was hung 120 cm above the maze to mimic a bird of prey; striped
247 mice were very wary and quickly looked for shelter when exposed to this toy (**Online Resource 2**).
248 During the control trial, the escape box was replaced by a black PVC panel to control for the use of
249 visual and olfactory cues from the escape box.

250
251 Before each trial, a mouse was placed in a circular and transparent starting box (diameter = 10 cm,
252 height = 10 cm) in the center of the Barnes maze. The mouse was able to see the holes from the center
253 of the arena but not which one was the correct hole giving access to the escape box. A trial started
254 when the mouse was released from the starting box that was lifted by pulling a string attached to the
255 box (**Online Resource 2**). To reduce disturbance of the tested mouse, the experimenter pulled the
256 string from behind the curtain. The neutral and bat trials ended when the mouse entered the escape
257 box. When the mouse did not enter the escape box within 5 minutes, the experimenter gently led the
258 mouse to the correct hole and encouraged it to enter the box. The control trial ended when the mouse
259 poked the correct hole.

260
261 The location of the correct hole was randomly determined for each mouse and remained constant for
262 all the trials and sessions for that individual mouse. Mice were videotaped using a Microsoft HD web-
263 camera connected to a laptop. For each trial, we recorded the number of errors (i.e. poke into another
264 hole than the correct hole) before the mouse nose-poked the correct hole and the latency to nose-poke
265 the correct hole. We considered that a mouse poked a hole when it placed its nose inside the hole or
266 less than 1 cm away from the hole, the head being oriented toward the hole. A second observer coded
267 5% of the videos (86 randomly selected videos): the weighted Cohen's kappa coefficient of agreement
268 between the two observers was 0.86.

269
270
271

272 **Statistical analyses**

273 All statistics were performed with R v. 3.0.2 (The R foundation for statistical computing,
274 <http://www.r-project.org/>). Mixed models were constructed using the lmer function in *lme4* package.

275

276 *Attention in the Orientation response test*

277 Seasonal differences in attention were analyzed by performing two linear mixed models, one with
278 number of orientation responses and the other with orientation time as dependent variable, and sex and
279 season specified as fixed effects. We specified group identification as a random factor to control for
280 potential confounding effects of group origin (litter and/or ecology). To obtain normality of residuals,
281 data were transformed using a logarithm + 1 transformation for the number of orientation responses
282 and a logarithm transformation for the orientation time.

283

284 *Spatial memory in the Barnes maze test*

285 We initially assessed whether spatial memory performance changed during the consecutive trials and
286 sessions of the Barnes maze test. Differences in spatial memory were analyzed by performing two
287 linear mixed models, one with number of errors and the other with latency to poke the correct hole for
288 each trial as the dependent variable, trial and session as fixed effects, and ID number of the mice as
289 random factor (i.e. repeated measures design).

290

291 For each session of the Barnes maze test, seasonal differences in spatial memory were analyzed by
292 performing two linear mixed models, with either number of errors or latency to poke the correct hole
293 as the dependent variable, season (i.e. summer and winter), sex and category of trials (i.e. N-I, N-II, B
294 and C; see results for description) specified as fixed effects, and ID number of the mice as random
295 factor (i.e. repeated measures design). To control for potential confounding effects of group origin of
296 the striped mice and location of the correct hole in the BM test, we constructed mixed models with
297 group identifications and the number of the correct hole specified as random factors. To obtain
298 normality of residuals, data were transformed using a logarithm + 1 transformation for the number of
299 errors and a logarithm transformation for the latency. In our study, we could not exclude age as a
300 confounding factor in our analyses because the individuals tested during winter were a few months
301 older than those tested during summer.

302

303 **Results**

304

305 **Seasonal variation in body condition**

306

307 The body mass and the blood glucose and ketone bodies levels did not differ between individuals
308 tested in summer or in winter (t-test: $p > 0.05$, **Table 2**), indicating that energy balance (energy intake

309 – energy expenditure) did not change between the two seasons (McCue 2010). Basal corticosterone
310 levels decreased from summer to winter (t-test: $p = 0.011$, **Table 2**), which is supposed to reduce
311 energy expenditure to enable individuals to cope with long periods of low food availability (Romero
312 2002).

