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1 **Seasonal changes in problem-solving in wild African striped mice**

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25  
26 Innovative problem-solving ability is a predictor of whether animals can successfully cope with  
27 environmental changes. These environmental changes can test the limits of animals, for example when  
28 energy availability decreases seasonally and, hence, problem-solving performance decreases because  
29 less energy is available for cognitive processes. Here, we investigated: (1) how problem-solving  
30 performance changed between seasons that differed significantly in food availability; (2) whether these  
31 changes were related to environmentally induced physiological changes in blood glucose and ketone  
32 levels, indicators of energy availability; and (3) whether individual variation in problem-solving was  
33 related to sex differences. We studied 99 free-ranging African striped mice, *Rhabdomys pumilio*, in the  
34 Succulent Karoo, South Africa, 55 during the hot dry summer with low food availability and 44 during  
35 the cold wet winter with higher food availability. We measured their problem-solving abilities using a  
36 food extraction task and found no seasonal differences in problem-solving success. However, mice  
37 solved the problem faster in summer *versus* winter. In summer, food availability was reduced and blood  
38 ketones increased but there was no seasonal difference in blood glucose levels. There were no correlation  
39 between problem-solving performance and blood glucose or ketone levels. Overall, more males solved

40 the task than females. It appears that in striped mice cognitive functions can be maintained under harsh  
41 environmental conditions.

42

43 **Key words:** cognition, glucose, innovation, ketone, seasonality, sex differences

44

45 Anthropogenically induced global climate change represents one of the most severe threats for  
46 biodiversity and causes rapid environmental change (Parmesan 2006). Consequently, wild animals face  
47 novel challenges related to habitat loss, new predators or novel food sources (Buchholz et al., 2019).  
48 Characterizing traits that enable successful animals to thrive in changing habitats will help to show the  
49 determinants of successful adaptation to human-induced rapid environmental change (Sih et al., 2011).

50 Innovation is defined as the use of novel behaviours to meet challenges or the application of existing  
51 behaviours to solve novel problems (Kummer & Goodall, 1985). Problem-solving commonly serves as  
52 a proxy for innovation (*e.g.*, Reader & Laland, 2003). Problem-solving has been proposed as a major  
53 predictor of the successful establishment of species in novel or altered habitats (Sol et al., 2005). For  
54 example, innovative responses to novel predators will aid survival under changing environmental  
55 conditions (Berger et al. 2001; Sol et al. 2016). Therefore, the ability to solve new problems might be  
56 critical for the survival of individuals (Reader & Laland 2003; Ramsey et al., 2007).

57 Behavioural changes, such as solving new problems in response to changing environmental  
58 conditions, can be cognitively demanding, which might explain the variation both within and between  
59 species in the ability to solve problems (Reader & Laland, 2003). However, the processes underlying  
60 problem-solving are unclear (*e.g.*, Camacho-Alpizar et al., 2020; Chen et al., 2020). Some authors  
61 suggest that an animal's performance in a problem-solving task might depend on non-cognitive traits  
62 such as persistence (Van Horik & Madden, 2016) *i.e.*, the time that an animal spends interacting with  
63 the task (Griffin & Guez, 2014), response to novelty (neophobia), and motivation to obtain the reward.  
64 Furthermore, motivation could increase persistence itself and thereby increase the likelihood of  
65 successfully solving a problem (Griffin & Guez, 2014). Nonetheless, there is wide support for the idea  
66 that cognitive processes such as perception, learning and information storage underlie problem-solving  
67 performance (Reader et al., 2016; Audet & Lefebvre, 2017) along with mechanical (*i.e.*, movements

68 required to solve problems) and/or morphological (*i.e.*, physical structure to manipulate objects to solve  
69 a problem) components as part of problem-solving ability (reviewed in Rowell et al., 2021).

70 Variation within and between species in problem-solving performance could be related to  
71 environmental factors. The “necessity drives innovation” hypothesis suggests that when resources are  
72 scarce, individuals will be more likely to exhibit novel problem-solving behaviour (Laland & Reader,  
73 1999). Individuals in poor condition may be more motivated to solve new problems because competitive  
74 ability may be directly linked to physiological condition and health (Laland & Reader, 1999). Habitat  
75 type can also influence problem-solving (Prasher et al., 2019). For example, in striped field mice,  
76 *Apodemus agrarius*, individuals living in urban environments exhibit increased problem-solving  
77 propensity (Mazza & Guenther, 2021). Mountain chickadees, *Poecile gambeli*, from high elevations  
78 solve new problems faster than individuals from low elevations (Kozlovsky et al., 2017), and black-  
79 capped chickadees, *Poecile atricapillus*, from northern latitudes solve new problems more efficiently  
80 than more southern conspecifics (Roth et al., 2010). These results suggest that animals which live under  
81 harsher climatic conditions might have enhanced problem-solving performance as an adaptation to meet  
82 specific environmental needs (Pravosudov et al., 2015), and in particular because finding food in harsh  
83 habitats was more challenging, and survival depends on plastic responses such as solving new problems  
84 in relation to these challenges (Kozlovsky et al., 2015).

85 Alternatively, living under harsh conditions necessitates a reduction in energy-demanding  
86 processes. Animals have to continuously adjust physiologically to their environment (*i.e.*, allostasis),  
87 and when energy expenditure exceeds energy acquisition, allostatic overload type I occurs and can alter  
88 health status (McEwen & Wingfield, 2010). The neuronal tissue development, which is the substrate of  
89 cognition, and the maintenance of cognitive processes (*e.g.*, propagation of neural signal) are  
90 energetically highly expensive (Laughlin 2001). Thus, environmentally induced energy trade-offs can  
91 influence how much energy is available and consumed by the brain, affecting cognitive processes  
92 involved in problem-solving (Buchanan et al., 2013). However, the environmental conditions under  
93 which animals might directly reduce energy investment into cognitive processes (cognitive impairment)  
94 and the conditions under which they might keep this energetic investment unchanged (cognitive  
95 resilience) or improved (cognitive enhancement) remain poorly understood (Maille & Schradin, 2016a).

106 One possibility to better understand the link between particular environmental demands and  
107 problem-solving performance is to study how seasonal variation in food availability induces  
108 physiological changes that could affect problem-solving performance. To date, only one laboratory  
109 study has explored the relationship between physiological state and problem-solving performance.  
110 Bókonyi et al., (2014) tested the necessity drives innovation hypothesis in wild-caught house sparrows,  
111 *Passer domesticus*, in four novel tasks of food acquisition and found that those sparrows with lower  
112 corticosterone levels (the main avian stress hormone) solved the most difficult task faster. Sparrows  
113 with higher concentrations of glutathione (a key antioxidant) solved easy tasks faster. Bókonyi et al.,  
114 (2014) concluded that the physiological state influenced problem-solving performance in a context-  
115 dependent manner and that individual differences in cognitive abilities were more likely to drive  
116 problem-solving success than the health status (Bókonyi et al., 2014).

