

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

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Abstract Cognitive flexibility describes the reversible changes of cognition in response to environmental changes. Although various environmental factors such as temperature, photoperiod and rainfall change seasonally, seasonal variation in cognitive performance has been reported in merely a few birds and mammals. We assessed whether cognitive performance in a wild population of African striped mice *Rhabdomys pumilio*, from the Succulent Karoo semidesert of South Africa, differed between summer and winter. In order to measure cognitive performance, striped mice were trapped in the field, tested under laboratory conditions at our research station and returned to the field within 5 h. We measured attention and spatial memory using the standardized orientation response test and the Barnes maze test. Males tested during summer oriented faster toward a predator-stimulus but made more errors and took longer to locate a shelter than males tested during winter. In contrast, females' performance did not differ between the two seasons. We discuss how the faster orientation in males during winter might be the consequence

of lower temperatures and/or prolonged food restriction. We suggest that the enhancement of spatial performance during winter might be due to a greater motivation for future dispersal in male striped mice, as spring represents the breeding season.

Keywords Cognitive flexibility · Seasonality · Orientation response · Spatial memory · Sex differences

Introduction

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

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

There are a number of factors, such as food availability and photoperiod, which are associated with the change of seasons and may serve as environmental cues leading to changes in cognitive functions. One important factor that changes seasonally in most environments is ambient temperature. Maintaining a constant body temperature is energetically highly expensive for endotherms, especially for smaller-bodied species, such as rodents (Canals et al. 1989). Numerous studies have demonstrated that the basal metabolic rate increases as the ambient temperature drops (e.g., Geiser 2004). In addition, endotherms face the necessity to invest more energy into thermoregulation in environments where ambient temperatures fall clearly below their thermoneutral zone (i.e., range of ambient temperatures at which the metabolic cost of maintaining body temperature is minimal). Individuals living in energy-restricted environments are expected to trade-off between investing energy either into cognition or into other life-sustaining processes, such as thermoregulation (Maille and Schradin, submitted). Increased thermoregulatory costs could thus affect the energy available for cognitive processing, especially in animals with a high surface/volume ratio, such as rodents. In the current study,

we aimed to establish whether a seasonal decrease in ambient temperature would lead to lower cognitive performance in a free-living population of rodents. In the northern hemisphere, the cold season is also a season of low food availability which leads to the difficulty of disentangling the influence of seasonal changes in food availability versus ambient temperature on cognitive performance. To study the effect of ambient temperature independent of food availability, one would need a study system where the ambient temperature changes seasonally but food availability does not.

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

The environmental conditions occurring during the study enabled us to assess the influence of seasonal changes in temperature on cognitive performance of striped mice, while food availability remained relatively stable. In the year of the study, temperatures dropped from 9 °C at night in the austral summer to 1 °C at night in the austral winter, in both cases being clearly below the striped mouse thermoneutral zone of 31 °C (Scantlebury et al. 2006). However, food plant density remained low during both seasons because winter precipitation, characteristic of our study site in the Succulent Karoo, arrived very late (in June that is 2 months later than usual). The striped mice that were tested thus experienced a 6-month period of low food availability. We assumed that striped mice faced a greater need to trade-off energy allocation for cognition in winter, because of the prolonged period of low food availability coupled with the increased energetic costs of thermoregulation. We therefore predicted a reduction in cognitive performance of striped mice from summer to winter.

Materials and methods

Study species

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

Study area and period

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

The study took place from 17th January to 8th July 2014. The weather was hot and dry during the austral summer months of the study (17th January to 8th April: average temperature \pm SE = 25.1 ± 2.0 °C, total rainfall = 35 mm p.a.), whereas a drop in temperature occurred during the austral winter months (15th May to 8th July: average temperature \pm SE = 14.6 ± 1.4 °C, total rainfall = 46 mm p.a., Table 1).