313

314 **Seasonal variation in attention (Orientation response test)**

315

316 *Number of orientation responses*

317 We excluded 11 males (summer: $N = 6$, winter: $N = 5$) and 6 females (summer: $N = 4$; winter: $N = 2$)
318 from the analyses because they never reacted to the raptor-stimulus within the 10 presentations. There
319 was no difference between summer and winter in the proportions of individuals that never oriented or
320 oriented to the raptor-stimulus (Fisher exact test: males $p = 0.744$, females: $p = 0.684$). There was no
321 significant seasonal effect on the number of orientation responses to the raptor-stimulus ($\chi^2 = 0.32$, $p =$
322 0.572) and no significant interaction between season and sex ($\chi^2 = 0.01$, $p = 0.946$).

323

324 *Orientation time*

325 Striped mice tested during winter tended to orient more slowly toward the raptor-stimulus than mice
326 tested during summer ($\chi^2 = 3.53$, $p = 0.060$). Although the interaction between season and sex was not
327 significant ($\chi^2 = 1.74$, $p = 0.187$), we found that the males tested during winter were significantly
328 slower to orient towards the raptor-stimulus than the males tested during summer (t-tests: $p = 0.037$)
329 while there was no difference for females (t-tests: $p = 0.670$; **Fig. 1**).

330

331 **Seasonal variation in spatial memory (Barnes maze test)**

332

333 Whatever the session, the number of errors and latency to poke the correct hole did not differ between
334 the control trial C and the last neutral trial N6 (pairwise-t-test: $p > 0.05$, **Fig. 2**) which indicates that
335 mice did not use olfactory or visual cues from the escape box to locate the correct hole. The latency to
336 poke the correct hole was significantly greater in the control trial than in the last bat trial B2 (pairwise-
337 t-test: short-term session: $p < 0.05$, **Fig. 2**) though the number of errors did not significantly differ
338 between these two trials (pairwise-t-test: short-term session: $p > 0.05$, **Fig. 2**).

339

340 Spatial memory performance significantly differed between the short-term memory session and the
341 long-term memory session (number of errors (E): $\chi^2 = 81.44$, $p < 0.001$; latency (L): $\chi^2 = 180.88$, $p <$
342 0.001) and among the 9 trials (E: $\chi^2 = 273.18$, $p < 0.001$; L: $\chi^2 = 476.09$, $p < 0.001$). Because the
343 analyses also revealed significant interactions between sessions and trials (E: $\chi^2 = 49.38$, $p < 0.001$; L:
344 $\chi^2 = 21.72$, $p = 0.005$), we decided to perform all the subsequent statistical analyses for the two
345 sessions separately.

346

347 To reduce the number of multiple comparisons, we grouped the N1 and N2 trials into a “neutral-I
348 trials” (N-I) category, the N3 to N6 trials into a “neutral-II trials” (N-II) category and the B1 and B2
349 trials into a “bat trials” (B) category based on significant differences between trials in the short-term
350 memory session (t-tests: $p < 0.05$: see **Fig. 2**). Within each category, there were no differences
351 between trials for either the number of errors (except in the N-I category) or the latency to poke the
352 correct hole.

353

354 *Short-term memory-session*

355 For the short-term memory session, there was no significant seasonal effect on either the number of
356 errors (E: $\chi^2 = 0.00$, $p = 0.966$) nor the latency to poke the correct hole (L: $\chi^2 = 0.73$, $p = 0.392$).
357 Regarding the number of errors, the analysis revealed no significant interaction between season and
358 category of trials (E: $\chi^2 = 0.33$, $p = 0.850$) and no significant interaction between sex, season and
359 category of trials (E: $\chi^2 = 0.91$, $p = 0.823$). In contrast, regarding the latency to poke the correct hole,
360 the analysis revealed significant interactions between the sex and the category of trials (L: $\chi^2 = 18.21$,
361 $p < 0.001$) and between the season, sex and category of trials (L: $\chi^2 = 10.92$, $p = 0.012$, **Fig.3**). We
362 thus analyzed the influence of the season on the latency to poke the correct hole for each category of
363 trials and for males and females separately.

