How does cognitive performance change in relation to seasonal and experimental changes in blood glucose levels?

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In some species, cognition can change flexibly in response to environmental changes. These changes can be adaptive or can result from physiological constraints, such as when energy availability decreases seasonally. Here, we investigated: 1. how cognitive performance changes between seasons that differ significantly in food availability; 2. how these changes are related to environmentally induced physiological changes (blood glucose); and 3. whether experimental increase of blood glucose levels during the dry season impacts cognitive performance. We studied 93 free-ranging African striped mice (*Rhabdomys pumilio*) in the Succulent Karoo, South Africa during the hot summer dry season with low food availability, and the cold wet winter with high food availability. Striped mice

had reduced blood glucose levels during the food-restricted dry season. We measured their attention using the standardized orientation response test and their spatial memory using the Barnes maze test. Neither attention nor spatial memory changed seasonally. However, high basal and experimentally increased blood glucose levels impaired cognition in most cases. We also found sex differences in cognitive performance. Even though food was restricted in the dry season and blood glucose levels were reduced, cognition was not affected by these changes, indicating cognitive resilience, which represents an evolved adaptation to cope with seasonally changing energy supply in striped mice.

Keywords

Attention, Blood glucose, Cognitive flexibility, Cognitive resilience, Seasonality, Sex differences, Spatial memory, *Rhabdomys pumilio*

Cognition is defined as the processes by which animals collect, retain and use information from their environment to guide their behaviour (Shettleworth, 2009). Behaviours, such as foraging, predator avoidance and mating, rely on cognition. An animal's cognitive performance can be affected by environmental conditions (Ferrari, 2014; Pravosudov, Roth, Ladage, & Freas, 2015; Tello-ramos et al., 2018). Individual variation in cognitive traits is likely to influence how animals react in their changing environment, and their survival and reproductive success (Cole, Cram, & Quinn, 2011; Maille & Schradin, 2016b). As a product of natural selection, cognitive abilities are adapted to closely match the cognitive demands imposed by the current environmental conditions (Cauchoix & Chaine, 2016). Cognitive flexibility, *i.e.* the ability to adapt cognitively-driven behaviour in response to changing situational demands (Klanker, Feenstra, Denys, Lo, & Tsing, 2013), may occur as a response to changing environmental conditions (Tello-ramos, Branch, Kozlovsky, Pitera, & Pravosudov, 2019).

One example of cognitive flexibility is seasonal variation in cognitive performance, which has been observed in bird and mammal species (Galea & McEwen, 1999; Sherry & Hoshooley, 2009). For instance, in the common shrew *Sorex araneus*, spatial learning abilities of individuals are higher in summer compared to winter, when individuals show a reduction in brain size (*i.e.* the Dehenel effect; Lázaro et al., 2017). Under harsh seasonal conditions, cognitive performance might be enhanced as an adaptation to meet specific ecological needs (Buchanan, Grindstaff, & Pravosudov, 2013). For example, food restriction leads to improved learning in cichlid fish *Simochromis pleurospilus* (Kotrschal & Taborsky, 2010). A comparison of two subspecies of white crowned sparrow, one migratory (*Zonotrichia leucophrys gambelii*) and the other non-migratory (*Z. l. nuttalli*), revealed that the migratory subspecies showed better spatial memory and larger relative size of the hippocampus, and have more hippocampal neurons (Pravosudov, Kitaysky, & Omanska, 2006).

Comparisons of two populations of food-caching chickadees (*Poecile atricapilla*) experiencing different winter climatic conditions showed that chickadees living under harsher conditions cached more food, were more efficient at cache recovery, performed more accurately on a spatial memory task, and had larger hippocampal volumes (Pravosudov & Clayton, 2002). Alternatively, a need to reduce energy-demanding physiological processes under harsh seasonal conditions might impair cognitive performance (Laughlin, 2001). Individuals spending more energy than they can currently obtain from their environment (allostatic overload type I; McEwen & Wingfield, 2010a), are expected to trade off energy investment between different processes, for example cognition and reproduction (Mery & Kawecki, 2004). In contrast, the cognitive resilience hypothesis predicts that cognition is so important for fitness that it is shielded from low energy availability, such that cognitive performance remains unvarying even if food availability is low and other traits suffer as a consequence (Buchanan et al., 2013). Although seasonal environmental changes are expected to influence cognition, previous studies have provided contrasting results about whether cognition is maintained, impaired, or improved when environment conditions harshen.

The ecophysiology of cognition considers how environmentally-induced physiological changes affect cognition (Maille & Schradin, 2016a). Several environmental factors (such as food availability and photoperiod) change seasonally, inducing physiological changes (Schradin, 2008; Wikelski & Ricklefs, 2001). For example, under natural conditions, blood glucose levels can be altered *via* food availability and ambient temperature (*e.g.* African striped mouse: Schradin et al., 2015; free-ranging goats: Pambu-Gollah, Cronjé, & Casey, 2000). Hence, these changes in blood glucose levels can occur over a long time period (Schradin et al., 2015). Changes in blood glucose might affect cognitive performance (Donohoe & Benton, 1999). One hypothesis is that a decrease in blood glucose induces cognitive impairment due to the high energy demand of brain function. For example, in humans poorer performance in a Stroop task was reported in individuals with lower blood glucose levels (Gluck et al., 2013) and low blood glucose levels were associated with poorer learning and memory performances in both rats and humans (Gold, 1995). In contrast, cognitive performance in both humans and rats has been shown to decrease following the ingestion of a high-glycemic-index meal, which significantly increased blood glucose levels (Benton et al., 2003). In rats, chronic sucrose

consumption induced deficits in spatial cognition that remained long after exposure (Kendig, Boakes, Rooney, & Corbit, 2013). The alternative cognitive resilience hypothesis suggests that cognitive functions will be maintained despite external environmental challenges induces changes in blood glucose levels, because of the high importance of good cognitive function (Buchanan et al., 2013). This could be achieved by physiological (*e.g.* reduced susceptibility of neurons to oxidative stress) and / or behavioural strategies (*e.g.* microhabitat choice) protecting the brain against detrimental environmental effects. Furthermore, the brain specific glucose transporter GLUT3 has a very high affinity to glucose (compared to other glucose transporters in other organs) that allows for a relatively constant glucose uptake independent of extracellular glucose concentration (Frayn, 2010), which might explain the mechanism of cognitive resilience in periods of low basal blood glucose level. It is unknown whether results obtained under artificial conditions using optimally fed individuals reflect the natural situation, especially in species experiencing seasons of low food availability causing low blood glucose levels (Schradin et al., 2015). Thus, investigating environmentally induced changes in blood glucose levels, *e.g.* during periods of low food availability, might indicate trade-offs between cognition and other energetically expensive processes.