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

Study animals

Cognitive tests were performed on 105 adult mice from nine different groups: 59 mice (30 males, 29 females) were tested in summer from 17th January to 8th April, and 46 mice (26 males, 20 females) were tested in winter from

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

	Tmin	Tmax	Rain	Pplants	Nfood	Population
<i>Jan</i>	8.8	42.6	22.2	16.2	4.4	240
<i>Feb</i>	9.5	43.2	0.7	14.6	2.3	228
<i>Mar</i>	5.3	42.9	17.2	14.3	1.6	196
<i>Apr</i>	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

Tmin, average daily minimum temperature in °C; Tmax, average daily maximum temperature in °C; Rain total precipitation in mm; Pplants, percentage of area covered by plants; Nfood: mean number of green food plant species; Population, total number of trapped individuals in the population. Data for Pplants and Nfood were collected twice a month in 8 distinct 4 m² plots (Schradin and Pillay 2006). Summer months of the study are marked in italic, winter months in bold

15th May to 8th July. None of the individuals was tested in both seasons to avoid any learning effect.

Trapping and marking

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

Body mass and metabolism

We measured body mass and performed blood sampling 5–20 days before cognitive testing to be able to measure metabolic indicators (glucose, ketone and corticosterone) while at the same time giving the mice enough time to rest between blood sampling and cognitive testing. Striped mice were trapped early in the morning before they left their nest to forage in order to obtain measurements after the overnight fast and before onset of foraging and pronounced physical activity. As soon as a mouse entered a trap, it was anaesthetized with diethyl ether and approximately 400 μ L of blood was obtained from a sublingual vein. Blood glucose and ketone bodies were directly

measured using the One Touch Ultra glucometer (Lifescan, Inc., Milpitas, CA, USA) and the Freestyle Optium Blood β -Ketone meter (Abbott Laboratories, Australia). Samples were collected within a 3-min delay and were transported to the research station where they were centrifuged twice for 10 min in order to obtain serum. Aliquots were stored at $-20\text{ }^{\circ}\text{C}$ and later analyzed at the Institut Pluridisciplinaire Hubert Curien using a validated commercial kit from IBL Hamburg.

Cognitive testing

Each morning, 2–3 striped mice were trapped at their nest within the first hour after sunrise and brought to a research room located a 5-min walking distance from the field site. Tests were performed in a specific laboratory room ($3.70 \times 3.10 \times 2.40\text{ m}$) constructed for this project. The laboratory room was split into two areas with a black non-translucent curtain hanging from the ceiling, one area being used for testing the mice (testing area: $1.60 \times 3.10 \times 2.40\text{ m}$) and the other area to serve as a hide for the experimenter. The temperature inside the laboratory room was not controlled and tracked the ambient outdoor temperatures (no heater used in winter). Individuals were first tested for the orientation response test (description below), lasting 10 min. Following an interval of 1–2 h during which mice were placed individually in a quiet room in a plastic cage ($22 \times 16.5 \times 14\text{ cm}$) with sand for bedding and an egg box as shelter, mice were brought back to the laboratory and tested in the Barnes maze test (description below), lasting 60–90 min. After testing, mice were given 10 sunflower seeds to compensate for missed foraging opportunities and were then released at their nest in the field site.

Orientation response test

The orientation response test uses the natural propensity of rodents to orient their head or whole body toward a salient stimulus (Rodríguez and Wetsel 2006). A mouse was placed in a perspex box ($18.5 \times 13 \times 11.5\text{ cm}$) that was centered in a black plastic chamber ($57 \times 38 \times 25\text{ cm}$). The lid and one lateral side of the box were transparent, whereas the other sides had been made opaque using black tape. The transparent lateral side of the box faced a computer screen (7 in. = $15 \times 9.5\text{ cm}$; distance box to screen: 17 cm) connected to a laptop (Online Resource 1). After a 5-min familiarization to the setup during which the mouse was exposed to a white screen, a raptor-stimulus was projected onto the screen. The raptor-stimulus was a photograph of flying jackal buzzard *Buteo rufofuscus*, a natural predator of the striped mouse, presented in a horizontal sliding motion (Online Resource 1). The raptor-stimulus presentation was repeated 10 times, once every 25 s, each