364

365 Males tested during winter poked the correct hole significantly faster in the Control trial than males
366 tested during summer (t-tests: Control: $p = 0.019$), whereas there were no differences for the other
367 categories of trials (t-tests: N-I: $p = 0.280$; N-II: $p = 0.470$, Bat: $p = 0.540$; **Fig. 3**). Females did not
368 differ between seasons in their latency to poke the correct hole, whatever the category of trials (t-tests:
369 N-I: $p = 0.730$, N-II: $p = 0.530$, Bat: $p = 0.580$, Control: $p = 0.410$; **Fig. 3**).

370

371 *Long-term memory-session*

372 For the long-term memory session, the analyses revealed a significant interaction between sex, season
373 and category of trials for both the number of errors and the latency to poke the correct hole (E: $\chi^2 =$
374 30.68 , $p < 0.001$; L: $\chi^2 = 7.97$, $p = 0.047$, **Fig. 3**). We thus analyzed the influence of the season on the
375 number of errors and the latency to poke the correct hole for each category of trials and for males and
376 females separately.

377

378 Males tested during winter made significantly fewer errors in the Neutral-II category than males tested
379 during summer (t-tests: N-II: $p = 0.009$) whereas there were no differences for the other categories (t-
380 tests: N-I: $p = 0.480$; Bat: $p = 0.720$, Control: $p = 0.560$; **Fig. 4a**). Males tested during winter poked
381 the correct hole significantly faster in the Neutral-II and Control category than males tested during
382 summer (t-tests: N-II: $p < 0.001$, Control: $p = 0.011$) whereas there were no differences for the other

383 categories (t-tests: N-I: $p = 0.290$, Bat: $p = 0.500$; **Fig. 4b**). In contrast, whatever the category of trials,
384 females tested during winter did not differ from those tested during summer for either the number of
385 errors (t-tests: N-I: $p = 0.150$, N-II: $p = 0.270$, Bat: $p = 0.380$, Control: $p = 0.810$; **Fig. 5a**) or the
386 latency to poke the correct hole (t-tests: N-I: $p = 0.940$, N-II: $p = 0.290$, Bat: $p = 0.890$, Control: $p =$
387 0.810 ; **Fig. 5b**).

388

389 **Discussion**

390

391 We assessed cognitive performance in attention and spatial memory in a free-living population of
392 African striped mice *Rhabdomys pumilio* that experienced seasonal changes in ambient temperature
393 while food availability remained relatively stable. Males tested during summer oriented faster toward a
394 predator-stimulus in an orientation response test but made more errors and took longer to locate the
395 shelter in some (but not all) trials of a Barnes maze test compared to males tested during winter. Thus,
396 the performance of males declined from summer to winter in a test assessing attention whereas they
397 improved from summer to winter in a test assessing spatial learning and memory. In contrast, the
398 performance of females did not differ between the seasons. Multiple potential proximate as well as
399 ultimate factors can be put forward to explain these results.

