Seasonal changes in problem-solving in wild African striped mice

Celine Rochais, Carsten Schradin, Neville Pillay

► To cite this version:

Celine Rochais, Carsten Schradin, Neville Pillay. Seasonal changes in problem-solving in wild African striped mice. *Animal Cognition*, 2021, 10.1007/s10071-021-01559-4 . hal-03364035

HAL Id: hal-03364035

<https://hal.science/hal-03364035>

Submitted on 4 Oct 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Seasonal changes in problem-solving in wild African striped mice

Celine Rochais^{a,*}, Carsten Schradin^{a,b} and Neville Pillay^a

^a School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

^b IPHC, UNISTRA, CNRS, 23 rue du Loess, 67200 Strasbourg, France

*Corresponding author:

Celine Rochais

School of Animal, Plant and Environmental Sciences,

University of the Witwatersrand,

Johannesburg, South Africa

celine.rochais@gmail.com

Published as

Rochais, C., Schradin, C. & Pillay, N. 2021. Seasonal changes in problem-solving in wild African striped mice. *Animal Cognition*.

10.1007/s10071-021-01559-4

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

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

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

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

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

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

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

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

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

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

Here, we aimed to investigate whether problem-solving performance changed between seasons and whether these changes were associated with environmentally induced physiological changes in a free-ranging population of the African striped mouse, *Rhabdomys pumilio*. The striped mouse is an ideal model to study the influence of seasonal, and hence, physiological state on problem-solving because it inhabits the semi desert Succulent Karoo in southern Africa where it faces marked seasonal changes in food availability (Schradin et al., 2012). The frequency and intensity of droughts has increased in this 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 food availability (lower quantity of plants leaves, flowers and seeds for striped mice) and the blood glucose levels of striped mice decrease due to decreased food availability (Schradin et al., 2015).

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

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

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

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

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

METHODS

Ethical note

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

Study population

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

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

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

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

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

Study location and period

Our study location was in Goegap Nature Reserve, near Springbok in the Northern Cape Province, South Africa (S 29 41.56, E 18 1.60). The area is arid, characterized by a hot and dry summer and a wet and cold winter. The vegetation is classified as Succulent Karoo. Up to sixteen social groups of striped mice occupied our 10ha study area. The study took place during the dry summer season from 1st January to 22th March 2019 and during the wet winter season from 20th June to 17th August 2019. We measured daily temperature and rainfall. Because striped mice mainly feed on all parts (leaves, flowers and seeds) of annual and perianual plants, food availability was assessed twice a month through plant surveys using the Braun-Blanquet method (Wikum & Shanholtzer 1978) on the 1st and the 15th of each month of the year. We recorded the number of food plant species for striped mice as a measure of food availability (palatability is known from behavioural observations, Schradin & Pillay, 2006), in eight monitoring plots of 4 m² each that were located within the home ranges of the different social groups (Schradin & Pillay, 2005).

Measurement of basal blood glucose and ketone levels

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

to the anus; mm) and reproductive status. Mice were trapped early in the morning before they left their nest to forage. Thus, blood samples were obtained after the mice had fasted overnight and before their onset of foraging and pronounced physical activity. Immediately after a mouse entered a trap, it was removed and anaesthetized by putting them in a jar containing diethyl ether on cotton wool (Schradin 2008) and a drop of blood was obtained from the sublingual vein within 3 minutes of trapping to limit handling influence. We measured blood glucose (mmol/Litre) and ketone bodies (mmol/Litre) in the field by using a One Touch Ultra glucometer (Lifescan, Inc., Milpitas, CA, U.S.A.) and a Freestyle Optium Blood β -Ketone meter (Abbott Laboratories, Australia). The mice were given a piece of the bait used in their trap just after the procedure and were released at their nest within 30 minutes. 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 (Maille et al., 2015; Rochais et al., 2019).

Cognitive testing

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

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

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

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

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

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

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

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

Statistical analyses

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

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

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

Seasonal changes in weather and food availability

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

Seasonal changes in body condition and physiology

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

Seasonal and physiological influence on problem-solving performance

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

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

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

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

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

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

RESULTS

Seasonal changes in weather and food availability

It was warmer and drier during summer (temperature: 24.42 ± 0.36 °C; total rainfall: 0.60 mm) compared to winter (temperature: 13.47 ± 0.45 °C; total rainfall: 39.60 mm; LM: N = 138, F = 368.40, $P < 0.001$; F = 4.31, $P = 0.039$, respectively). Food availability increased within the study period from summer (2.35 ± 0.11 food plants/plot) to winter (3.27 ± 0.24 food plants/plot; LM: N_{summer plots} = 48, N_{winter plots} = 48, F = 12.12, $P < 0.001$).