presentation lasting 5 s. To reduce habituation to the raptor-stimulus, a different starting location on the screen was used for each presentation. In addition, the raptor-stimulus moved either leftward or rightward (five presentations each). Mice were videotaped using a high-speed Casio camera EX-ZR200 recording at 120 frames/s. Light for videotaping was provided by a 11-W lamp mounted above the setup. For each presentation, we recorded whether the mouse showed an orientation response toward the raptor-stimulus and the time for the mouse to start orienting toward the raptor-stimulus. We considered that a mouse showed an orientation response when it turned its head toward the raptor-stimulus.

Barnes maze test

The Barnes maze test (Barnes 1979) measures spatial learning and memory by assessing the ability of rodents to relocate a hole giving access to a shelter among numerous available holes. The maze consisted of a circular platform 110 cm in diameter raised 60 cm from the ground (Online Resource 2). The maze was surrounded by a 30-cm-high transparent perspex cylinder because striped mice, unlike laboratory mice and rats, would otherwise have jumped off the platform. The platform was made of white perspex bored with 12 equidistant circular holes 5 cm in diameter and 7 cm from the outer edge (Online Resource 2). One hole provided access to a dark escape box underneath ($15 \times 13 \times 9\text{ cm}$), but the 11 remaining holes were closed with black PVC panels made of the same perspex as the escape box ($15 \times 13 \times 0.1\text{ cm}$, placed under the holes). To provide visual landmarks for the mice, we placed six pictures of rocks or plants from the field site on the walls and curtains surrounding the setup, 50 cm above the platform of the Barnes maze (mice could see the landmarks whatever their location in the maze; Online Resource 2).

Individuals were tested for two sessions, the second session (i.e., long-term memory session) occurring 8 ± 3 days after the first session (i.e., short-term memory session). The mice were released into the field after the first session and were re-trapped before the second session. Each session consisted of 9 trials separated by a 5-min delay during which the maze and escape box were cleaned using 70 % alcohol and the mouse was transferred from the escape box to the starting box. Trials were always conducted in the same order: 6 neutral trials N1 to N6 (i.e., with the escape box) that were followed by 2 bat trials B1 and B2 (i.e., with the escape box and a bat toy hanging above the maze) and finally a control trial C (i.e., no escape box and no bat toy). During the bat trials, an automated flapping battery run bat-like toy (out of the Blue KG, Germany) was hung 120 cm above the maze to mimic a bird of prey; striped mice were very wary and quickly

looked for shelter when exposed to this toy (Online Resource 2). During the control trial, the escape box was replaced by a black PVC panel to control for the use of visual and olfactory cues from the escape box.

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

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

Statistical analyses

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

Attention in the orientation response test

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

Spatial memory in the Barnes maze test

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

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

Results

Seasonal variation in body condition

The body mass and the blood glucose and ketone bodies levels did not differ between individuals tested in summer or in winter (t test: $p > 0.05$, Table 2), indicating that energy balance (energy intake – energy expenditure) did not change between the two seasons (McCue 2010). Basal corticosterone levels decreased from summer to winter (t test: $p = 0.011$, Table 2), which is supposed to reduce energy expenditure to enable individuals to cope with long periods of low food availability (Romero 2002).

Seasonal variation in attention (orientation response test)

Number of orientation responses

We excluded 11 males (summer: $N = 6$, winter: $N = 5$) and 6 females (summer: $N = 4$; winter: $N = 2$) from the analyses because they never reacted to the raptor-

Table 2 Body mass and metabolic indicators measured 5–20 days before cognitive testing in the striped mice tested in summer and winter (mean \pm SE)

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

Significant seasonal differences are marked in bold (* $p < 0.05$)

stimulus within the ten presentations. There was no difference between summer and winter in the proportions of individuals that never oriented or oriented to the raptor-stimulus (Fisher's exact test: males $p = 0.744$, females: $p = 0.684$). There was no significant seasonal effect on the number of orientation responses to the raptor-stimulus ($\chi^2 = 0.32$, $p = 0.572$) and no significant interaction between season and sex ($\chi^2 = 0.01$, $p = 0.946$).