400

401 Although seasonal variation in attention of male African striped mice must be interpreted with caution
402 (because of a non-significant interaction between the sex and the season), males tested in winter were
403 slower to orient toward the predator-stimulus in the orientation response test than males tested in
404 summer. The increased orientation time of males tested in winter might be a consequence of seasonal
405 changes in ambient temperature. Ambient temperature has a significant effect on the activity of striped
406 mice, which use sun-basking to warm up especially when mornings are cold (Schradin et al. 2007),
407 thereby reducing their energy expenditure (Scantlebury et al. 2010). The importance of sun-basking
408 for thermoregulation and energy balance has been considered for diverse small mammals taxa (Geiser
409 et al. 2002). Moreover, ambient temperature can be related to cognition in both birds and mammals.
410 For example, short-term decrease in ambient temperatures affects foraging decisions in European
411 starling *Sturnus vulgaris* (Chatelain et al. 2013) and induces both motor and cognitive impairment in
412 humans (Solianik et al. 2014). Indeed, human reaction time is longer in cold environmental conditions,
413 men being more affected by low temperatures than women (Solianik et al. 2014). Such sex differences
414 in reaction time in response to cold might explain why only male striped mice were slower to orient
415 toward a predatory-stimulus when tested during winter (low temperatures) compared to summer (high
416 temperatures). However, we cannot exclude the possibility that orientation time of male striped mice
417 may have been influenced by at least two other proximate factors than the ambient temperature. First,
418 attention of male striped mice might be influenced by the photoperiod (daylight length). Photoperiod
419 is usually a highly reliable cue in predictable environments, enabling individuals to respond to

420 seasonal changes (Yaskin 2011). For example, marsh tits *Parus palustris* that cache food during winter
421 perform better in spatial learning during short compared to long daylight cycles (Clayton and Cristol
422 1996). However, we believe that photoperiod does not determine the attentional variation that we
423 reported in male striped mice because photoperiod is not a reliable cue for seasonal changes in rainfall
424 and consequently food availability in the Succulent Karoo. This lack of predictability may explain
425 why food availability itself and not photoperiod regulates hormone secretion and reproduction in
426 striped mice (Raynaud and Schradin 2013). Second, the increase in orientation time from summer to
427 winter in male striped mice may alternatively be the consequence of prolonged food restriction within
428 the study period, lasting from January to July. Cognitive impairments were reported in rats that had
429 experienced at least 5 months of food restriction (Yanai et al. 2004). Since stress-induced changes in
430 cognition are often sexually differentiated (Bowman 2005), the negative influence of prolonged food
431 restriction on orientation time may have been more pronounced in males than females in the African
432 striped mouse.

433 At the evolutionary level, seasonal cognitive flexibility in attention might have an adaptive value in
434 species facing seasonal changes in predation risk. Faster detection of predators during summer in male
435 striped mice may have evolved in response to the higher predation pressure that probably occurs in
436 this season because of high predator density (i.e. most predators of striped mice reproduce in late
437 spring, leading to high population densities of predators in summer).

438
439 Striped mice showed spatial learning and long-term memory in the Barnes maze test, similar to other
440 rodent species, such as deer mice *Peromyscus maniculatus* and *P. californicus* (Jašarević et al. 2012)
441 and *Octodon degus* (Popović et al. 2010). Surprisingly, seasonal variation in spatial performance were
442 opposite to our predictions since male striped mice tested in winter located the shelter faster in the
443 long-term memory session of the Barnes maze test than males tested in summer. The seasonal
444 differences that we reported are not necessarily due to seasonal changes in cognition but alternatively
445 to seasonal differences in perception, motor performance or motivation. The fact that performance of
446 striped mice did not differ seasonally in the trials where they were exposed to an artificial predator (i.e.
447 bat trials) indicates that spatial learning during the previous neutral trials did not differ between
448 seasons, but that all individuals learned the maze equally well. It is also unlikely that the differences
449 that we reported in the neutral and control trials result from perceptive or motor impairment because
450 the individuals tested in summer were as fast to locate the shelter in the bat trial as the individuals
451 tested in winter. Seasonal differences in motivation better explain the reported seasonal variation in
452 spatial performance because male striped mice tested in summer took longer to poke the correct hole
453 in the control trial than in the bat trials despite a lack of changes in the number of errors. We thus
454 assume that seasonal variation in males' spatial performance result from a higher motivation to locate
455 the shelter during winter.