In the present study, we investigated the eco-physiology of cognition in free-ranging African striped mice (*Rhabdomys pumilio*). Striped mice inhabit semi-desert areas in southern Africa where they face marked seasonal changes in food availability (Cowling, Esler, & Rundel, 1999).The summer dry season is characterized by low food availability when striped mice have low blood glucose levels, while both food and blood glucose rise in the winter wet season (Schradin et al., 2015). Striped mice breed in spring (from August to December). The striped mouse is an interesting species to study cognitive flexibility in free-ranging mammals because of its seasonal environment and as it is diurnal, which enables behavioural testing during the day. Importantly, recent studies in this species showed seasonal changes in cognitive performance of males between early winter and summer (Maille, Pillay, & Schradin, 2015) and striped mice survival increased with higher attention and spatial memory performances (Maille & Schradin, 2016b).

Several eco-physiological hypotheses can be considered when studying seasonal changes in cognition. Impaired cognition when food availability is low (*i.e.* positive relationship between

156 cognitive performance and blood glucose) might arise from a need to reduce energy-demanding
157 processes while facing allostatic overload type I (energy consumption higher than energy uptake;
158 McEwen & Wingfield, 2010). Alternatively, enhanced cognitive performance when food availability
159 is low (*i.e.* negative relationship between cognitive performance and blood glucose) might be selected
160 in animals living under energetically challenging environmental conditions, when improved cognitive
161 performance helps to improve energy saving or foraging ability (Pravosudov, 2003; Pravosudov &
162 Clayton, 2002). These two alternative hypotheses can be tested against the null-hypothesis of
163 cognitive resilience, *i.e.* the ability to maintain cognitive function despite external environmental
164 challenges (Buchanan et al., 2013), which would predict no seasonal changes in cognition.
165 Here, we considered the extent to which attention (*i.e.* the ability to process selectively one
166 aspect of the environment over others, Bushnell, 1998) and spatial learning and memory (*i.e.* the
167 ability to store spatial mental representations either for a small amount of time - short term memory, or
168 a large amount of time - long term memory, Shettleworth, 2009) changes seasonally in striped mice.
169 We tested striped mice outside of their breeding season to avoid possible cognitive and physiology
170 differences due to breeding activity (Schradin, 2008). We investigated whether variation in attention,
171 spatial learning and memory was related to environmentally-induced changes in physiology (*i.e.*
172 glucose levels), and whether an experimental increase of blood glucose levels in the dry season (when
173 these levels are typically low) influenced attention, spatial learning and memory. We focused on traits
174 which would be important to reduce predation risk and for foraging during harsh conditions in a small
175 diurnal mammal living in an open environment (Maille & Schradin, 2016b): attention (measured as
176 reaction time) to a dangerous situation such as an approach by a bird of prey and spatial learning and
177 memory of the location of a shelter. We made three predictions. First, we predicted that blood glucose
178 levels would be lower during the dry season compared to the wet season, indicating that energy intake
179 is constrained. Second, we predicted that cognitive performance would be impaired during the dry
180 season compared to the wet season because of a need to reduce energy-demanding processes. Third,
181 we predicted that cognitive performance would be positively correlated with basal blood glucose
182 levels and would be improved by an experimental increase in blood glucose levels.
183

METHODS

Ethical note

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. This study also complies with the ASAB/ABS Guidelines for the Use of Animals in Research. We took care in ensuring the animals' welfare throughout the experimental procedure and afterwards. Following marking using ear tags and equipping them with radio transceivers, we usually trapped the mice again on the same day to check their welfare state (*e.g.* checked ears, neck, eyes, no external airway obstruction). During blood sampling, mice were anaesthetized to limit pain and stress. They received a piece of food after the procedure. We checked their awareness, breathing rate and released them at their nest within maximum 30 minutes. During cognitive tests, mice were transported in their traps and we checked mice behaviour continuously *via* the video recording. No injury occurred due to the cognitive apparatus. Mice were fed with sunflower seeds to compensate for missed foraging opportunities and were released at their nest within maximum 80 minutes after cognitive tests.

Study species

One population comprising of several distinct social groups of African striped mice was studied in the semi-arid Succulent Karoo, South Africa. Social groups of striped mice (2–30 adult individuals of both sexes) share one nest and territory which they defend against neighbouring groups but forage solitarily (Schradin, 2006). Striped mice usually breed in the next year of their birth when they are 10–12 months old (Schradin & Pillay, 2005). The date of birth of individuals was estimated from the first time a mouse was trapped and according to its body mass (Schradin, Schneider, & Yuen, 2009). It was not possible to estimate their exact age but all mice studied were born during the previous breeding season (spring 2014). Because of communal breeding and extra-group paternity (Schradin et al., 2012) we did not know kinship in our population.

Study area and period

We conducted the study in Goegap Nature Reserve (S 29 41.56, E 18 1.60) in a 10 ha study area. In this area, summer is the dry season and winter is the wet season. Hence, the weather was hot and dry during the austral summer period of our study (30th January to 24th March 2015: average ± SE temperature = 23.9 ± 0.1°C, rainfall = 0.08mm/day), and temperature dropped during the austral winter months of the study (2nd July to 17th August 2015: 12.2 ± 0.1 °C, rainfall = 0.30 mm/day). Because striped mice mainly feed on plants, we assessed their food availability through plant surveys. We used the Braun-Blanquet method (Wikum & Shanholtzer, 1978) to conduct plant surveys on the 1st and on the 15th of each month at our field site. We recorded the number of food plants species for striped mice in each of eight monitoring plots of 4 m^2 each (Schradin & Pillay, 2005).

Study animals

We assessed cognitive performance using the orientation response test and the Barnes maze test. We tested 93 adult mice representing 17 different social groups for each season: 53 mice (27 females and 26 males) were tested in summer from 30th January to 24th March and 40 other mice (18 females and 22 males) were tested in winter from 2nd July to 17th August. None of the individuals were tested in both seasons to avoid any learning effects. There was an equal distribution of males and females for each social group (GLM: χ^2_1=0.0001, P=0.99). We chose to test 1/3 of the entire population in summer to ensure that there were sufficient naïve (untested) mice in the population for the winter season tests, particularly since predation and dispersal both impact population size. All tested individuals were non-breeding adults during the experimental period to avoid possible cognitive and physiological differences due to breeding activity. We permanently marked mice using ear tags (National Band and Taf Co., Newport, KY, USA). Monitoring of the population and determination of group association was performed by routinely trapping individuals at their nests, direct behavioural observations, and radio-tracking (for details see Schradin, König, & Pillay, 2010).