117 Here, we aimed to investigate whether problem-solving performance changed between seasons  
118 and whether these changes were associated with environmentally induced physiological changes in a  
119 free-ranging population of the African striped mouse, *Rhabdomys pumilio*. The striped mouse is an ideal  
120 model to study the influence of seasonal, and hence, physiological state on problem-solving because it  
121 inhabits the semi desert Succulent Karoo in southern Africa where it faces marked seasonal changes in  
122 food availability (Schradin et al., 2012). The frequency and intensity of droughts has increased in this  
123 area, and the Succulent Karoo biome has been identified as being at great risk from climate change  
(Rutherford et al., 2000; Midgley & Thuiller 2007). The dry summer season is characterized by low  
124 food availability (lower quantity of plants leaves, flowers and seeds for striped mice) and the blood  
125 glucose levels of striped mice decrease due to decreased food availability (Schradin et al., 2015).

126 Glucose is the most important energy source for the brain, and thus cognitive processes (McNay  
127 et al., 2000). Unexpectedly, in striped mice, higher blood glucose levels have been associated with lower  
128 attentional state and spatial learning and memory performance (Rochais et al., 2019). Low food  
129 availability not only influences blood glucose levels, but also blood ketone levels in striped mice  
130 (Schoepf et al., 2017). Ketone bodies are derived from stored fat, and are indicators of energy  
131 availability, but their role in striped mouse cognition has not been investigated. Blood ketone levels  
132 could be used to investigate metabolic switching from utilization of liver-derived glucose to a ketogenic  
133

124 state under starvation (McCue 2010). This state is characterized by the use of ketones by neurons and  
125 muscle cells as cellular fuels to sustain cognitive performance and physical endurance under harsh food  
126 availability conditions (Mattson 2019).

127         The dry seasons are energetically challenging periods for striped mice living in the Succulent  
128 Karoo in southern Africa. Because of low food availability, they show physiological signs of fasting,  
129 such as increased ketone body concentrations (Rimbach et al., 2018). When food resources decline and  
130 conditions become harsher, their health deteriorates and non-survivor mice exhibit signs of permanent  
131 pathology (Schoepf et al., 2017). To reduce their daily energy expenditure, striped mice also reduce their  
132 metabolism and activity during the dry season (Rimbach et al., 2018a, b, c). Furthermore, philopatric  
133 striped mice do not seem to accumulate fat during winter to better survive the dry season (Rimbach et  
134 al., 2019), and invest heavily in body growth (Rimbach et al., 2021). Finally, previous studies in striped  
135 mice also showed sex differences in attention and spatial learning: males tested during summer showed  
136 faster attention toward a predator-stimulus but made more errors and took longer in a spatial learning  
137 and memory task than males tested during winter (Maille et al., 2015). In contrast, females did not differ  
138 between the two seasons, but their survival was correlated with faster attention to a predator stimulus  
139 whereas male survival was correlated with greater spatial memory (Maille & Schradin, 2016b).  
140 Therefore, seasonal variation in cognitive performance in striped mice could be related to sex-specific  
141 behavioural characteristics, such as male biased dispersal (Solmsen et al., 2011), that could increase  
142 demands on problem-solving since males will be more likely to encounter novel challenges.

143         We developed a novel food extraction task for striped mice to assess problem-solving and tested  
144 one distinct group of striped mice by season. This testing regime allowed us to test individuals with the  
145 same developmental profile and avoided any learning effects between seasons. We aimed to investigate  
146 whether free-living striped mice differed in their problem-solving ability during the dry and wet seasons,  
147 and whether problem-solving was correlated with their blood glucose and ketone levels. We also aimed  
148 to identify the potential mechanisms underpinning between-individual differences in problem-solving,  
149 focusing on the influence of non-cognitive traits *i.e.*, persistence, neophobia and motivation (Van Horik  
150 & Madden, 2016). We made three predictions: 1) Problem-solving performance would vary seasonally  
151 and would be enhanced during the dry summer, following the harsh environment hypothesis described

152 in birds (*e.g.*, Pravosudov et al., 2015). 2) Based on our previous research (*e.g.*, Rochais et al., 2019),  
153 problem-solving performance would be negatively correlated with blood glucose levels and positively  
154 correlated with ketone levels. 3) Seasonal variation in problem-solving would be influenced by non-  
155 cognitive traits: more persistent, neophilic and food motivated mice would show higher problem-solving  
156 success. Additionally, as shown for spatial memory performance (Maille et al., 2015), we expected that  
157 males would show better problem-solving performance in winter, whereas females would not differ  
158 between seasons.

159

## 160 **METHODS**

### 161 *Ethical note*

162

163 Animal ethics clearance was provided by the University of the Witwatersrand, Johannesburg,  
164 South Africa (No. 2018/09/46B). All procedures were in accordance with the ethical standards of the  
165 institution. Throughout the experimental procedures and thereafter, we took care in ensuring the animals'  
166 welfare. We usually re-trapped the mice again on the same day after marking them with ear tags to check  
167 their welfare state (*e.g.*, checked ears, neck, eyes, external airway for obstructions). When trapped for  
168 blood sampling, mice were anaesthetized with diethyl ether to limit pain and distress. They received a  
169 piece of food after the procedure. We checked their awareness and breathing rate and released them at  
170 their nest within 30 minutes. When trapped latter for cognitive testing, mice were transported in their  
171 traps to the field laboratory, and we checked their behaviour continuously during cognitive testing *via*  
172 video recordings. No injuries or mortality occurred due to the cognitive apparatus. Mice were fed with  
173 pieces of bait (*i.e.*, a small piece of bran flake soaked in sunflower oil) to compensate for missed foraging  
174 opportunities.

175

### 176 *Study population*

177

178 We studied a free-living population of African striped mice, consisting of several distinct social  
179 groups. Groups comprised of one breeding male, one to four breeding females and their non-

180 reproductive offspring of both sexes that remained in their natal group after reaching adulthood  
181 (Schradin & Pillay, 2004). Groups contained 2 to 30 (mean  $\pm$  SEM:  $14.92 \pm 0.93$ ) adult individuals of  
182 both sexes. Striped mice typically breed in the austral winter / spring (August – November / December),  
183 corresponding to the period of highest rainfall (Schradin & Pillay, 2005). The age of mice was  
184 determined by using long-term continuous trapping data (*i.e.*, all year long). Upon first capture after  
185 birth, body mass (if less than 30 g) and the date of first capture were used to estimate an individual's  
186 birth date using a species-specific growth curve (Schradin et al., 2009). For mice with body mass of  
187 more than 30 g, age cannot be determined reliably. Striped mice are diurnal and inhabit an open habitat,  
188 allowing for direct behavioural observations in the field (Schradin & Pillay, 2004).