Seasonal changes in body condition and physiology

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

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

Seasonal and physiological influence on problem-solving performance

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

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

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

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

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

DISCUSSION

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

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

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

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

Currently, it is debated whether the speed of solving a problem is a suitable method to measure cognitive proficiency (Griffin et al., 2015; Rowe & Healy, 2014), because of the influence of non-cognitive factors, including persistence, neophobia, motivation and motor diversity (Van Horik & Madden, 2016; Rowell et al., 2021). Thus, we assessed whether possible non cognitive factors, such as 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.

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

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

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

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

Acknowledgments: This study was made possible by the administrative and technical support of the Succulent Karoo Research Station (registered South African NPO 122-134). We thank Javed Anver, Noor Den hartog, Leon Kotze, Gildas Lemonnier, Jonas Sommer, Richard Weil and Lindy Wolhuter for assistance in the field. We are grateful to Margaux Duparcq and Leon Kotze for the blind video analyses and to Pierre Uhrich for building the device. We are grateful to the anonymous reviewers for insightful comments that greatly improved the manuscript.

Author contribution: All the authors participated to the conception and the design of the experiments. C.R. performed the experiments and analysed the data. All the authors contributed to writing the paper.

Funding: This research was supported by a fellowship (to C.R.) by the University of the Witwatersrand, the National Research Foundation (South Africa) and by the CNRS (France).

Conflict of Interest: The authors declare no conflict of interest.

Ethics approval: Animal ethical clearance was provided by the University of the Witwatersrand, Johannesburg, South Africa (No.2018/09/46B).

References

- Amici F, Widdig A, Lehmann J, Majolo B (2019) A meta-analysis of interindividual differences in innovation. *Anim Behav* 155:. <https://doi.org/10.1016/j.anbehav.2019.07.008>
- Audet J-N, Lefebvre L (2017) What's flexible in behavioral flexibility? *Behav Ecol* 28:943–947. <https://doi.org/10.1093/beheco/arx007>
- Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:. <https://doi.org/10.18637/jss.v067.i01>
- Berger J, Swenson JE, Persson IL (2001) Recolonizing carnivores and naïve prey: Conservation lessons from pleistocene extinctions. *Science* (80-) 291:1036–1039. <https://doi.org/10.1126/science.1056466>
- Bókony V, Lendvai ÁZ, Vágási CI, et al (2014) Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. *Behav Ecol* 25:124–135. <https://doi.org/10.1093/beheco/art094>
- Boogert NJ, Reader SM, Laland KN (2006) The relation between social rank, neophobia and individual learning in starlings. *Anim Behav* 72:1229–1239. <https://doi.org/10.1016/j.anbehav.2006.02.021>
- Buchanan KL, Grindstaff JL, Pravosudov V V. (2013) Condition dependence, developmental

592 plasticity, and cognition: implications for ecology and evolution. *Trends Ecol Evol* 28:290–296.
593 <https://doi.org/10.1016/j.tree.2013.02.004>

594 Buchholz R, Banusiewicz JD, Burgess S, et al (2019) Behavioural research priorities for the study of
595 animal response to climate change. *Anim Behav* 150:127–137.
596 <https://doi.org/10.1016/j.anbehav.2019.02.005>

597 Camacho-Alpízar A, Griffin AS, Guillette LM (2020) Are cognitive abilities under selection by
598 female choice? A comment on Chen et al. (2019). *Anim Behav* 165:e1–e3.
599 <https://doi.org/10.1016/j.anbehav.2020.03.017>

600 Chen J, Zou Y, Sun YH, ten Cate C (2020) On problem solving and the evolution of cognitive abilities
601 by mate choice: a reply to Camacho-Alpízar et al. (2020). *Anim Behav* 165:e5–e7.
602 <https://doi.org/10.1016/j.anbehav.2020.05.003>

603 Fox J, Weisberg S (2019) *An R Companion to Applied Regression* (3 ed.). Sage

604 Griffin AS, Guez D (2014) Innovation and problem solving: A review of common mechanisms. *Behav*
605 *Processes* 109:121–134. <https://doi.org/10.1016/J.BEPROC.2014.08.027>