Measurement of basal blood glucose

Blood sampling was done regularly in our study population and we obtained basal blood glucose levels from 105 (56 males, 49 females) striped mice in summer (dry season: high temperature,

low precipitation, low food availability) and 64 (34 males, 30 females) striped mice in winter (wet season: low temperature, high precipitation, high food availability). We collected blood from all mice which were tested for their cognitive performance. We trapped the mice early in the morning before they left their nest to forage. Thus, blood sample measurements were obtained after the mice fasted overnight and before their onset of foraging and pronounced physical activity. Immediately after a mouse entered a trap, we anaesthetized it with diethyl ether and a maximum of 500µL of blood was obtained from the sub-lingual vein within 3 min from trapping. We needed this blood quantity for our study and additional hormonal measurements for another study. We measured basal blood glucose in the field by using the One Touch Ultra glucometer (Lifescan, Inc., Milpitas, CA, USA). The mice were given a piece of the bait used in their trap just after the procedure and were released at their nest. We measured basal blood glucose levels 4 ± 2 days before the cognitive tests to give the mice sufficient time to recuperate between blood sampling and cognitive testing. In striped mice, no diurnal variation in blood glucose levels has been found between the morning and afternoon in spring (paired t-test: N=11, t_{10}=0.042, P=0.97) or summer (paired t-test: N=20, t_{19}=0.65, P=0.52, Schradin, unpublished data).

Experimentally-induced changes in blood glucose: sucrose or saccharine treatment

The aim of experimentally-induced changes in blood glucose was to test whether increasing blood glucose levels during the dry season, which had already been shown to be low compared to the wet season with high food availability (Schradin *et al*., 2015), improves cognitive performance. There was no justification to increase blood sugar levels in the wet season, when blood glucose levels were already high, as we wanted to test whether decreased blood glucose levels during the dry season affect cognition. In summer (low food availability), we experimentally increased blood glucose using a sucrose treatment in 25 individuals (13 females and 12 males) out of the 53 mice that were tested for cognition. The other 28 mice (12 females and 13 males) received a saccharine treatment as an experimental control. In winter (high food availability - when blood glucose levels are already high), 35 mice (16 females and 19 males) received a saccharine treatment as a control for comparison with

mice that had received sucrose in summer. Treatments were allocated to generate the same number of males and females originating from different social groups in each treatment.

Each day, during the summer and winter study period, we trapped 2 striped mice at their nest within the first hour after sunrise and brought them to the research station located a 5-min walking distance from the field site. Mice were transported in their traps. We weighed each mouse and then placed them in a quiet room in a plastic cage (22 x 16.5 x 14 cm) with sand for bedding. An individual received the experimental blood glucose level change treatment for which it was allocated as follows: After a 15-minute (first mouse) or a 90-minute (second mouse) period, a jam jar lid containing a piece of jelly was placed in the centre of the cage. We prepared the jelly by diluting 2 grams of agar-agar and either 20 grams of sugar (sucrose treatment) or 4 pills (Ø5mm, 60mgof saccharine, which is approximately 333 times as sweet as sucrose) of Cologran from Lidl Germany (saccharine treatment) in 100 mL of water. Each individual mouse was given 0.025 grams of jelly per gram of body mass (*e.g.* 1 g of jelly for a 40 g individual), thus representing 5 grams of sucrose or 4 grams of saccharin per kilogram of body mass. Treatment groups were alternated every day (1st received sucrose, 2nd received saccharine and *vice versa* on different days). One hour after receiving the sucrose or saccharine treatment, we took each mouse to the research room and tested them in the orientation response and Barnes maze tests, as described below. After completion of cognitive tests, we assessed experimental increase of blood glucose. Approximately 2 drops of blood were obtained from either the facial vein or the sub-lingual vein exactly 120 minutes after providing mice the jelly. We needed only 2 drops of blood to measure glucose levels.

We conducted a pilot study to confirm that our sucrose treatment increased blood glucose in the 60-minute interval that we used between providing mice with jelly and starting cognitive tests. We measured blood glucose 60 minutes after giving jelly to 35 individuals (16 females and 19 males, different individuals to those used in the present study). Blood glucose level was higher in mice that received the sucrose treatment (N=17; blood glucose: 7.4 ± 0.5 mmol/litre) than mice that received the saccharine treatment (N=18; blood glucose: 5.8 ± 0.5 mmol/litre, t-test: T=-2.17, P=0.037).

Cognitive testing

For each mouse, two cognitive tests were performed in succession, firstly the orientation response test to evaluate attention performance, lasting 10 minutes and secondly (*i.e*. 10 min later) the Barnes maze test to evaluate spatial learning and memory, lasting 35 to 55 minutes depending on individuals' performance. At the end of tests and after the blood glucose measurement, we fed mice with 10 sunflower seeds to compensate them for missed opportunities of foraging and we released them at their nests after experiments.

Each mouse was tested individually for cognition in a research room (L 3.70 x B 3.10 x H 2.40 m) that was split into two areas with a black opaque curtain hanging from the ceiling. One area was dedicated to mice testing (testing area: 1.60 x 3.10 x 2.40 m) and the other area was used to hide the experimenter. All cognitive tests were video recorded and analysed later by the experimenter (who was aware of the experimental treatments).

Attention: the orientation response test

We placed a mouse in a perspex box (18.5 x 13 x 11.5 cm) that was located in the centre of a black plastic chamber (57 x 38 x 25 cm). All box sides were opaque except the lid and one lateral side of the box that were transparent. Above the box, we attached a computer screen (15 x 9.5 cm; distance box to screen: 17 cm) connected to a laptop. The mouse was exposed to a white screen for a 5-minute familiarization phase. Then, we displayed a raptor-stimulus onto the screen. This was a photograph of a jackal buzzard (*Buteo rufofuscus)* in flight*,* a natural predator of the striped mouse. We presented the raptor in a horizontal sliding motion. In order to explore individual differences in number of reactions and to increase the chance that the mice reacted at least once to the raptor-stimulus, we presented the photograph 10 times for each mouse, once every 25 s, and for 5 s each time (for details, see online resource of Maille et a. 2015; https://download-tls-cdn.edge-cdn.net/videodb/5501/videodb_5501_53500_6624641_16x9_hq.mp4). We used a different starting location on the screen for each presentation to reduce habituation to the raptor-stimulus. In addition, the raptor-stimulus moved either leftwards or rightwards in a pseudorandom order (5 presentations each). We videotaped mice using a high speed Casio camera EX-ZR200, recording at 120 frames/s. A 11W lamp was mounted above the experimental set-up. We recorded whether the mouse showed an

orientation response toward the raptor-stimulus for each presentation, and the time for the mouse to start orienting toward the raptor-stimulus (*i.e*. reaction time). We considered an orientation response when a mouse turned its head towards the raptor-stimulus (83 of the 93 tested mice reacted to at least one presentation of the raptor-stimulus).