189 The study population has been continuously monitored since 2005 using a combination of  
190 behavioural observations, trapping and radiotracking (Schradin & Pillay, 2004). Each striped mouse  
191 group was trapped for a minimum of 6 trap days per month and observed directly at its nesting site at  
192 least 2 days per month. Striped mice were trapped using baited (*i.e.*, small piece of bran flake soaked in  
193 sunflower oil) metal (Sherman-like) live traps (26 X 9 X 9 cm) placed in shade under bushes where  
194 striped mice were nesting. We used numbered metal ear tags (National Band and Tag Co., Newport,  
195 KY, USA) to permanently marked individuals. Additionally, each individual was marked on the pelage  
196 with commercial hair dye (Rapido, Pinetown, South Africa) for visual identification that had no long-  
197 term effects on mouse fitness or mortality (Schradin, 2006). At least one female of each group was fitted  
198 with a collar-mounted radiotransmitter (models BD-2C and PD-2C, Holohil, Ontario, Canada) to  
199 determine group nesting sites (Schradin & Pillay, 2005; Schradin & Pillay, 2005). However, no  
200 individuals were collared when tested for the problem-solving task.

201 We assessed problem-solving using a novel lid opening task that required a mouse to reach food  
202 (see below). We tested the cohort of striped mice born in the 2018 breeding season, split into two  
203 different groups: 55 mice (26 females and 29 males, originating from 13 different social groups) were  
204 tested in summer and 44 other mice (18 females and 26 males, originating from 16 groups including the  
205 same 13 groups as in summer) in winter. Testing every mouse only in one season was necessary to  
206 ensure that they were naive to the problem-solving device when tested in winter. Thus, in order to avoid  
207 any learning effects, none of the individuals were tested in both seasons. Furthermore, it was not possible

208 to test the same individual in both seasons because striped mice disperse in early winter (Lonnstedt et  
209 al., 2012; Vuarin et al., 2019) or disappear due to predation (*e.g.*, 22 of 55 mice (40%) tested in summer  
210 were either dispersed or dead at the beginning of winter). Mice tested in winter were inevitably older  
211 than those tested in winter. All tested individuals were non breeding adults during the experimental  
212 period to avoid possible confounding effects of breeding activity on cognition. We checked for  
213 reproductive status by observing signs of sexual activity (open vagina or pregnancy in females and being  
214 scrotal in males).

215

#### 216 *Study location and period*

217

218 Our study location was in Goegap Nature Reserve, near Springbok in the Northern Cape Province,  
219 South Africa (S 29 41.56, E 18 1.60). The area is arid, characterized by a hot and dry summer and a wet  
220 and cold winter. The vegetation is classified as Succulent Karoo. Up to sixteen social groups of striped  
221 mice occupied our 10ha study area. The study took place during the dry summer season from 1<sup>st</sup> January  
222 to 22<sup>th</sup> March 2019 and during the wet winter season from 20<sup>th</sup> June to 17<sup>th</sup> August 2019. We measured  
223 daily temperature and rainfall. Because striped mice mainly feed on all parts (leaves, flowers and seeds)  
224 of annual and perianual plants, food availability was assessed twice a month through plant surveys  
225 using the Braun-Blanquet method (Wikum & Shanholtzer 1978) on the 1<sup>st</sup> and the 15<sup>th</sup> of each month of  
226 the year. We recorded the number of food plant species for striped mice as a measure of food availability  
227 (palatability is known from behavioural observations, Schradin & Pillay, 2006), in eight monitoring  
228 plots of 4 m<sup>2</sup> each that were located within the home ranges of the different social groups (Schradin &  
229 Pillay, 2005).

230

#### 231 *Measurement of basal blood glucose and ketone levels*

232

233 We routinely conducted blood sampling in our entire study population, and we obtained basal  
234 blood glucose and ketone levels from 97 (37 females, 60 males) striped mice in summer and 67 (32  
235 females, 35 males) in winter. We recorded body mass to the nearest 0.1 g, length (from tip of the nose

236 to the anus; mm) and reproductive status. Mice were trapped early in the morning before they left their  
237 nest to forage. Thus, blood samples were obtained after the mice had fasted overnight and before their  
238 onset of foraging and pronounced physical activity. Immediately after a mouse entered a trap, it was  
239 removed and anaesthetized by putting them in a jar containing diethyl ether on cotton wool (Schradin  
240 2008) and a drop of blood was obtained from the sublingual vein within 3 minutes of trapping to limit  
241 handling influence. We measured blood glucose (mmol/Litre) and ketone bodies (mmol/Litre) in the  
242 field by using a One Touch Ultra glucometer (Lifescan, Inc., Milpitas, CA, U.S.A.) and a Freestyle  
243 Optium Blood  $\beta$ -Ketone meter (Abbott Laboratories, Australia). The mice were given a piece of the bait  
244 used in their trap just after the procedure and were released at their nest within 30 minutes. We measured  
245 basal blood glucose levels  $4 \pm 2$  days before the cognitive tests to give the mice sufficient time to  
246 recuperate between blood sampling and cognitive testing (Maille et al., 2015; Rochais et al., 2019).

247

#### 248 *Cognitive testing*

249

250 Each day of testing, 2-4 striped mice (that had blood taken samples  $4 \pm 2$  days before), were trapped  
251 at their nest within the first hour after sunrise and brought to a field laboratory (3.70 X 3.10 X 2.40 m)  
252 within 40 minutes after trapping. The laboratory was located within a 5 minutes walking distance from  
253 the field site. The laboratory was split into two areas with a black opaque curtain hanging from the  
254 ceiling, one area being used for testing (1.60 X 3.10 X 2.40 m) and the other area to serve as a hide for  
255 the experimenter. Before tests, mice were placed individually in a separate quiet room next to the field  
256 laboratory, in a plastic cage (22 X 16.5 X 14 cm) with sand for bedding and an empty egg carton as  
257 shelter. Mice were kept between 10 and 80 minutes in the separate room to allow them to habituate to  
258 the test conditions. There is no influence of holding time on striped mouse behaviour (see Rochais et  
259 al., 2021). Mice were then brought individually to the laboratory to perform the food-extraction  
260 problem-solving test. The order of testing of individuals was randomly assigned and did not influence  
261 individual performance. Each mouse was tested in the same neutral arena made of white chipboard (80  
262 X 65 X 94 cm). The arena was cleaned with 70% alcohol after each test. The behaviour of mice was  
263 video recorded using a Microsoft HD web camera mounted over the centre of the arena and connected

264 to a laptop. On each day of testing, the time from capture in the trap to testing and final release to the  
265 nest was a maximum of 2 hours.

266 Each mouse was first placed in the right corner of the empty arena and given 5-minutes to habituate.  
267 A food extraction problem-solving device was then put into the arena (electronic supplementary material  
268 1). The device consisted of a grey PVC foraging grid (20 X 8 X 3.5cm) containing 4 wells (each with a  
269 3.5 cm diameter and 2.5 cm depth) that were covered with grey PVC lids. A short cotton string (3 cm)  
270 was attached to each lid, which the mice could pull to open the lid (Rochais et al., 2021). Each well  
271 contained a small piece of bran flake soaked in sunflower oil (the bait used during trapping) and a  
272 sunflower seed (highly preferred by striped mice).