456 Male striped mice might have been more motivated to hide and less motivated to perform exploration
457 during winter because of a necessity to reduce energy expenditure. At the evolutionary level, improved
458 spatial performance in winter may be adaptive in species where males disperse and breed in spring
459 (Galea et al. 1996). In the deer mouse *Peromyscus maniculatus*, a polygynous seasonal breeder in
460 which mostly the males disperse, spatial performance improves during the breeding season relative to
461 the non-breeding season in males but not females (Galea et al. 1994). *Rhabdomys pumilio* is also
462 polygynous, and male dispersal starts in winter, several weeks before reproduction in spring (Schradin,
463 unpubl. data). Male striped mice travel distances of up to several kilometers during dispersal to
464 colonize new territories (Solmsen et al. 2011), which is likely to increase demands on spatial learning
465 and memory processing. We thus hypothesize that the enhanced spatial performance is due to greater
466 motivation in male striped mice tested during winter relative to males tested during summer because
467 of male dispersal during this season and the following spring.

468

469 **Conclusions**

470

471 We demonstrated the existence of seasonal variation in attention and spatial performance in male but
472 not female African striped mice. This suggest that winter provides diverse challenges for males and
473 females in this rodent species. In males, the enhanced orientation time is associated with reduced
474 ambient temperature and better spatial performance appears to suggest a greater dispersal motivation
475 before breeding. Females were seasonally unvarying suggesting that they were buffered from
476 thermoregulatory challenges and were under different behavioural motivations of nesting in a colony.
477 The presence of both seasonal and sex differences in cognitive traits that are crucial to avoid predation,
478 suggest that the African striped mouse *Rhabdomys pumilio*, living in the Succulent Karoo semi-desert
479 of South Africa, could be an ideal rodent model for investigating flexibility in cognition and
480 behavioural motivation under natural and seasonally changing conditions.

481

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483

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493 **Ethical note**

494

495 Animal ethical clearance was provided by the University of the Witwatersrand, Johannesburg, South
496 Africa (no. 2013/50/2A). All procedures were in accordance with the ethical standards of the
497 institution or practice at which the studies were conducted. All applicable international, national,
498 and/or institutional guidelines for the care and use of animals were followed. The authors declare that
499 they have no conflict of interest.

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645 **Table 1. Monthly weather, plant data and population size at the field site (Goegap Nature**
 646 **Reserve, Northern Cape, South Africa) during the study period.**

647

	Tmin	Tmax	Rain	Pplants	Nfood	Population
Jan	8.8	42.6	22.2	16.2	4.4	240
Feb	9.5	43.2	0.7	14.6	2.3	228
Mar	5.3	42.9	17.2	14.3	1.6	196
Apr	5.8	37.4	3.7	13.5	2.1	178
May	3.9	35.9	5.9	12.7	3	164
Jun	0.7	27.8	35.7	13.1	3.6	147
Jul	-0.1	27.1	22.1	15.3	5.4	119

658 Notes. Tmin: average daily minimum temperature in °C, Tmax: average daily maximum temperature in °C,
 659 Rain: total precipitation in mm, Pplants: Percentage of area covered by plants, Nfood: mean number of green
 660 food plant species, Population: total number of trapped individuals in the population. Data for Pplants and Nfood
 661 were collected twice a month in 8 distinct 4 m²-plots (Schradin and Pillay 2006). Summer months of the study
 662 are marked in light grey shading, winter months in dark grey shading.

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672 **Table 2. Body mass and metabolic indicators measured 5 to 20 days before cognitive testing in**
 673 **the striped mice tested in summer and winter (mean ± SE).**

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	Summer (N=64)	Winter (N=42)	t-test (p-value)
Body mass (g)	36.3 ± 1.1	38.1 ± 1.3	0.310
Blood glucose (mmol/L)	5.7 ± 0.2	6.3 ± 0.4	0.130
Ketone bodies (mmol/L)	0.5 ± 0.0	0.5 ± 0.0	0.460
Basal corticosterone (ng/mL)	753.4 ± 43.6	556.7 ± 48.8	0.011 *

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 682 Notes. Significant seasonal differences are marked in bold (* p < 0.05)

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694 **Figure captions**

695

696 **Fig. 1 Orientation time in seconds (means + SE) for the first orientation response toward the**
697 **raptor-stimulus in the orientation response test in males (left) and females (right).** A total of 80
698 individuals were tested: individuals tested during summer are depicted in dark grey (males: N=23,
699 females: N=22) and individuals tested during winter in light grey (males: N=16, females: N=19).*: $p <$
700 0.05.