Spatial learning and memory: the Barnes maze test

During the Barnes maze test, we investigated the spatial learning, short-term spatial memory under predation pressure as well as the long-term spatial memory under predation pressure occurring 4±2 days later. We used 75 of the 93 mice in the long-term spatial memory test since the remaining 18 were not re-trapped within 6 days. The maze was placed on a table top 60 cm above the floor and consisted of a circular platform of 110 cm in diameter. We surrounded the maze with a 30 cm high transparent perspex cylinder to prevent striped mice jumping off the platform. The platform was made of white perspex with 24 equidistant circular holes 4 cm in diameter and located 7 cm from the outer edge. No landmarks were available except one curtain that separated the room in two areas and a second curtain that concealed the window on the opposite wall. One hole provided access to a dark escape box (15 x 13 x 9 cm) beneath the maze and the 23 remaining holes were closed with black perspex panels (15 x 13 x 0.1 cm) placed under the holes, and of the same color as the escape box.

We tested individuals for 6 trials separated by a 5-minute interval during which the maze and escape box were cleaned using 70% alcohol, when we transferred the mouse from the escape box to a waiting cage. We always conducted trials in the same order: 1) spatial learning phase: 4 neutral trials N1 to N4 (*i.e.* with the escape box); 2) short term spatial memory test under predation pressure: the bat trial test (*i.e.* with the escape box and a bat toy hanging above the maze to mimic predator presence to increase mice motivation to find the shelter); 3) one control trial C (*i.e.* no escape box and no bat toy); 4) long term spatial memory test under predation pressure: the 2nd bat trial test, 4±2 days later. During bat trials, an automated flapping battery powered bat-like toy (Out of the Blue KG, Germany) was hung 120 cm above the maze to mimic a bird of prey since we could not find a moving toy shaped like a buzzard. During the control trial, we replaced the escape box with a black PVC panel to control for the use of visual and olfactory cues from the escape box. We re-trapped mice 4±2 days later and we

tested them again for one bat trial only. We randomly located the location of the correct hole for each mouse and it remained constant for all the trials for that individual mouse.

Before each trial, we placed the mouse in a circular and transparent starting box (diameter = 10 cm, height = 10 cm) in the centre of the Barnes maze. A trial started when we released the mouse from the starting box that was lifted by pulling a string attached to the box. We pulled the string from behind the curtain to reduce disturbance of the test mouse. The end of the neutral and the bat trials occurred when the mouse entered in the escape box. When the mouse did not enter the escape box within 5 minutes, we gently led the mouse to the correct hole and encouraged it to enter the box. In the tests, 12 of the 93 mice showed a freezing behaviour or refused to enter the escape box in the first bat trial. The control trial ended when the mouse poked its nose in the correct hole.

We videotaped the behaviours of the tested mouse using a Microsoft HD web-camera mounted above the experimental set-up and connected to a laptop. For each trial, we recorded the latency to poke the correct hole and the number of errors (*i.e.* poke into a hole other than the correct hole) before the mouse poked the correct hole, which was used to assess spatial learning (during the neutral trials N1, N2, N3, N4) and short (1st bat trial) and long term memory (2nd bat trial). A mouse was considered to have poked a hole when it placed its nose inside the hole or less than 1 cm away from the hole with its head being orientated towards the hole.

2.7. Statistical analyses

All statistics were performed with R v. 3.5.0 (The R foundation for statistical computing, http://www.r-project.org/). The significance level was set at 0.05. Mean and standard error values are provided the descriptive statistics. Mixed models were constructed using the lmer or glmer function in the *lme4* package and statistical tests were performed using the Anova function in the *car* package. Post-hoc tests were performed using the emmeans function in *emmeans* package, with a Tukey correction. Independence and homogeneity of variances of the mixed models were assessed by inspection of fitted residuals using the plotresid function in *RVAideMemoire* package. To obtain better fitted residuals, we used log transformation for the latency variable in the Barnes maze test. We specified social group identification as a random factor in all mixed models with repeated

measurements to control for potential confounding effects of social group origin (litter and/or ecology).

We compared food availability between summer and winter by performing a linear mixed model with food availability as a dependent variable and season as a fixed effect. The influence of the season on basal blood glucose was analysed for all samples available from our entire study population (N=105 mice in summer and N=64 in winter) using a linear mixed model with basal blood glucose level as the dependent variable and season, sex and the interaction between season and sex specified as fixed effects, body mass as a covariate and the identity of the mice nested in the group of the mice as a random effect (to account repeated blood measurement on the same individual). The influence of the experimental condition (*i.e.* summer-sucrose, summer-saccharine and winter-saccharine) on blood glucose level was analysed using a linear mixed model with blood glucose as dependant variable, sampling time (2 days before receiving the treatment or 2 hours after receiving the treatment), experimental condition, sex and the interaction between experimental condition and sex as fixed effects and the identity of the mice nested in the group of the mice as random effect.

To assess the association between basal blood glucose and cognitive performance, analyses were performed only on mice that received the saccharine treatment either in summer or winter. The association between basal blood glucose level and attention performance in the orientation response test was analysed using a linear mixed model with either orientation time in the first orientation response (linear mixed model) or number of orientation responses (generalized mixed model for Poisson data) as the dependent variable, basal blood glucose and body mass as a co-variates, sex and the interaction between basal blood glucose and sex as fixed effects and group of the mice as random effect. The association between basal blood glucose level and spatial learning and memory performance in each of the two bat trials of the Barnes maze test was analysed using a mixed model with either latency to poke the correct hole (log latency - linear mixed model) or number of errors (generalized mixed model for Poisson data) as the dependent variable, basal blood glucose and body mass as co-variates, sex and the interaction between basal blood glucose and sex as fixed effect and group of the mice as random factor.