273 The problem-solving device was placed alongside a wall as striped mice tend to avoid the middle  
274 of the arena. Mice were first trained for 5 minutes to search the wells where they could gain access to a  
275 food incentive (one small piece of food for each opened well) by first being exposed to the lids only  
276 partially covering the well, so the animal could associate the set-up with a reward and learn its location.  
277 We considered that a mouse explored a well when it placed its nose inside the hole. After these 5 minutes  
278 with lids partially opened, the mouse stayed in the testing arena and wells were filled by the experimenter  
279 with food, if necessary, all the lids of the wells were closed and the mouse was tested for 30 minutes  
280 and thereafter released at its nest at the study site. In order to provide the mice with sufficient time to  
281 perform the task in an unfamiliar field laboratory environment and not keeping them in captivity for too  
282 long, mice were tested twice on 2 consecutive days with the same food extraction procedure (see also  
283 Huebner et al., 2018) (*i.e.*, 2 x 5 minutes with lids partially opened and 2 x 30 minutes of testing). We  
284 managed to trap most mice on two consecutive days (92% of individuals in summer, 100% in winter)  
285 to avoid a longer period between tests which could have increased the chances of mice disappearing  
286 from the field site, for example, because of predation.

287 Problem-solving was analysed from video footage. The video-recordings of the cognitive tests were  
288 scored using the software Kinovea (Kinovea 0.8.15). Scoring of all videos was done by one observer  
289 (C.R.) and 10% of these videos were also scored by one field assistant who was naïve to the experimental  
290 treatment. We found high inter-observer reliability of  $N = 12$ ,  $0.85 < r_s < 0.99$ .

291 We recorded whether a mouse opened at least one lid (solving outcome coded as 1/0 for success/fail)  
292 and the total number of lids opened (0–4 lids). We measured the latency (in minutes) of opening the 1<sup>st</sup>  
293 lid. Latency of opening was measured from the start of the trial until a successful lid opening. Both trials  
294 (day 1 and 2) were added, and thus latencies could be up to 60 minutes. We considered only the latency  
295 for the 1<sup>st</sup> lid opening, since opening of subsequent lids was no longer novel.

296 As a measure of a subject's efficiency in solving the task, we additionally measured solving time,  
297 defined as how long it took an individual that was manipulating a lid until it opened it for the 1<sup>st</sup>  
298 successful attempt (Huebner et al., 2018). Solving time (in seconds), was measured from the time the  
299 mouse touched the lid/string with its mouth and/or front legs to the time the lid was opened.

300 Since problem-solving can be related to other non-cognitive factors (Van Horik & Madden, 2016)  
301 we assessed: 1) individual persistence, defined as the time that an animal spent interacting with the task  
302 (Griffin & Guez 2014) by recording the total duration (in % of time according to total testing time),  
303 mice spent in contact with the device (*i.e.*, sniffing, climbing, scratching), using continuous focal  
304 sampling (Martin & Bateson, 1993), 2) neophobia, by scoring the latency (in seconds), of each mouse,  
305 to contact the device once it was placed in the arena, and 3) motivation for food, by scoring the  
306 presence/absence (yes/no) of feeding when lids were opened (71% of mice eat when lids were opened).  
307 Mice that successfully opened at least one lid were characterized as 'solvers', whereas those which failed  
308 were characterized as 'non-solvers', with a maximum latency of 60 minutes (2 \* 30 minutes of testing).  
309 Prior to release at the nest, mice were given 5 pieces of bait.

310

### 311 *Statistical analyses*

312

313 All statistics were performed with R v. 3.6.1 (The R foundation for statistical computing,  
314 <http://www.r-project.org/>, Team 2019). The significance level was set at 0.05. Descriptive statistics are  
315 reported as means and standard error of mean (SEM). Independence and homogeneity of variances of  
316 the models were assessed by inspection of fitted values residuals using the *plotresid* function in  
317 *RVAideMemoire* package (Hervé, 2019). Mixed models were constructed using the *lm* or *glm* function  
318 in *lme4* package (Bates et al., 2015) and statistical tests were performed using the *Anova* function in *car*

319 package (Fox & Weisberg, 2019). *Post hoc* tests were performed using the *emmeans* function in the  
320 *emmeans* package (Lenth, 2019), with a Tukey correction. Cox models were built using the *coxme*  
321 (Therneau, 2020) and *survival* (Therneau, 2020b) packages.

322 Thereafter, we ran multiple models excluding non-significant factors, based on stepwise  
323 backward model selection using log-likelihood ratio tests and the Akaike's Information Criterion (AIC)  
324 comparison ('lrttest', 'lmttest' package; Hothorn et al., 2019) to help determine models of best fit. We  
325 also assessed for seasonal differences of non-cognitive traits by using t-test for persistence and  
326 neophobia and Chi-square for motivation for food. Non-cognitive traits did not differ between seasons  
327 ( $P > 0.05$  for all).

328

#### 329 *Seasonal changes in weather and food availability*

330 The seasonal changes in weather and food availability were analysed using separate linear  
331 models (LM) with daily temperature, daily rainfall and bi-monthly food availability measurements as  
332 the dependent variables and season as the fixed effect.

333

#### 334 *Seasonal changes in body condition and physiology*

335 The relationship between season and blood glucose and ketone levels was analysed for all  
336 samples available from our entire study population during the study period ( $N = 97$  mice in summer and  
337  $N = 67$  in winter) using a separate linear mixed model (LMM) with blood glucose or ketone level as the  
338 dependent variable and season, sex and the interaction between season and sex specified as fixed effects,  
339 age and body mass as a covariate and the identity of the mice as a random effect (to account for repeated  
340 blood measurement on the same individual). The seasonal changes in body condition were analysed by  
341 using a separate LMM with body mass and length as the dependent variables and season, sex and the  
342 interaction between season and sex as fixed effects. We specified group identity as a random factor to  
343 account for potential confounding effects of group origin (litter and/or ecology).

344

#### 345 *Seasonal and physiological influence on problem-solving performance*

346 In all original models analysing the predictors of problem-solving performance, season, sex, the  
347 interaction between season and sex to test sex-specific seasonal variation, the interaction between sex  
348 and body condition (ratio body mass / length; as males are bigger than females), age, glucose and ketone  
349 levels were included as fixed effect and non-cognitive traits (persistence, neophobia, motivation) as  
350 covariates. We specified group identity as a random factor. We first performed a separate generalized  
351 linear mixed model (GLMM) for Binomial data with general success (solving outcome coded as 1/0 for  
352 success/fail) as the dependent variable.