606 Griffin AS, Guillette LM, Healy SD (2015) Cognition and personality: an analysis of an emerging
607 field. *Trends Ecol Evol* 207–2014. <https://doi.org/https://doi.org/10.1016/j.tree.2015.01.012>

608 Healy SD, Bacon IE, Haggis O, et al (2009) Explanations for variation in cognitive ability:
609 Behavioural ecology meets comparative cognition. *Behav Processes* 80:288–294.
610 <https://doi.org/10.1016/j.beproc.2008.10.002>

611 Hervé M (2019) *RVAideMemoire: Testing and Plotting Procedures for Biostatistics*. R package
612 version 0.9-73.

613 Hothorn T, Zeileis A, Farebrother RW, et al (2019) Package ‘lmtest’ (Version 0.9-37). [https://CRANR-](https://CRANR-project.org/Packag)
614 [project.org/ Packag](https://CRANR-project.org/Packag)

615 Huebner F, Fichtel C, Kappeler PM (2018) Linking cognition with fitness in a wild primate: Fitness
616 correlates of problem-solving performance and spatial learning ability. *Philos Trans R Soc B*
617 *Biol Sci* 373:. <https://doi.org/10.1098/rstb.2017.0295>

618 Kozlovsky DY, Branch CL, Pravosudov V V. (2015) Problem-solving ability and response to novelty
619 in mountain chickadees (*Poecile gambeli*) from different elevations. *Behav Ecol Sociobiol*
620 69:635–643. <https://doi.org/10.1007/s00265-015-1874-4>

621 Kozlovsky DY, Weissgerber EA, Pravosudov V V. (2017) What makes specialized food-caching
622 mountain chickadees successful city slickers? *Proc R Soc B Biol Sci* 284:.
623 <https://doi.org/10.1098/rspb.2016.2613>

624 Kummer H, Goodall J (1985) Conditions of Innovative Behaviour in Primates. *Philos Trans R Soc B*
625 308:203–214. <https://doi.org/10.1098/rstb.1985.0020>

626 Laland KN, Reader SM (1999) Foraging innovation in the guppy. *Anim Behav* 57:331–340.
627 <https://doi.org/10.1006/anbe.1998.0967>

628 Laughlin SB (2001) Energy as a constraint on the coding and processing of sensory information. *Curr*
629 *Opin Neurobiol* 11:475–480. [https://doi.org/10.1016/S0959-4388\(00\)00237-3](https://doi.org/10.1016/S0959-4388(00)00237-3)

630 Lenth R (2019) emmeans: Estimated Marginal Means, aka Least-Squares Means. [https://cran.r-](https://cran.r-project.org/package=emmeans)
631 [project.org/package=emmeans](https://cran.r-project.org/package=emmeans)

632 Lonnstedt OM, McCormick MI, Meekan MG, et al (2012) Learn and live : predator experience and
633 feeding history determines prey behaviour and survival. *Proc R Soc B Biol Sci* 279:2091–2098.
634 <https://doi.org/10.1098/rspb.2011.2516>

635 Maille A, Pillay N, Schradin C (2015) Seasonal variation in attention and spatial performance in a
636 wild population of the African striped mouse (*Rhabdomys pumilio*). *Anim Cogn* 18:1231–1242.
637 <https://doi.org/10.1007/s10071-015-0892-y>

638 Maille A, Schradin C (2016a) Ecophysiology of cognition: How do environmentally induced changes
639 in physiology affect cognitive performance? *Biol Rev* 92:1101–1112.
640 <https://doi.org/10.1111/brv.12270>

641 Maille A, Schradin C (2016b) Survival is linked with reaction time and spatial memory in African
642 striped mice. *Biol Lett* 12:20160346. <https://doi.org/10.1098/rsbl.2016.0346>

643 Martin P, Bateson P (1993) *Measuring behaviour*. Cambridge University Press, Cambridge

644 Mattson MP (2019) An Evolutionary Perspective on Why Food Overconsumption Impairs Cognition.
645 *Trends Cogn. Sci.* 23:200–212

646 Mazza V, Guenther A (2021) City mice and country mice: innovative problem solving in rural and
647 urban noncommensal rodents. *Anim Behav* 172:197–210.
648 <https://doi.org/10.1016/j.anbehav.2020.12.007>