Orientation time

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

Seasonal variation in spatial memory (Barnes maze test)

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

Spatial memory performance significantly differed between the short-term memory session and the long-term memory session [number of errors (E): $\chi^2 = 81.44$, $p < 0.001$; latency (L): $\chi^2 = 180.88$, $p < 0.001$] and among the 9 trials (E : $\chi^2 = 273.18$, $p < 0.001$; L : $\chi^2 = 476.09$, $p < 0.001$). Because the analyses also revealed significant interactions between sessions and trials (E : $\chi^2 = 49.38$, $p < 0.001$; L : $\chi^2 = 21.72$, $p = 0.005$), we

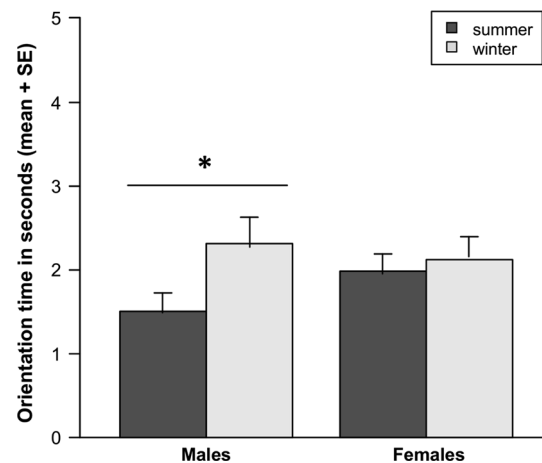


Fig. 1 Orientation time in seconds (means + SE) for the first orientation response toward the raptor-stimulus in the orientation response test in males (*left*) and females (*right*). A total of 80 individuals were tested: Individuals tested during summer are depicted in dark gray (males: $N = 23$, females: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

decided to perform all the subsequent statistical analyses for the two sessions separately.

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

Short-term memory session

For the short-term memory session, there was no significant seasonal effect on either the number of errors (E : $\chi^2 = 0.00$, $p = 0.966$) nor the latency to poke the correct hole (L : $\chi^2 = 0.73$, $p = 0.392$). Regarding the number of errors, the analysis revealed no significant interaction between season and category of trials (E : $\chi^2 = 0.33$, $p = 0.850$) and no significant interaction between sex,