353 In a second step, we performed a separate GLMM for Poisson data for the total number of  
354 success (0-4 lids opened) as the dependent variable.

355 To further investigate individual problem-solving efficiency, we used a LMM with solving time  
356 as a dependent variable.

357 We checked if mice chose a particular lid location on the device by using Fisher exact tests  
358 among the 4 different locations and for each lid opened (1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup> and 4<sup>th</sup>).

359 We conducted an extended Cox proportional hazards regression on latency to open the first lid.  
360 This is a semi-parametric survival analysis approach that makes no assumptions about the distribution  
361 of the response variable (Therneau & Grambsch, 2000). We used this approach as an alternative to  
362 assigning capped latencies to individuals that did not solve a problem and use solving performance (yes  
363 *versus* no) as the censored variable. In previous studies investigating problem-solving performances,  
364 latencies were usually analysed with ordinary regressions or ANOVAs, but these approaches are  
365 inappropriate because censored variables are unlikely to meet the assumption of normality. In addition,  
366 regressions and ANOVAs give the same response value to all individuals that failed to complete the  
367 task; however, it is quite likely that the individual values would have differed if individuals had been  
368 given more time to solve the task. Thus, Cox proportional hazards regressions have been used to analyse  
369 problem-solving performance (*e.g.*, Bókony et al., 2014; Prasher et al., 2019). We used the latency to  
370 solve the task as the dependent variable, expressed as the time (in minutes) elapsed from the start of the  
371 test until first lid opening. Mice which did not solve a task were treated as censored observations in the  
372 analyses since we did not know their true latency to solve the well opening (*e.g.*, Prasher et al., 2019).  
373 We included season, sex, the interaction between season and sex, the interaction between sex and body

374 condition, age, glucose and ketone levels as fixed effect and non-cognitive traits (persistence, neophobia,  
375 motivation) as covariates. Cox analyses model the probability of not solving the task as a function of  
376 test time; positive parameter estimates indicate shorter latencies (*i.e.*, faster decrease of probability of  
377 not solving during the test), whereas negative parameter estimates indicate longer latencies.

378

## 379 RESULTS

380

### 381 *Seasonal changes in weather and food availability*

382

383 It was warmer and drier during summer (temperature:  $24.42 \pm 0.36$  °C; total rainfall: 0.60 mm)  
384 compared to winter (temperature:  $13.47 \pm 0.45$  °C; total rainfall: 39.60 mm; LMM: N = 138, F = 368.40,  
385  $P < 0.001$ ; F = 4.31,  $P = 0.039$ , respectively). Food availability increased within the study period from  
386 summer ( $2.35 \pm 0.11$  food plants/plot) to winter ( $3.27 \pm 0.24$  food plants/plot; LMM: N<sub>summer plots</sub> = 48,  
387 N<sub>winter plots</sub> = 48, F = 12.12,  $P < 0.001$ ).

388

### 389 *Seasonal changes in body condition and physiology*

390

391 Body mass and length were greater in winter than summer (body mass: summer:  $41.33 \pm 1.04$   
392 g; winter:  $47.17 \pm 1.36$  g; LMM: N = 99,  $\chi^2_1 = 11.93$ ,  $P < 0.001$ ; Length: summer:  $106.21 \pm 0.98$  mm;  
393 winter:  $113.91 \pm 1.28$  mm; LMM: N = 99,  $\chi^2_1 = 21.48$ ,  $P < 0.0001$ ). Males were heavier than females in  
394 both seasons (summer: males:  $44.46 \pm 1.52$  g; females:  $38.09 \pm 1.13$  g; LMM: N = 55,  $\chi^2_1 = 10.96$ ,  $P =$   
395  $0.002$ ; winter: males:  $52.20 \pm 1.46$  g; females:  $40.29 \pm 1.51$  g; LMM: N = 44,  $\chi^2_1 = 31.54$ ,  $P < 0.0001$ ).  
396 Males were longer than females in both seasons (summer: males:  $109.21 \pm 1.35$  mm; females:  $102.00$   
397  $\pm 0.99$  mm; LMM: N = 55,  $\chi^2_1 = -3.62$ ,  $P = 0.003$ ; winter: males:  $118.12 \pm 1.52$  mm; females:  $108.37 \pm$   
398  $1.47$  mm; LMM: N = 44,  $\chi^2_1 = 4.71$ ,  $P < 0.0001$ ). As expected, mice tested in summer were younger  
399 than those tested in winter (summer:  $4.51 \pm 0.16$  months; winter:  $8.60 \pm 0.55$  months; LMM: N = 99,  
400  $\chi^2_1 = 208.07$ ,  $P < 0.0001$ ).

401 For the entire striped mouse population at our study site (97 mice sampled in summer and 67 in  
402 winter; including the mice tested for cognition), glucose level tended to be influenced by an interaction  
403 between season and sex: males had higher blood glucose levels in winter ( $9.54 \pm 0.58$  mmol/litre) than  
404 females sampled in winter ( $7.43 \pm 0.37$  mmol/litre; LMM: N = 164;  $\chi^2_1 = 3.60$ , P = 0.054, Fig 1a). There  
405 was no effect of body mass or age on the glucose level (LMM: N = 164;  $\chi^2_1 = 3.47$ , P = 0.062;  $\chi^2_1 =$   
406  $0.55$ , P = 0.459, respectively). Mice had higher blood ketone levels in summer ( $0.63 \pm 0.04$  mmol/litre)  
407 than winter ( $0.41 \pm 0.02$  mmol/litre; LMM: N = 164;  $\chi^2_1 = 9.86$ , P = 0.001, Fig 1b). There was no effect  
408 of sex or body mass or age on ketone levels (LMM: N = 164;  $\chi^2_1 = 0.37$ , P = 0.541;  $\chi^2_1 = 2.19$ , P = 0.139;  
409  $\chi^2_1 = 3.09$ , P = 0.079, respectively).

410

#### 411 *Seasonal and physiological influence on problem-solving performance*

412

413 Of the 55 mice tested in summer, 38 (69%) were non-solvers and 17 (31%) were solvers (*i.e.*,  
414 opened at least 1 lid). Among the solvers, 5 (28%) opened just one lid, 5 (28%) opened 2 lids, 2 (11%)  
415 opened 3 lids and 6 (33%) opened all 4 lids (Table 1). There was no significant difference in lid location  
416 choice (Fisher exact test: 1<sup>st</sup> lid: P = 0.232; 2<sup>nd</sup> lid: P = 0.259; 3<sup>rd</sup> lid: P = 0.541; 4<sup>th</sup> lid: 0.410). In winter,  
417 of the 44 mice tested, 27 (61%) were non-solvers and 17 (39%) were solvers, of which 3 (18%) opened  
418 just one lid, 6 (35%) opened 2 lids, 1 (6%) opened 3 lids and 7 (41%) opened all 4 lids (Table 1). There  
419 was no significant difference in lid location choice (Fisher exact test: 1<sup>st</sup> lid: P = 0.138; 2<sup>nd</sup> lid: P = 0.240;  
420 3<sup>rd</sup> lid: P = 0.426; 4<sup>th</sup> lid: 0.1).