649 McCue MD (2010) Starvation physiology: Reviewing the different strategies animals use to survive a
650 common challenge. *Comp. Biochem. Physiol. - A Mol. Integr. Physiol.* 156:1–18

651 McEwen BS, Wingfield JC (2010) What is in a name? Integrating homeostasis, allostasis and stress.
652 *Horm Behav* 57:105–111. <https://doi.org/10.1016/j.yhbeh.2009.09.011>

653 McNay EC, Fries TM, Gold PE (2000) Decreases in rat extracellular hippocampal glucose
654 concentration associated with cognitive demand during a spatial task. *Proc Natl Acad Sci*

97:2881–2885. <https://doi.org/10.1073/pnas.050583697>

Midgley GF, Thuiller W (2007) Potential vulnerability of Namaqualand plant diversity to anthropogenic climate change. *J Arid Environ* 70:615–628. <https://doi.org/10.1016/j.jaridenv.2006.11.020>

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Evol Syst* 37:637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>

Prasher S, Evans JC, Thompson MJ, Morand-Ferron J (2019) Characterizing innovators: Ecological and individual predictors of problem-solving performance. *PLoS One* 14:. <https://doi.org/10.1371/journal.pone.0217464>

Pravosudov V V., Clayton NS (2002) A test of the adaptive specialization hypothesis: Population differences in caching, memory, and the hippocampus in black-capped chickadees (*Parus atricapilla*). *Behav Neurosci* 116:515–522. [https://doi.org/https://doi.org/10.1037/0735-7044.116.4.515](https://doi.org/10.1037/0735-7044.116.4.515)

Pravosudov V V., Roth TCI, LaDage LD, Freas CA (2015) Environmental influences on spatial memory and the hippocampus in food-caching chickadees. *Comp Cogn Behav Rev* 10:25e43

Ramsey G, Bastian ML, Van schaik C (2007) Animal innovation defined and operationalized. *Behav Brain Sci* 30:. <https://doi.org/10.1017/S0140525X07002373>

Reader SM, Laland KN (2003) *Animal Innovation*. Oxford University Press, New York, NY

Reader SM, Morand-Ferron J, Flynn E (2016) Animal and human innovation: Novel problems and novel solutions. *Philos Trans R Soc B Biol Sci* 371:. <https://doi.org/10.1098/rstb.2015.0182>

Rimbach R, Blanc S, Zahariev A, et al (2018a) Seasonal variation in energy expenditure in a rodent inhabiting a winter-rainfall desert. *J Comp Physiol B Biochem Syst Environ Physiol* 188:877–888. <https://doi.org/10.1007/s00360-018-1168-z>

Rimbach R, Blanc S, Zahariev A, et al (2019) Fat content of striped mice decreased during the breeding season but not during the food-restricted dry season. *J Exp Biol* jeb.208504. <https://doi.org/10.1242/jeb.208504>

Rimbach R, Jäger J, Pillay N, Schradin C (2018b) Food availability is the main driver of seasonal changes in resting metabolic rate in African striped mice (*Rhabdomys pumilio*). *Physiol Biochem Zool* 91:826–833. <https://doi.org/10.1086/696828>

Rimbach R, Pillay N, Schradin C (2018c) Both thyroid hormone levels and resting metabolic rate decrease in African striped mice when food availability decreases. *J Exp Biol* 220:837–843. <https://doi.org/10.1242/jeb.185363>

687 Rimbach R, Pillay N, Schradin C (2021) Prolonged growth during the food-restricted dry season in a
688 small African mammal. *J Mammal* 102:296–307. <https://doi.org/10.1093/jmammal/gyaa169>

689 Rochais C, Maille A, Jäger J, et al (2019) How does cognitive performance change in relation to
690 seasonal and experimental changes in blood glucose levels? *Anim Behav* 158:149–159.
691 <https://doi.org/10.1016/j.anbehav.2019.10.011>

692 Rochais C, Pillay N, Schradin C (2021) Do alternative reproductive tactics predict problem-solving
693 performance in African striped mice? *Anim Cogn*. <https://doi.org/10.1007/s10071-020-01459-z>

694 Roth TC, LaDage LD, Pravosudov V V. (2010) Learning capabilities enhanced in harsh environments:
695 A common garden approach. *Proc R Soc B Biol Sci* 277:3187–3193.
696 <https://doi.org/10.1098/rspb.2010.0630>