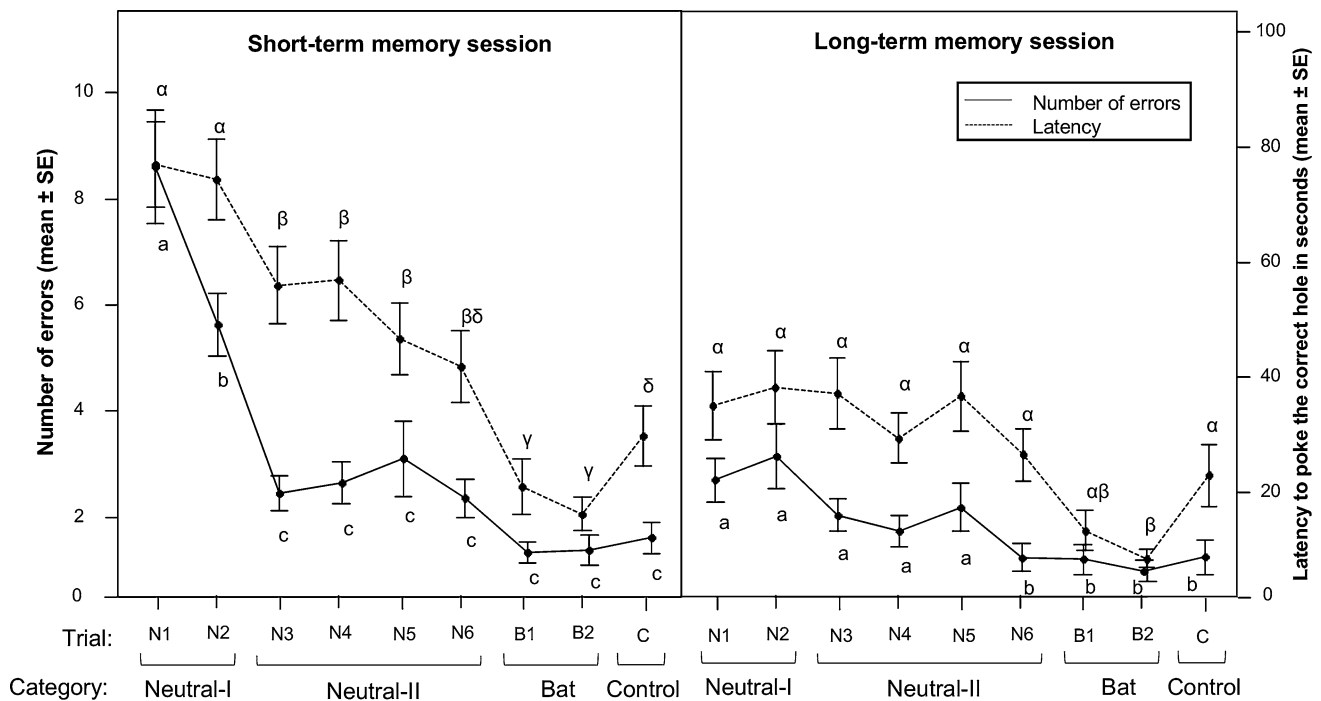


Fig. 2 Number of errors (*black line*) and latency in seconds to poke the correct hole (*dash line*) for each trial of the short-term memory (*left*) and long-term memory (*right*) sessions of the Barnes maze test, depicted as mean \pm SE. A total of 89 individuals were tested. The long-term memory session occurred 8 ± 3 days after the short-term memory session. Trials N1 to N6 were neutral trials, trials B1 and B2 were bat trials (animated predator-like toy above the maze), and trial

C was a control trial (no escape box); trials were separated from one other using a 5-min delay. The results of the pairwise *t* tests (number of errors: $a \neq b \neq c, p < 0.05$; latency: $\alpha \neq \beta \neq \gamma \neq \delta, p < 0.05$) allowed us to group the trials in 4 distinct categories: the N-I category consisting of trials N1 and N2, the N-II category consisting of trials N3, N4, N5 and N6, the bat category consisting of trials B1 and B2 and the control category consisting of the trial C

season and category of trials ($E: \chi^2 = 0.91, p = 0.823$). In contrast, regarding the latency to poke the correct hole, the analysis revealed significant interactions between the sex and the category of trials ($L: \chi^2 = 18.21, p < 0.001$) and between the season, sex and category of trials ($L: \chi^2 = 10.92, p = 0.012, \text{Fig. 3}$). We thus analyzed the influence of the season on the latency to poke the correct hole for each category of trials and for males and females separately.

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

Long-term memory session

For the long-term memory session, the analyses revealed a significant interaction between sex, season and category of

trials for both the number of errors and the latency to poke the correct hole ($E: \chi^2 = 30.68, p < 0.001$; $L: \chi^2 = 7.97, p = 0.047, \text{Fig. 3}$). We thus analyzed the influence of the season on the number of errors and the latency to poke the correct hole for each category of trials and for males and females separately.

Males tested during winter made significantly fewer errors in the neutral-II category than males tested during summer (*t* tests: N-II: $p = 0.009$), whereas there were no differences for the other categories (*t* tests: N-I: $p = 0.480$; bat: $p = 0.720$, control: $p = 0.560$; Fig. 4a). Males tested during winter poked the correct hole significantly faster in the neutral-II and control category than males tested during summer (*t* tests: N-II: $p < 0.001$, control: $p = 0.011$), whereas there were no differences for the other categories (*t* tests: N-I: $p = 0.290$, bat: $p = 0.500$; Fig. 4b). In contrast, whatever the category of trials, females tested during winter did not differ from those tested during summer for either the number of 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 latency to poke the correct hole (*t* tests: N-I: $p = 0.940$, N-II: $p = 0.290$, bat: $p = 0.890$, control: $p = 0.810$; Fig. 5b).