406 To assess the influence of experimental condition (*i.e.* summer-sucrose, summer-saccharine
407 and winter-saccharine) on cognitive performance, analyses were performed on all mice tested. The
408 influence of experimental condition on attention in the orientation response test was analysed using a
409 linear mixed model with either orientation time in the first orientation response (linear mixed model)
410 or number of orientation responses (generalized mixed model for Poisson data) as the dependent
411 variable, body mass as a co-variate, sex, experimental condition and the interaction between sex and
412 experimental condition specified as fixed effects and group of the mice as a random effect. The
413 influence of the experimental condition on short-term and long-term spatial memory in the Barnes
414 maze test was analysed by performing two mixed models, with either latency to poke the correct hole
415 (log latency -linear mixed model) or number of errors (generalized mixed model for Poisson data)
416 measured in each bat trial as the dependent variable, body mass as a co-variate, sex, experimental
417 condition and the interaction between sex and experimental condition as fixed effects, and group of the
418 mice as a random effect. We analysed spatial memory only in the two bat trials because these trials
419 indicated whether striped mice quickly remembered the location of an escape hole under potential
420 predation risk, either a few minutes (first bat trial occurring 5 minutes after the last neutral trial, *i.e.*
421 short-term spatial memory) or several days (second bat trial 4±2 days after the last neutral trial, *i.e.*
422 long-term spatial memory) after learning to find this escape hole in the maze.
423 Spatial learning during the four neutral trials of the Barnes maze test was confirmed using a
424 mixed model with either number of errors (generalized mixed model for Poisson data) or latency to
425 poke the correct hole (log latency - linear mixed model) measured in each neutral trial as the
426 dependent variable, trial number (N1, N2, N3, N4) as a co-variate, sex, experimental condition and the
427 interaction between trial number and experimental condition as fixed effects and the identity of the
428 mice nested in the group of the mice as a random factor (*i.e.* repeated measures design).
429
430 **RESULTS**
431
432 *Changes in physiology*
433

434 *Seasonal changes in food availability and blood glucose level*

435 Food availability for the striped mice increased within the study period from summer (1.31±0.78 food
436 plants/plot) to winter (6.25 ± 1.75 food plants/plot) (LMM, $N_{\text{summer plots}} = 32$, $N_{\text{winter plots}} = 32$, χ^2_1
437 =214.25, P<0.0001). For the entire striped mice population in our study site (105 mice in summer and
438 64 in winter; including mice tested for cognition), body mass increased from summer to winter (LMM:
439 N=169; χ^2_1=178.06, P<0.001) and mice had higher basal blood glucose levels in winter (July-Aug
440 2015: 5.86 $\pm$ 0.18 mmol/litre) than in summer (Feb-March 2015: 5.07 $\pm$ 0.13 mmol/litre, LMM:
441 N=169; χ_1^2=13.20, P=0<0.001). There was no effect of sex and body mass on the glucose level (LMM:
442 N=169; sex: χ^2_1=0.29, P=0.58; body mass: χ^2_1=155.85, P=0.15).
443 In our subsample of striped mice tested for cognition, body mass increased in winter (LMM: N=93, χ^2
444 $_1$=50.81, P<0.001). There was no difference in the basal blood glucose levels between the summer
445 (N=55) and winter seasons (N=38, LMM: χ^2_1=0.88, P=0.34; Fig. 1.a). There was no effect of sex and
446 body mass on blood glucose levels (LMM: N=93; sex: χ^2_1=0.97, P=0.32; body mass: χ^2_1=0.17,
447 P=0.68). Males were heavier than females (males : 39.16 ± 6.44g; females : 34.00 ± 5.47g; LM: N=93,
448 χ^2_1=16.5, P=0<001).
449
450 *Experimentally-induced changes in blood glucose level*
451 Blood glucose level measured in striped mice 2 hours after being fed jelly (and after cognitive tests
452 were completed) differed between experimental conditions (LMM: N=93, χ^2_1=7.06, P=0.007): blood
453 glucose was higher in individuals that received the sucrose (only done in summer, 8.25 ± 0.71
454 mmol/litre, [3.78 – 23.11 mmol/litre]) than in mice that received the saccharine in summer (5.23 ±
455 0.29 mmol/litre, [2.50 – 10.28 mmol/litre]) (t-test: $N_{\text{summer-sucrose}}$=27, $N_{\text{summer-saccharine}}$=28, t_{175} = -3.89,
456 P=0<001, Fig 1.b) and in winter (5.49 ± 0.27 mmol/litre, [2.67 – 9.00 mmol/litre]) (t-test: $N_{\text{summer-}}$
457 $_{\text{sucrose}}$=27, $N_{\text{winter-saccharine}}$= 38, t_{175} = 5.14, P<0.001, Fig 1.b). Blood glucose level measured after the
458 cognitive tests did not differ between mice that received the saccharine treatment in summer and
459 winter (t-test: $N_{\text{summer-saccharine}}$=28, $N_{\text{winter-saccharine}}$=38, t_{175} = 0.98, P=0.58, Fig 1.b). There was no effect
460 of sex (LMM: N=93, χ^2_1=2.38, P=0.30).
461

Changes in cognitive performance

Attention in the orientation response test:

Association between basal blood glucose and attention performance

The number of orientation responses towards the raptor stimulus did not differ according to blood glucose level, sex, and body mass (GLMM, N=60, P>0.05). The orientation time for the first response to the raptor stimulus was related to basal blood glucose level (LMM: N=60; χ^2_1=4.88, P=0.03): the higher the basal blood glucose level, the faster the mice orientated toward the stimulus (Fig 2). There was no effect of sex (LMM: N=60; χ^2_1=1.19, P=0.28) nor body mass (LMM: N=60; χ^2_1=2.14, P=0.14) and no interaction between sex and glucose level (LMM: N_{males}=32, $N_{females}$=28; χ^2_1=0.29, P=0.59) on this orientation time.