697 Rowe C, Healy SD (2014) Measuring variation in cognition. *Behav Ecol* 25:1287–1292.
698 <https://doi.org/10.1093/beheco/aru090>

699 Rowell MK, Pillay N, Rymer TL (2021) Problem solving in animals: Proposal for an ontogenetic
700 perspective. *Animals* 11:1–21. <https://doi.org/10.3390/ani11030866>

701 Rutherford M, Midgley G, Bond W, et al (2000) South African Country Study on Climate Change:
702 Plant Biodiversity Vulnerability and Adaptation Assessment. *Clim Chang impacts South Africa*
703 Rep to Natl Clim Chang Comm

704 Rymer TL, Pillay N, Schradin C (2016) Resilience to droughts in mammals: a conceptual framework
705 for estimating vulnerability of a single species. *Q Rev Biol* 91:133–176

706 Schoepf I, Pillay N, Schradin C (2017) Trade-offs between reproduction and health in free-ranging
707 African striped mice. *J Comp Physiol B Biochem Syst Environ Physiol* 187:625–637.
708 <https://doi.org/10.1007/s00360-016-1054-5>

709 Schradin C (2006) Whole-day follows of striped mice [*Rhabdomys pumilio*], a diurnal murid rodent. *J*
710 *Ethol* 24:37–43. <https://doi.org/10.1007/s10164-005-0158-2>

711 Schradin C (2008) Seasonal changes in testosterone and corticosterone levels in four social classes of
712 a desert dwelling sociable rodent. *Horm Behav* 53:573–579.
713 <https://doi.org/10.1016/j.yhbeh.2008.01.003>

714 Schradin C (2004) Territorial defense in a group-living solitary forager: Who, where, against whom?
715 *Behav Ecol Sociobiol* 55:439–446. <https://doi.org/10.1007/s00265-003-0733-x>

716 Schradin C, Lindholm AK, Johannesen J, et al (2012) Social flexibility and social evolution in
717 mammals: A case study of the African striped mouse (*Rhabdomys pumilio*). *Mol Ecol* 21:541–
718 553. <https://doi.org/10.1111/j.1365-294X.2011.05256.x>

719 Schradin C, Pillay N (2005a) Demography of the striped mouse (*Rhabdomys pumilio*) in the succulent
720 karoo. *Mamm Biol* 70:84–92. <https://doi.org/10.1039/DT9850000663>

721 Schradin C, Pillay N (2004) The Striped Mouse (*Rhabdomys pumilio*) From the Succulent Karoo,
722 South Africa: A Territorial Group-Living Solitary Forager With Communal Breeding and
723 Helpers at the Nest. *J Comp Psychol* 118:37–47. <https://doi.org/10.1037/0735-7036.118.1.37>

724 Schradin C, Pillay N (2005b) Intraspecific Variation in the Spatial and Social Organization of the
725 African Striped Mouse. *J Mammal* 86:99–107. [https://doi.org/10.1644/1545-](https://doi.org/10.1644/1545-1542(2005)086<0099:IVITSA>2.0.CO;2)
726 [1542\(2005\)086<0099:IVITSA>2.0.CO;2](https://doi.org/10.1644/1542(2005)086<0099:IVITSA>2.0.CO;2)

727 Schradin C, Pillay N (2006) Female striped mice (*Rhabdomys pumilio*) change their home ranges in
728 response to seasonal variation in food availability. *Behav Ecol* 17:452–458.
729 <https://doi.org/10.1093/beheco/arj047>

730 Schradin C, Pillay N, Kondratyeva A, et al (2015) Basal blood glucose concentration in freelifving
731 striped mice is influenced by food availability, ambient temperature and social tactic. *Biol Lett*
732 11:. <https://doi.org/10.1098/rsbl.2015.0208>

733 Schradin C, Schneider C, Yuen CH (2009) Age at puberty in male African striped mice: the impact of
734 food, population density and the presence of the father. *Funct Ecol* 23:1004–1013.
735 <https://doi.org/10.1111/j.1365-2435.2009.01569.x>

736 Schubert M, Pillay N, Schradin C (2009) Parental and Alloparental Care in a Polygynous Mammal. *J*
737 *Mammal* 90:724–731. <https://doi.org/10.1644/08-mamm-a-175r1.1>