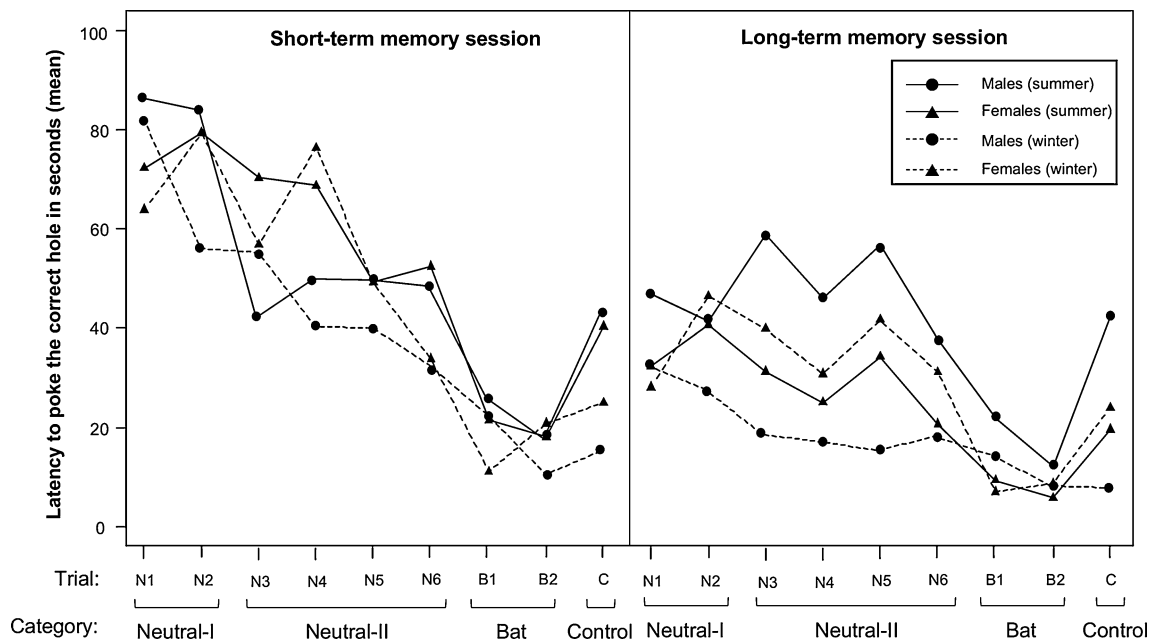


Fig. 3 Latency in seconds to poke the correct hole depicted as means for each trial of the short-term memory (*left*) and long-term memory (*right*) sessions of the Barnes maze test, in each sex and for each season. A total of 89 individuals were tested: Individuals tested during summer are depicted with a full line (males: $N = 26$, circles; females: $N = 22$, triangles) and those tested during winter with a dashed line

(males: $N = 25$, circles; females: $N = 16$, triangles). The long-term memory session occurred 8 ± 3 days after the short-term memory session. Trials N1 to N6 were neutral trials, trials B1 and B2 were bat trials (animated predator-like toy above the maze), and trial C was a control trial (no escape box); trials were separated from one other using a 5-min delay