Influence of experimentally-induced increase in blood glucose on attention performance

The number of orientation responses towards the raptor stimulus did not differ according to the experimental condition (*i.e.* summer-sucrose, summer-saccharine, winter-saccharine), sex and body mass (GLMM, N=93, P>0.05). There was an interaction between the sex and the experimental condition on the orientation time for the first response to the raptor-stimulus (LMM: N_{males}=48, $N_{females}$=40; χ^2_2=19.13, P<0.001). Males that received the sucrose treatment in summer reacted slower to the raptor-stimulus than males that received the saccharine treatment in summer (t-test: $N_{summer\text{-}sucrose}$=12, $N_{summer.saccharine}$=13, t_{24} = -7.38, P<0.001; Fig.3) and in winter (t-test: $N_{summer\text{-}sucrose}$=12, $N_{winter.saccharine}$=19, t_{30} = 5.13, P<0.001; Fig.3) while there was no difference between males that received the saccharine in summer compared to winter (t-test: $N_{summer.saccharine}$=13, $N_{winter.saccharine}$=19, t_{31} = -1.24, P=0.43; Fig.3). In contrast, orientation time in females did not differ between sucrose and saccharine treatments (t-test: $N_{summer\text{-}sucrose}$=12, $N_{summer.saccharine}$=12, $N_{winter.saccharine}$=16, P>0.1; Fig.3).

Spatial learning and memory in the Barnes maze test:

490 *Association between basal blood glucose and spatial learning performance*

491 Striped mice progressively learnt the location of the correct hole during the four neutral trials
492 of the Barnes maze test as shown by a decrease of both the number of errors (GLMM: N=90,
493 χ^2_1=401.37, P<0.001; Fig.4.a) and the latency to poke the correct hole (LMM: N=90, χ^2_1=6.35,
494 P=0.01; Fig.4.b). In addition, we found an interaction between trials and basal blood glucose levels on
495 the number of errors (LMM: N=90, χ^2_1=13.43, P=0<0.001): the higher the blood glucose level of the
496 mice, the greater their number of errors in the Barnes maze during the first trial.

497

498 *Influence of experimentally-induced increase in blood glucose on spatial learning performance*

499 We found an interaction between trials and experimental condition on the number of errors
500 (LMM: N=90, χ^2_2=59.95, P<0.001): mice that received the sucrose in summer made more errors in the
501 neutral trials than mice that received the saccharine in winter (t-test: $N_{summer.sucrose}$=27,
502 $N_{winter.saccharine}$=38, t_{54}=2.43, P=0.04; Fig.4.a). No difference was found between males and females
503 (N_{males}=47, $N_{females}$=43; errors: GLMM: χ^2=0.98, P=0.32; latency: LMM: χ^2=0.10, P=0.75).

504

505 *Association between basal blood glucose and spatial memory performance*

506 In the first bat trial (short-term spatial memory), basal blood glucose levels were positively
507 associated with the number of errors (GLMM: N=63; χ^2_1=6.64, P=0.01) but not with the latency to
508 poke the correct hole (LMM: N=63; χ^2_1=3.02, P=0.08): the higher the blood glucose level of the mice,
509 the greater their number of errors in the Barnes maze (Fig.5.a). There was no sex effect (N_{males}=33,
510 $N_{females}$=30; errors: GLMM: χ^2_1=3.11, P=0.08; latency: LMM: χ^2_1=0.23, P=0.63; fig. 5) and no
511 significant interaction between blood glucose level and sex (errors: GLMM: χ^2_1=2.19, P=0.14; latency:
512 LMM: χ^2_1=3.09, P=0.08).

513 In the second bat trial (4±2 days after the neutral trials and the first bat trials, *i.e.* long-term
514 spatial memory), there was an association between the basal blood glucose level and the latency to
515 poke the correct hole (LMM: N=52; χ^2_1=4.44, P=0.035): the higher the blood glucose level of the
516 mice, the higher their latency to poke the correct hole. There was an interaction between the sex and
517 the basal blood glucose on the number of errors (N_{males}=27, $N_{females}$=25; GLMM: χ^2_1=5.85, P=0.02;

latency: LMM: χ^2_1=1.91, P=0.17): the higher the blood glucose level, the greater the number of errors in females but not in males (t-test: $N_{females}$=25, N_{males}=27; t_{51}= 2.35, P=0.02; Fig.5.b).

Heavier mice made a lower number of errors in the first bat trial (GLMM: N=63; χ^2_1=11.43, P<0.001). In contrast, heavier mice made a higher number of errors in the second bat trial (GLMM: N=52; χ^2_1=6.32, P=0.01).

Influence of experimentally-induced increase in blood glucose on spatial memory performance

In the first bat trial (short-term spatial memory), experimental condition had an effect on both the number of errors and the latency to poke the correct hole ($N_{summer.sucrose}$=24, $N_{summer.saccharine}$=23, $N_{winterr.saccharine}$=34; errors: GLMM: χ^2_2=75.42, P<0.001; latency: LMM: χ^2_2=6.09, P=0.048): mice that received the sucrose in summer made more errors and took longer to poke the correct hole than individuals that received the saccharine in summer (*t*-test: $N_{summer.sucrose}$=24, $N_{summer.saccharine}$=23; errors: t_{46}=-6.68, P<0.001; latency: t_{46}=-2.46, P=0.04; Fig.6.a) or in winter (*t*-test: $N_{summer.sucrose}$=24, $N_{winterr.saccharine}$=34; errors: t_{57}=7.17, P<0.001; latency: t_{57}=1.41, P=0.34; Fig.6.a), while there was no difference between mice that received the saccharine in summer or winter (t-test: $N_{summer.saccharine}$=23, $N_{winterr.saccharine}$=34; t_{56}=0.66, P>0.1; Fig.6.a). There was no sex effect (N_{males}=41, $N_{females}$=40; errors: GLMM: χ^2_1=2.04, P=0.153; latency: LMM: χ^2_1=0.22, P=0.64) and no interaction between sex and experimental condition (errors: GLMM: χ^2_2=2.66, P=0.27; latency: LMM: χ^2_2=0.58, P=0.75).