421 There was no seasonal difference in the proportion of solvers (GLMM, N = 99;  $\chi^2_1 = 1.30$ , P =  
422 0.253). The proportion of male solvers was greater than the proportion of female solvers (males: 43.64%;  
423 females: 22.73%; GLMM, N = 99;  $\chi^2_1 = 4.05$ , P = 0.044), but there was no significant interaction  
424 between season and sex (GLMM, N = 99;  $\chi^2_1 = 0.17$ , P = 0.676) (Table 2). There was no influence of  
425 physiological state on any measure of problem-solving (Table 2). Mice which were more persistent  
426 showed greater problem-solving success (GLMM, N = 99;  $\chi^2_1 = 5.30$ , P = 0.021), while neophobia and  
427 motivation for food did not predict general success (Table 2).

428           There was an influence of sex (GLMM,  $N = 99$ ;  $\chi^2_1 = 3.99$ ,  $P = 0.045$ ) on the total number of  
429 successes, but no seasonal difference (0-4 lids; GLMM,  $N = 99$ ;  $\chi^2_1 = 0.89$ ,  $P = 0.345$ ) and no significant  
430 interaction between season and sex (GLMM,  $N = 99$ ;  $\chi^2_1 = 0.97$ ,  $P = 0.325$ ) (Table 2). There was no  
431 influence of physiological state on the total number of success (Table 2). However, there was a  
432 significant influence of the body condition (GLMM,  $N = 99$ ;  $\chi^2_1 = 5.27$ ,  $P = 0.021$ ) and a significant  
433 interaction between body condition and sex (GLMM,  $N = 99$ ;  $\chi^2_1 = 7.27$ ,  $P = 0.007$ ): bigger males opened  
434 more lids. Mice which were more persistent opened more lids (GLMM,  $N = 99$ ;  $\chi^2_1 = 7.94$ ,  $P = 0.005$ )  
435 while neophobia and motivation did not predict the total number of successes (Table 2).

436           There was an influence of the season on the solving time for the 1<sup>st</sup> lid opened: mice tested in  
437 summer required less time than those tested in winter (LMM,  $N = 99$ ;  $\chi^2_1 = 20.42$ ,  $P < 0.001$ , Fig 2).  
438 There was no influence of sex (LMM,  $N = 99$ ;  $\chi^2_1 = 1.67$ ,  $P = 0.196$ ) but there was a significant  
439 interaction between season and sex (LMM,  $N = 99$ ;  $\chi^2_1 = 4.85$ ,  $P = 0.027$ ): females tested in summer  
440 required more time to open the 1<sup>st</sup> lid than males tested in summer (t-test:  $N_{\text{females}} = 26$ ,  $N_{\text{males}} = 29$ ,  $t_{20} =$   
441  $2.93$ ,  $P = 0.037$ , Fig 2). There was no influence of physiological state, body condition or non-cognitive  
442 traits on the solving time for the 1<sup>st</sup> lid opened (Table 2).

443           Latency to open the device was not significantly related to any physiological variables, but mice  
444 tested in summer opened the lids quicker compared to those tested in winter (Cox proportional hazard  
445 model,  $N = 99$ ; Fig. 3), with no influence of sex (Table 3). Latency was not affected by persistence,  
446 neophobia or motivation for food (Table 3).

447

## 448 **DISCUSSION**

449

450           In this study we tested whether free-ranging African striped mice differed seasonally in their  
451 success rate in an innovative problem-solving test, whether problem-solving was related to blood  
452 glucose and ketone levels, and whether possible intrinsic factors mediate problem-solving performance.  
453 We found no correlation between problem-solving performance and physiological parameters of energy  
454 availability. Overall, more males solved the problem than females and more persistent mice were more  
455 successful. We found partial support for seasonal differences in problem-solving performance but not

456 success. The number of successful individuals, and the number of lids opened did not differ between  
457 seasons, but in summer striped mice solved the problem faster than those in winter.

458 In accordance with our first prediction, problem-solving performance varied seasonally with  
459 regards to the time it took to solve the problem. The number of successful individuals was low for both  
460 seasons (summer: 31%; winter: 37%) suggesting that the task was difficult to solve, not ecologically  
461 relevant and/or conditions in a field lab were stressful. Nevertheless, a previous study based on the same  
462 protocol, showed that 57% of the tested striped mice were successful (Rochais et al., 2021) suggesting  
463 that striped mice are able to perform the task. The success rate itself did not differ seasonally, since the  
464 number of successful individuals and the number of lids opened did not differ between season. These  
465 results suggest that even when natural food availability was very low, problem-solving success was not  
466 affected. This finding supports the cognitive resilience hypothesis, which predicts that cognitive  
467 processes such as problem-solving are protected from low energy availability (Buchanan et al., 2013),  
468 suggesting that cognition could help to stabilize or improve the physiological state in challenging  
469 environments (Maille & Schradin, 2016a)

470 Of the successful solvers, striped mice solved problems significantly faster in summer than in  
471 winter. Previous findings on avian species suggested that faster cognitive performance in tasks like  
472 problem-solving could help individuals cope with harsh conditions when food supply is limited and  
473 unpredictable (Pravosudov & Clayton, 2002). Quicker cognitive performance during periods of food  
474 shortage, enabling animals to detect both food and potential dangers more easily, might have a greater  
475 net benefit under harsh conditions, decreasing allostatic load and increasing survival probability (Healy  
476 et al., 2009). Thus, individuals with faster problem-solving performance in the present study might cope  
477 better and increase their survival chances in their changing environment (Maille & Schradin, 2016b).

478 Currently, it is debated whether the speed of solving a problem is a suitable method to measure  
479 cognitive proficiency (Griffin et al., 2015; Rowe & Healy, 2014), because of the influence of non-  
480 cognitive factors, including persistence, neophobia, motivation and motor diversity (Van Horik &  
481 Madden, 2016; Rowell et al., 2021). Thus, we assessed whether possible non cognitive factors, such as  
482 persistence, mediate problem-solving performance. In our study, independent of season, more persistent

483 striped mice were more successful and opened more lids which supports previous studies showing that  
484 performance in a problem-solving task might depend on the extent of an individual interacting with the  
485 problem itself (reviewed in Amici et al., 2019, Rowell et al., 2021). Male striped mice solved problems  
486 faster in the food restricted summer than in winter, which could be due to other factors such as  
487 motivation to feed rather than cognition (Van Horik & Madden, 2016). We would have expected striped  
488 mice tested in summer to show increased motivation to feed, but there was no seasonal difference in  
489 persistence, neophobia or motivation for food. Thus, the most parsimonious explanation for the faster  
490 problem-solving performance in summer could be enhanced cognitive performance (*e.g.*, Reader et al.,  
491 2016).