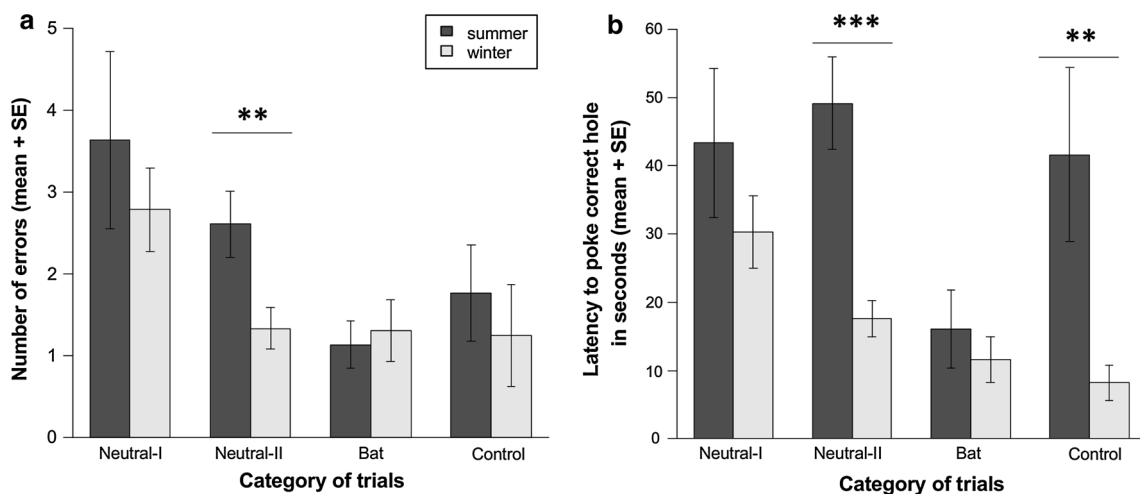


Fig. 4 Spatial performance of males for the neutral-I, neutral-II, bat and control categories of trials of the long-term memory session in the Barnes maze test: **a** Number of errors (mean + SE) and **b** latency to poke the correct hole in seconds (mean + SE). A total of 51 males

were tested: Individuals tested during summer are depicted in dark gray ($N = 26$) and those tested during winter in light gray ($N = 25$); $**p < 0.01$; $***p < 0.001$

Discussion

We assessed cognitive performance in attention and spatial memory in a free-living population of African striped mice *R. pumilio* that experienced seasonal changes in ambient temperature, while food availability remained relatively

stable. Males tested during summer oriented faster toward a predator-stimulus in an orientation response test but made more errors and took longer to locate the shelter in some (but not all) trials of a Barnes maze test compared to males tested during winter. Thus, the performance of males declined from summer to winter in a test assessing

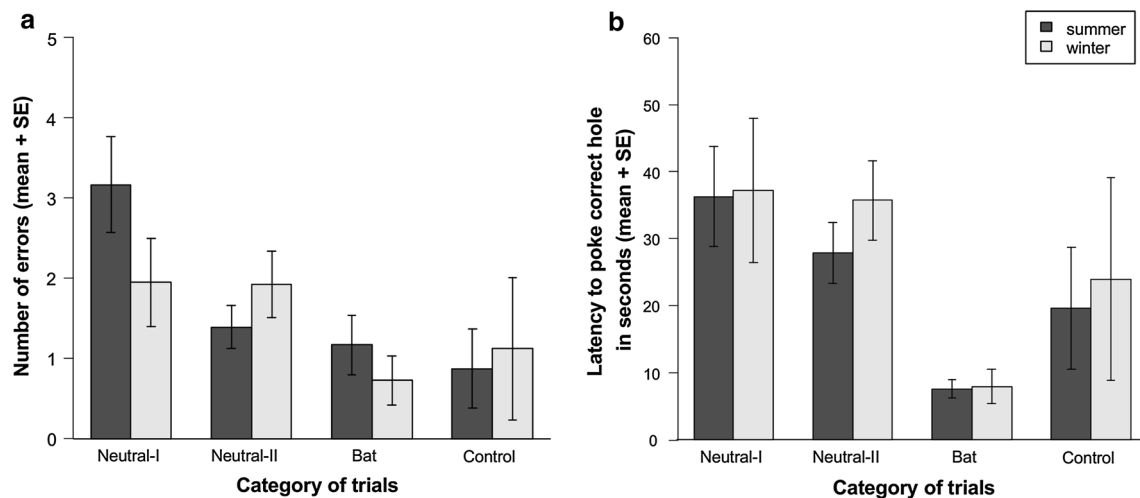


Fig. 5 Spatial performance of females for the neutral-I, neutral-II, bat and control categories of trials of the long-term memory session in the Barnes maze test: **a** Number of errors (mean + SE) and **b** latency to poke the correct hole in seconds (mean + SE). A total of 38