In the second bat trial (long-term spatial memory), there was an interaction between sex and experimental condition on the number of errors ($N_{summer.sucrose}$=20, $N_{summer.saccharine}$=23, $N_{winterr.saccharine}$=29; errors: GLMM: χ^2_2=26.21, P<0.001; latency: LMM: χ^2_2=2.10, P=0.35). Males that received the sucrose in summer made more errors than males that received the saccharine either in summer (*t*-test: $N_{summer\text{-}sucrose}$=9, $N_{summer\text{-}saccharine}$=11, t_{19}=-3.20, P=0.004; Fig.6.b) or in winter (*t*-test: $N_{summer\text{-}sucrose}$=9, $N_{winter\text{-}saccharine}$=16, t_{24}=3.16, P=0.005; Fig.6.b) while there was no difference between males that received the saccharine in summer or in winter (*t*-test: $N_{summer\text{-}saccharine}$=11, $N_{winter\text{-}saccharine}$=16, t_{26}=-0.34, P=0.94; Fig.6.b). In females, the mice that received the saccharine in summer made more errors than those that received the sucrose in summer (*t*-test: $N_{summer\text{-}sucrose}$=11, $N_{summer\text{-}saccharine}$=12, t_{22}=4.24, P<0.001; Fig.6.b) or the saccharine in winter (*t*-test: $N_{summer\text{-}saccharine}$=12, $N_{winter\text{-}saccharine}$=13, t_{24}=3.96,

546 $P<0.001$; Fig.6.b) while there was no difference between female mice that received the sucrose in
547 summer and those that received the saccharine in winter (*t*-test: $N_{summer\text{-}sucrose}=11$, $N_{winter\text{-}saccharine}=13$,
548 $t_{23}=0.08$, $P=0.99$; Fig.6.b). Body mass was positively related to the number of errors (GLMM: $N=72$,
549 $\chi^2_1=26.31$, $P<0.001$). In contrast, the latency to poke the correct hole in the second bat trial was not
550 affected by the experimental condition (LMM: $N_{summer.sucrose}=20$, $N_{summer.saccharine}=23$, $N_{winterr.saccharine}=29$,
551 $\chi^2_1=0.04$, $P=0.981$, Fig 4) and there was no interaction between sex and experimental condition
552 (LMM: $N=72$, $\chi^2_2=2.10$, $P=0.350$).
553
554 **DISCUSSION**
555
556 We found that blood glucose levels were reduced during the dry season in our study
557 population of free-ranging African striped mice, supporting the findings of a previous study (Schradin
558 et al 2015). Yet, within our subsample of striped mice tested for cognition, this difference was not
559 apparent, probably due to a lower sample size leading to lower statistical power to detect this moderate
560 effect. Nevertheless, as significant seasonal variation in blood glucose levels occur in our study
561 species, it is interesting to investigate how differences in blood glucose levels influence cognition and
562 whether cognition changes seasonally. We found no seasonal effect on attention and spatial learning
563 and short- or long-term spatial memory. However, we found sex differences in cognitive performance.
564 Finally, we found that high basal and experimentally increased blood glucose levels impaired spatial
565 learning and memory.
566 In the present study, attention did not change seasonally. One explanation could be that prey
567 species, such as striped mice, should show constantly high attention towards environmental stimuli,
568 independent of the season (Emery, 2000). Interestingly, survival during the dry season seems to be
569 related to striped mice attention abilities (Maille & Schradin, 2016b). Independent of season, striped
570 mice with high basal blood glucose levels reacted faster to the predator stimulus. Glucose is an
571 important energy resource for the brain (Gold, 1995). High basal blood glucose levels result in
572 accelerated absorption of glucose by the brain when there is an increase in cognitive demand such as
573 during attentional processes (McNay, Fries, & Gold, 2000). Furthermore, metabolic hormones are

574 released when an individual is exposed to acute stress such as a predator stimulus display, which will
575 have a secondary effect on cognition *via* the regulation of blood glucose levels (Sapolsky, Romero, &
576 Munck, 2000). This stressful situation could also be associated with glucose level variation in muscles
577 due to the fight and flight response to the predator stimulus display (Sapolsky et al., 2000) suggesting
578 an alternative non-cognitive explanation. Thus, we found that attention remains high in striped mice
579 regardless of season and might be impaired in individuals with low basal blood glucose levels.

580 Unlike basal blood glucose levels, experimentally-increased blood glucose levels did not
581 affect attention in females, and it even decreased attention in males. This might indicate that glucose
582 has a dose-dependent biphasic effect on cognition, *i.e*. an inverted U-shaped relationship (known as
583 the Yerkes–Dodson law; Mendl, 1999). Such a relationship is known for corticosteroids that take part
584 in glucose regulation (Mateo, 2008). Our experimental increase of blood glucose levels might have led
585 to too high levels of blood glucose (e.g. for the experimental increase of glucose, the maximal value
586 was 23 mmol/litre and for the basal blood glucose the maximal value was 10 mmol/litre) leading to a
587 decrease of attention performance in males.

588 In contrast to previous studies on free-living animals showing better cognitive performance
589 under harsh conditions (Lázaro et al., 2017; Pravosudov, 2003; Tello-ramos et al., 2018), spatial
590 learning and short- and long-term spatial memory did not change between seasons. This is also in
591 contrast to a previous study in which male striped mice tested during summer showed worse short-
592 term spatial memory performance than males tested during early winter, the time males disperse
593 (Maille et al., 2015). However, Maille et al., (2015) suggested that this finding was not necessarily due
594 to seasonal changes in cognition but to seasonal differences in perception, motor performance or
595 motivation related to male dispersal. Furthermore, this previous study showed a decrease of basal
596 corticosterone levels from summer to winter, which is known to impact cognitive performance
597 (Pravosudov, 2003). Decreased corticosteroids impairs spatial learning in Belding's ground squirrels
598 *Spermophilus beldingi* (Mateo, 2008). Conversely, moderately elevated levels of corticosterone
599 enhance spatial memory in food-caching birds (Pravosudov, 2003). Environmental variations could
600 also be involved. Variation of daily temperature seemed to be higher in the Maille et al., (2015) study
601 which could have impacted physiological state and hence cognition. Colder daily morning

temperatures are associated with higher basal blood glucose levels in striped mice, which might be attributed to higher energy expenditure during colder nights (Schradin et al., 2015). The Maille et al., (2015) study indicated a need to reduce energy-demanding activities. In contrast, the lack of seasonal changes in cognitive traits in our present study highlights the resilience of these traits to environmental harshness, such as decrease in food availability.

Blood glucose levels had an impact on spatial learning and memory. Striped mice with high basal blood glucose levels made more errors and needed more time to find the correct escape hole in the learning phase and during short and long term memory tests. Our results are similar to those obtained under artificial conditions in well fed laboratory rats, where deficits in spatial learning were associated with chronic elevations in blood glucose levels (Kendig et al., 2013). Similarly, experimentally increased blood glucose levels in striped mice lead to a worsening in learning and short and long term memory. Our experiment involved acute temporary increases of blood glucose levels. Such acute changes impacting cognition have also been reported for humans and for rats where the ingestion of a high-glycaemic-index meal lead to reduced spatial learning and memory performance (Benton et al., 2003). The authors suggested that the energy intake as such may modulate cognitive performance (Benton et al., 2003).