492 Summer in our study site was characterized by hot and dry weather with low food availability  
493 for the striped mice. Glucose levels changed seasonally in our entire population but the difference was  
494 significant only for males which showed an increased blood glucose level with increased food  
495 availability in winter. Increased blood glucose could also be related to increased corticosterone levels,  
496 previously found in dispersing male striped mice (Vuarin et al., 2019). However, increased blood  
497 glucose was not related to fat storing in winter (Rimbach et al. 2019). Yet, within our subsample of  
498 striped mice tested for problem-solving, this difference was not apparent, probably related to a lower  
499 sample size leading to lower statistical power. Furthermore, food availability was still very low in the  
500 winter months included in the present study. Further, we found significantly higher ketone body levels  
501 in summer. This indicates lipid metabolism, *i.e.* the breakdown of stored fat to obtain ketone bodies for  
502 energy, a metabolic state that occurs during extended food deprivation or fasting (Mattson 2019).  
503 Ketones are an energy source for neurons, and can affect learning and memory, synaptic plasticity, and  
504 hippocampal neurogenesis, but can also enhance neuronal stress resistance (Sleiman et al., 2016), which  
505 could have influenced problem-solving performance. Higher ketone body levels in summer in striped  
506 mice is related to deterioration of health status and decreased survival (Schoepf et al., 2017), particularly  
507 because mice do not accumulate fat during winter (Rimbach et al. 2019). Thus, we found considerable  
508 variation in energy containing blood metabolites that at least partly were related to environmental  
509 differences in food availability and which could affect energy consuming cognitive processes.

510 In a previous study, we showed that attention and spatial memory performance are negatively  
511 correlated with basal blood glucose levels (Rochais et al., 2019), and we expected the same relationship  
512 between problem-solving and blood glucose levels and an inverse relationship with ketone levels that  
513 were significantly higher in summer. Unexpectedly, there were no correlations between physiological  
514 state (*i.e.* blood glucose or ketone levels) and problem-solving performance. One explanation could be  
515 that the lower blood glucose level in summer did not alter problem-solving performance. Another  
516 explanation could be related to the low (though significant) seasonal difference in food availability  
517 together with the significantly higher ketone body levels in summer, which might have compensated for  
518 the lower environmental energy availability in summer. Finally, some specific physiological  
519 mechanisms allowing for the maintenance of high glucose levels within the brain despite a reduced  
520 energy intake could have been involved: the brain-centered gluco-regulatory system, with the glucose  
521 transporter GLUT3, is able to modulate brain glucose levels *via* both insulin-dependent and independent  
522 mechanisms (Schwartz et al., 2013). These mechanisms can contribute to cognitive resilience and are  
523 predicted to have evolved as cognition helps to stabilize or improve the physiological state in  
524 challenging environments (Buchanan et al., 2013).

525 Male striped mice often performed better than females in the present problem-solving task. The  
526 proportion of solver males was greater than the proportion of solver females, larger males opened more  
527 lids than females and solver males solved the problem faster, especially in the summer. These results  
528 support previous studies showing that more competitive individuals and individuals of the larger sex (in  
529 sexually dimorphic species) innovate more than smaller individuals due to an “excess of energy”  
530 availability (Boogert et al., 2006). However, although the competitive ability of striped mice is body  
531 mass dependant (Schradin, 2004), they do not have a dominance hierarchy (Schradin & Pillay, 2004;  
532 Schubert et al., 2009). Another explanation could be that problem-solving tendencies may be enhanced  
533 in the dispersing sex, which is more likely to encounter novel challenges (Thornton & Samson, 2012).  
534 In striped mice, dispersal is male biased (Solmsen et al., 2011). Alternatively, male success in problem-  
535 solving could be related to their large size and better motor ability to open the device. However, a  
536 previous study using the same device showed that younger and smaller males striped mice solved the

537 task better than bigger males (Rochais et al., 2021). Finally, male striped mice showed faster attentional  
538 shifts in summer (Maille et al., 2015) which could have been related to faster problem-solving.  
539 Attentional shifting is, like innovative problem-solving, a measure of cognitive flexibility but different  
540 neural circuits are involved in the two cognitive processes (Audet & Lefebvre, 2017). In sum, male  
541 striped mice are larger than females and they are the dispersing sex, which might be an ecological  
542 explanation why they are better problem solvers.

543 In conclusion, our findings support the cognitive resilience hypothesis (Buchanan et al., 2013),  
544 as problem-solving success did not change seasonally in our free-ranging population of striped mice  
545 despite external environmental challenges that affect metabolism. We suggest that this could represent  
546 an adaptation to cope with seasonally changing energy supply. Problem-solving was faster in the drier  
547 summer, indicating that striped mice are able to respond seasonally to challenges, which could provide  
548 a pre-adaptation to cope with rapidly changing ecological needs in harsher climatic conditions  
549 (Pravosudov et al., 2015; Rymer et al., 2016). The absence of a relationship between physiological state  
550 (glucose and ketone) and problem-solving supports the cognitive resilience hypothesis, potentially  
551 involving mechanisms protecting the brain against seasonal variation in energy availability (Maille &  
552 Schradin, 2016a). Interestingly, problem-solving resilience is particularly relevant in the Succulent  
553 Karoo semi desert, where the frequency and intensity of droughts has increased and is at greatest risk  
554 from climate change (Rutherford et al., 2000; Midgley & Thuiller, 2007). Further studies are required  
555 to explore whether selection for cognitive resilience is the same for different cognitive traits in relation  
556 to different physiological predictors (*e.g.*, glucocorticoids) and take into account life history trade-offs.

557

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569

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571

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574

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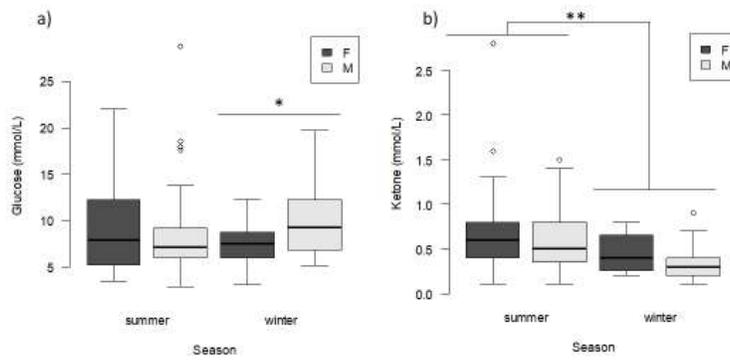
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771 **Figure captions**



772

773 **Figure 1:** Blood a) glucose and b) ketone levels (mean  $\pm$  SEM; mmol/litre) according to season and sex

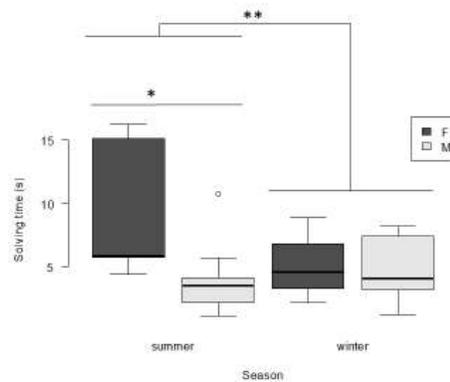
774 (summer:  $N_{\text{females}} = 37$ ,  $N_{\text{males}} = 60$ ; winter:  $N_{\text{females}} = 32$ ,  $N_{\text{males}} = 35$ ; LMM:  $T: P \leq 0.1$ ;  $**P \leq 0.01$ ). The

775 box corresponds to the first and third quartiles, the line is the median, the whiskers are 1.5 x the

776 difference between the third and first quartiles and circles are extreme individuals' data.