females were tested: Individuals tested during summer are depicted in dark gray ($N = 22$) and those tested during winter are depicted in light gray ($N = 16$)

attention, whereas they improved from summer to winter in a test assessing spatial learning and memory. In contrast, the performance of females did not differ between the seasons. Multiple potential proximate as well as ultimate factors can be put forward to explain these results.

Although seasonal variation in attention of male African striped mice must be interpreted with caution (because of a nonsignificant interaction between the sex and the season), males tested in winter were slower to orient toward the predator-stimulus in the orientation response test than males tested in summer. The increased orientation time of males tested in winter might be a consequence of seasonal changes in ambient temperature. Ambient temperature has a significant effect on the activity of striped mice, which use sun-basking to warm up especially when mornings are cold (Schradin et al. 2007), thereby reducing their energy expenditure (Scantlebury et al. 2010). The importance of sun-basking for thermoregulation and energy balance has been considered for diverse small mammals taxa (Geiser et al. 2002). Moreover, ambient temperature can be related to cognition in both birds and mammals. For example, short-term decrease in ambient temperatures affects foraging decisions in European starling *Sturnus vulgaris* (Chatelain et al. 2013) and induces both motor and cognitive impairment in humans (Solianik et al. 2014). Indeed, human reaction time is longer in cold environmental conditions, men being more affected by low temperatures than women (Solianik et al. 2014). Such sex differences in reaction time in response to cold might explain why only male striped mice were slower to orient toward a predatory-stimulus when tested during winter (low temperatures) compared to summer (high temperatures). However, we

cannot exclude the possibility that orientation time of male striped mice may have been influenced by at least two other proximate factors than the ambient temperature. First, attention of male striped mice might be influenced by the photoperiod (daylight length). Photoperiod is usually a highly reliable cue in predictable environments, enabling individuals to respond to seasonal changes (Yaskin 2011). For example, marsh tits *Parus palustris* that cache food during winter perform better in spatial learning during short compared to long daylight cycles (Clayton and Cristol 1996). However, we believe that photoperiod does not determine the attentional variation that we reported in male striped mice because photoperiod is not a reliable cue for seasonal changes in rainfall and consequently food availability in the Succulent Karoo. This lack of predictability may explain why food availability itself and not photoperiod regulates hormone secretion and reproduction in striped mice (Raynaud and Schradin 2013). Second, the increase in orientation time from summer to winter in male striped mice may alternatively be the consequence of prolonged food restriction within the study period, lasting from January to July. Cognitive impairments were reported in rats that had experienced at least 5 months of food restriction (Yanai et al. 2004). Since stress-induced changes in cognition are often sexually differentiated (Bowman 2005), the negative influence of prolonged food restriction on orientation time may have been more pronounced in males than females in the African striped mouse.

At the evolutionary level, seasonal cognitive flexibility in attention might have an adaptive value in species facing seasonal changes in predation risk. Faster detection of predators during summer in male striped mice may have

evolved in response to the higher predation pressure that probably occurs in this season because of high predator density (i.e., most predators of striped mice reproduce in late spring, leading to high population densities of predators in summer).

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

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

of male dispersal during this season and the following spring.

Conclusions

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

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Compliance with Ethical Standards

Ethical approval Animal ethical clearance was provided by the University of the Witwatersrand, Johannesburg, South Africa (No. 2013/50/2A). All procedures were in accordance with the ethical standards of the institution or practice at which the studies were conducted. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Conflict of interest The authors declare that they have no conflict of interest

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