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702

703 **Fig. 2 Number of errors (black line) and latency in seconds to poke the correct hole (dash line)**
704 **for each trial of the short-term memory (left) and long-term memory (right) sessions of the**
705 **Barnes maze test, depicted as means \pm SE.** A total of 89 individuals were tested. The long-term
706 memory session occurred 8 ± 3 days after the short-term memory session. Trials N1 to N6 were
707 neutral trials, trials B1 and B2 were bat trials (animated predator-like toy above the maze) and trial C
708 was a control trial (no escape box); trials were separated from one other using a 5-minute delay. The
709 results of the pairwise-t-tests (number of errors: $a \neq b \neq c$, $p < 0.05$; latency: $\alpha \neq \beta \neq \gamma \neq \delta$, $p < 0.05$)
710 allowed us to group the trials in 4 distinct categories: the N-I category consisting of trials N1 and N2,
711 the N-II category consisting of trials N3, N4, N5 and N6, the Bat category consisting of trials B1 and
712 B2 and the Control category consisting of the trial C.

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715 **Fig.3 Latency in seconds to poke the correct hole depicted as means for each trial of the short-**
716 **term memory (left) and long-term memory (right) sessions of the Barnes maze test, in each sex**
717 **and for each season.** A total of 89 individuals were tested: individuals tested during summer are
718 depicted with a full line (males: N= 26, circles; females: N=22, triangles) and those tested during
719 winter with a dashed line (males: N= 25, circles; females: N=16, triangles). The long-term memory
720 session occurred 8 ± 3 days after the short-term memory session. Trials N1 to N6 were neutral trials,
721 trials B1 and B2 were bat trials (animated predator-like toy above the maze) and trial C was a control
722 trial (no escape box); trials were separated from one other using a 5-minute delay.

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725 **Fig. 4. Spatial performance of males for the Neutral-I, Neutral-II, Bat and Control categories of**
726 **trials of the long-term memory session in the Barnes maze test: (a) Number of errors (mean +**
727 **SE) and (b) latency to poke the correct hole in seconds (mean + SE).** A total of 51 males were
728 tested: individuals tested during summer are depicted in dark grey (N = 26) and those tested during
729 winter in light grey (N = 25); **: $p < 0.01$, ***: $p < 0.001$.

730

731 **Fig. 5. Spatial performance of females for the Neutral-I, Neutral-II, Bat and Control categories**
732 **of trials of the long-term memory session in the Barnes maze test: (a) Number of errors (mean +**
733 **SE) and (b) latency to poke the correct hole in seconds (mean + SE).** A total of 38 females were
734 tested: individuals tested during summer are depicted in dark grey (N = 22) and those tested during
735 winter are depicted in light grey (N = 16).

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739 **Electronic supplementary material captions**

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741 **Online resource 1: Orientation response test.**

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743 A mouse (identified with ear tags and red/blonde hair dye) placed in a transparent box facing a white
744 screen, orients its head towards the raptor-stimulus that appeared at the left-bottom of the screen and
745 slides in a rightward motion. The raptor-stimulus presentation lasts 5 seconds.

746

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748 **Online resource 2: Barnes maze test – Bat trial**

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750 A mouse (placed in transparent circular box at the center of the Barnes maze) is released, nose-pokes 4
751 incorrect holes and then locates the correct hole providing access to an escape box. A bat toy hanging
752 above the maze mimics the presence of a flying predator. Pictures of rocks and plants (photographed
753 in the natural habitat of the population of mice tested) that are placed on the walls and curtains
754 surrounding the maze provide visual landmarks to the mice.