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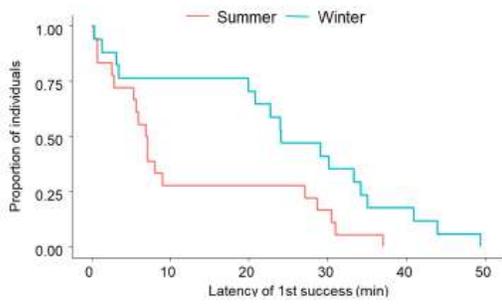
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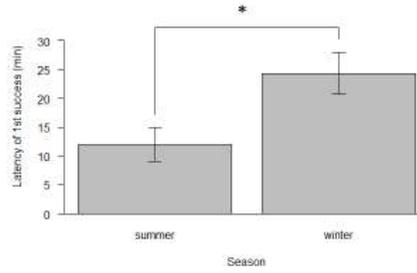
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781 **Fig 2.** Solving time *i.e.*, time, in seconds, took by a mouse that was manipulating a lid until it opened it  
 782 for the 1<sup>st</sup> successful attempt, by season and sex (summer:  $N_{\text{females}} = 26$ ,  $N_{\text{males}} = 29$ ; winter:  $N_{\text{females}} = 18$ ,  
 783  $N_{\text{males}} = 26$ ; LMM:  $*P \leq 0.05$ ;  $**P \leq 0.01$ ). The box corresponds to the first and third quartiles, the line  
 784 is the median, the whiskers are 1.5 x the difference between the third and first quartiles and circles are  
 785 extreme individuals' data.

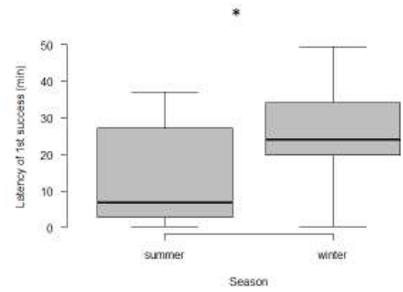
786



or



or



787

788 **Fig 3.** Relationship between season and proportion of individuals that solved the problem-solving task  
 789 in two trials for the latency of 1<sup>st</sup> success. Latency of opening was measured from the start of the trial  
 790 until a successful lid opening. These results suggest that summer conditions had a greater effect on  
 791 problem-solving performance, with more individuals tested in summer having a higher probability of  
 792 solving the task faster compared to individuals tested in winter, (Cox's proportional hazards models, \*  
 793  $P < 0.05$ ).

794

795

796 **Tables**

797 **Table 1:** Proportion of mice which solved the task (solvers: mice which opened at least 1 lid).

	Among solvers					
	% solvers	% non-solvers	% opened 1 lid	% open 2 lids	% opened 3 lids	% opened 4 lids
Winter	38.64	61.36	6.82	13.64	2.27	15.91
Summer	30.91	67.27	9.09	9.09	3.64	10.91

798

799

800

801 **Table 2:** Results from GLMM and LMM analysed for the influence of season, sex, body condition (ratio  
802 body mass / length), the physiological state (blood glucose and ketone levels) and “non-cognitive traits”  
803 (persistence, neophobia, motivation) on problem-solving performance, group is included as a random  
804 factor. The Likelihood Ratio Test statistics ( $\chi^2$ ), the denominator degrees of freedom (Df), and P values  
805 are shown (**bold values:**  $P \leq 0.05$ ); – Reflect untestable data.

806

<b>Variables</b>	<b><math>\chi^2</math></b>	<b>Df</b>	<b>P</b>
<i>Success (yes/no)</i>			
Season	0.01	1	0.925
Sex	4.04	1	<b>0.044</b>
Season*sex	0.17	1	0.676
Glucose	0.33	1	0.565
Ketone	1.15	1	0.283
Body condition	2.96	1	0.084
Sex*body condition	0.87	1	0.351
Age	0.69	1	0.406
Persistence	5.30	1	<b>0.021</b>
Neophobia	0.57	1	0.451
Motivation	0.01	1	0.982
<i>Total number of success (0-4 lids)</i>			
Season	0.89	1	0.345
Sex	3.99	1	<b>0.045</b>
Season*sex	0.97	1	0.325
Glucose	1.46	1	0.227
Ketone	0.07	1	0.784
Body condition	5.27	1	<b>0.021</b>
Sex*body condition	7.27	1	<b>0.007</b>
Age	2.27	1	0.131
Persistence	7.94	1	<b>0.005</b>
Neophobia	0.67	1	0.412
Motivation	0.02	1	0.967
<i>Solving time 1<sup>st</sup> success</i>			
Season	20.42	1	<b>&lt;0.001</b>
Sex	1.67	1	0.196
Season*sex	4.85	1	<b>0.027</b>
Glucose	2.05	1	0.151
Ketone	1.73	1	0.187
Body condition	3.91	1	0.058
Sex*body condition	2.73	1	0.098
Age	3.44	1	0.063
Persistence	1.09	1	0.296
Neophobia	0.99	1	0.319
Motivation	-	-	-

807

808 **Table 3:** Results from Cox proportional hazard model analysing problem-solving latency differences  
809 according to the season, sex, the physiological state (blood glucose and ketone levels) and “non-  
810 cognitive traits” (persistence, neophobia, motivation) on latency to solve the problem-solving task. The  
811 Likelihood Ratio Test statistics ( $\chi^2$ ), the denominator degrees of freedom (Df), and P values are shown  
812 (**bold values:**  $P \leq 0.05$ ).

813

	$\chi^2$	Df	P
<b>Variables</b>			
<i>Latency of 1<sup>st</sup> success</i>			
Season	4.44	1	<b>0.035</b>
Sex	0.42	1	0.516
Season*sex	0.07	1	0.791
Glucose	0.15	1	0.700
Ketone	0.14	1	0.705
Age	0.01	1	0.950
Persistence	0.82	1	0.365
Neophobia	0.38	1	0.539
Motivation	0.05	1	0.812

814

815