738 Schwartz MW, Seeley RJ, Tschöp MH, et al (2013) Cooperation between brain and islet in glucose
739 homeostasis and diabetes. *Nature* 503:59–66. <https://doi.org/10.1038/nature12709>

740 Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid
741 environmental change. *Evol Appl* 4:367–387. <https://doi.org/10.1111/j.1752-4571.2010.00166.x>

742 Sleiman SF, Henry J, Al-Haddad R, et al (2016) Exercise promotes the expression of brain derived
743 neurotrophic factor (BDNF) through the action of the ketone body β -hydroxybutyrate. *Elife* 5:.
744 <https://doi.org/10.7554/eLife.15092>

745 Sol D, Lefebvre L, Rodríguez-Teijeiro JD (2005) Brain size, innovative propensity and migratory
746 behaviour in temperate Palearctic birds. *Proc R Soc B Biol Sci* 272:1433–1441.
747 <https://doi.org/10.1098/rspb.2005.3099>

748 Sol D, Sayol F, Ducatez S, Lefebvre L (2016) The life-history basis of behavioural innovations. *Philos*
749 *Trans R Soc B Biol Sci* 371:. <https://doi.org/10.1098/rstb.2015.0187>

750 Solmsen N, Johannesen J, Schradin C (2011) Highly asymmetric fine-scale genetic structure between

751 sexes of African striped mice and indication for condition dependent alternative male dispersal
752 tactics. *Mol Ecol* 20:1624–1634. <https://doi.org/10.1111/j.1365-294X.2011.05042.x>

753 Team RC (2019) A language and environment for statistical computing. R Foundation for Statistical
754 Computing, Vienna, Austria. <https://www.r-project.org/>.

755 Therneau T, Grambsch P (2000) *Modeling Survival Data: Extending the Cox Model*, Springer.
756 Springer-Verlag New York, New York, NY

757 Therneau TM (2020a) Mixed Effects Cox Models [R package coxme version 2.2-16]

758 Therneau TM (2020b) Survival Analysis [R package survival version 3.2-7]

759 Thornton A, Samson J (2012) Innovative problem solving in wild meerkats. *Anim Behav* 83:1459–
760 1468. <https://doi.org/10.1016/j.anbehav.2012.03.018>

761 Van Horik JO, Madden JR (2016) A problem with problem solving : motivational traits , but not
762 cognition , predict success on novel operant foraging tasks. *Anim Behav* 114:189–198.
763 <https://doi.org/10.1016/j.anbehav.2016.02.006>

764 Vuarin P, Pillay N, Schradin C (2019) Elevated basal corticosterone levels increase disappearance risk
765 of light but not heavy individuals in a long-term monitored rodent population. *Horm Behav*
766 113:95–102. <https://doi.org/10.1016/J.YHBEH.2019.05.001>

767 Wikum DA, Shanholtzer GF (1978) Application of the Braun-Blanquet cover-abundance scale for
768 vegetation analysis in land development studies. *Environ Manage* 2:323–329.
769 <https://doi.org/10.1007/BF01866672>

770

771 **Figure captions**

Figure 1: Blood a) glucose and b) ketone levels (mean $\pm$ SEM; mmol/litre) according to season and sex (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 box corresponds to the first and third quartiles, the line is the median, the whiskers are 1.5 x the difference between the third and first quartiles and circles are extreme individuals' data.

779

780

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 1st 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 1st 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

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

Variables	χ^2	Df	P
<i>Success (yes/no)</i>			
Season	0.01	1	0.925
Sex	4.04	1	0.044
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	0.021
Neophobia	0.57	1	0.451
Motivation	0.01	1	0.982
<i>Total number of success (0-4 licks)</i>			
Season	0.89	1	0.345
Sex	3.99	1	0.045
Season*sex	0.97	1	0.325
Glucose	1.46	1	0.227
Ketone	0.07	1	0.784
Body condition	5.27	1	0.021
Sex*body condition	7.27	1	0.007
Age	2.27	1	0.131
Persistence	7.94	1	0.005
Neophobia	0.67	1	0.412
Motivation	0.02	1	0.967
<i>Solving time 1st success</i>			
Season	20.42	1	<0.001
Sex	1.67	1	0.196
Season*sex	4.85	1	0.027
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	-	-	-

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

	χ^2	Df	P
Variables			
<i>Latency of 1st success</i>			
Season	4.44	1	0.035
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