We found sex differences in some cognitive traits, and blood glucose level seems to impact cognitive performance of males and females differently. Females showed faster attention than males. Interestingly, experimentally-increased blood glucose levels did not affect attention in females, and it even decreased attention in males. Overall, females showed faster attention in the orientation test than did males, but females expressed worse long term spatial memory abilities when they had higher basal blood glucose levels. Experimental increases in blood glucose levels had a negative effect on long-term memory performance in males and a positive effect in females. Higher body mass was associated with worse long term memory performance, which can be related to long-term memory performance in males since males are heavier than females. One explanation could be that the increase in blood glucose level in males leads to lower task retention ability during the learning phase that would have an impact during the long-term memory test. For example, in humans, deficits in concentration and problem solving occur when there is a high daily sugar consumption (Kendig et al., 2013).

Alternatively, it is possible that either the experimental conditions lead to long-term changes in blood glucose or that the experimental elevation of blood glucose would have ended 4±2 days after, and hence reflects the basal individual state. Sex differences could also be due to the fact that males and females were under different behavioural motivations (Maille et al., 2015). In species with male biased dispersal, such as in the deer mouse *Peromyscus maniculatus*, spatial performance improves during the breeding season relative to the non-breeding season in males but not females (Galea et al., 1994). Mechanistically, sexual dimorphism in the hippocampus has been related to females performing less well than males during spatial learning and memory tasks (*e.g.* Gaulin & FitzGerald, 1995). Striped mice are polygynous and male-biased dispersal peaks in winter (Vuarin, Pillay, & Schradin, in press), before reproduction in spring. Male striped mice travel long distances during dispersal (Solmsen, Johannesen, & Schradin, 2011), which is likely to increase demands on spatial learning and memory processing. It has been proposed that the higher spatial performance by male striped mice in early winter is related to greater motivation to disperse (Maille et al., 2015), and our results support this hypothesis.

CONCLUSION

The absence of seasonal influence on cognition is in support of the cognitive resilience hypothesis. This study also showed that high basal (chronic) and experimentally (acute) increased blood glucose levels can impaire cognition, in agreement with high glucose levels being an indicator of metabolic imbalance. Our findings suggest that cognitive capacity in striped mice is set at a lower threshold of metabolic requirements, since better cognitive performance was associated with lower blood glucose levels. Optimizing cognition during harsh (low food availability – low blood glucose levels) environmental conditions could influence a wide range of behaviours such as foraging and/or avoiding predators and hence has a direct impact on animals' fitness.

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CONFLICT OF INTEREST

The authors declare no conflict of interest

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Figure captions

Figure 1. Blood glucose level (Mean ± SE) in mmol/litre measured in striped mice (**a)** 4 ± 2 days before experimental changes in blood glucose level and (**b**) 2 hours after they received the jelly containing sucrose in summer (dry season) (dotted, *N*=27), saccharine in summer (white, *N*=28) or saccharine in winter (wet season) (dark grey, *N*=38). Tests t: ** $P < 0.01$ Boxplot correspond to the 1st and 3rd quartiles, the line is the median, the whiskers is 1.5 * the difference between 3rd and 1st quartile, dots are extreme individuals' data.

Figure 2. Relationship between the blood glucose level in mmol/litre and the orientation time (in seconds) for the first orientation of striped mice towards the raptor-stimulus in the orientation response test. Males are shown in black squares and line (*N*=32) and females in grey dots and line (*N*=30).

Figure 3. Orientation time in seconds, depicted as mean + standard error, for the first orientation response of the striped mice toward the raptor-stimulus in females and males that received the sucrose during summer (dry season) (dotted, N_{males} =12, $N_{females}$ =12), the saccharine in summer (white, N_{males} =13, $N_{females}$ =12) or the saccharine in winter (wet season) (grey, N_{males} =19, $N_{females}$ =16). *t*-test: *** $P<0.001$.

Figure 4. (a) Mean number of errors and **(b)** latency to poke the correct hole in seconds in the successive trials (neutral trials N1 to N4, first bat trial, control trial, second bat trial occurring 4±2 days later) in the Barnes maze test in striped mice that received the sucrose in summer (dry season) (dashed line and dotted squares, *N*=27), the saccharine in summer (full line and white dot, *N*=25) or the saccharine in winter (wet season) (full line and black triangle, *N*=38).

Figure 5. Relationship between basal blood glucose level in mmol/litre and **(a)** the number of errors during the 1st bat trial **(b)** the number of errors during the 2nd bat trial in the Barnes maze test in males (black squares and full line, *N*=33) and females (grey dots and dashed line, *N*=30) that received the saccharine treatment.

Figure 6. Mean number of errors in **(a)** the 1st bat trial and **(b)** the 2nd bat trial in the Barnes maze test in striped mice that received different experimental condition: striped mice that received the sucrose in summer (dry season) (dotted, *N*=27), saccharine in summer (white, *N*=28) or saccharine in winter (wet season) (dark grey, *N*=38). Tests t: *** $P < 0.001$.

Table

Table 1. S: summary of the results of the different models. (bold values are: P<0.05).

	Orientation test		Barnes Maze test			
			Bat 1		Bat2	
	No. of Orientation response	Orientation time (s)	No. of Errors	Latency (s)	No. of Errors	Latency (s)
Experimental condition	χ^2_2=0.27, *P*=0.87	χ^2_2=39.68, ***P*<0.001**	χ^2_2=75.41, ***P*<0.001**	χ^2_2=6.09, ***P*=0.04**	χ^2_2=8.83, ***P*=0.01**	χ^2_2=0.04, *P*=0.98
Experimental condition:sex	χ^2_2=0.18, *P*=0.91	χ^2_2=19.12, ***P*<0.001**	χ^2_2=2.65, *P*=0.26	χ^2_2=0.58, *P*=0.74	χ^2_2=26.21, ***P*<0.001**	χ^2_2=2.10, *P*=0.35
Sex	χ^2_1=0.66, *P*=0.41	χ^2_1=21.34, ***P*<0.001**	χ^2_1=2.03, *P*=0.15	χ^2_1=0.22, *P*=0.64	χ^2_1=4.60, ***P*=0.03**	χ^2_1=1.59, *P*=0.21
Body mass	χ^2_1=0.21, *P*=0.64	χ^2_1=0.04, *P*=0.83	χ^2_1=0.56, *P*=0.45	χ^2_1=0.69, *P*=0.40	χ^2_1=26.31, ***P*<0.001**	χ^2_1=1.17, *P*=0.28

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