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SHORT COMMUNICATION

Cognitive skills of common shrews (*Sorex araneus*) vary with seasonal changes in skull size and brain mass

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ABSTRACT

In a rare phenomenon, shrews and a few other species cope with seasonal environments by reducing and regrowing brain size, potentially at the cost of changes in cognitive abilities. Here, we confirm an extensive seasonal shrinkage (21.4%) and regrowth (17.0%) of brain mass in winter and spring, respectively, in the common shrew (*Sorex araneus* L.) in Southern Germany. In a spatial learning task experiment, individuals with reduced winter brain size covered larger distances to find food, compared with the relatively large-brained summer juveniles and regrown spring adults. By reducing their brain mass, these shrews may reduce their energetic demands, but at the cost of cognitive performance, implying a complex trade-off for coping with seasonally fluctuating resources. These results are relevant for our understanding of evolution and the dynamics of mammalian nervous systems in response to environmental changes.

KEY WORDS: Dehnel's phenomenon, Brain size, Seasonal adaptation, Spatial cognition, Braincase size, Learning task

INTRODUCTION

Organisms have developed a wide range of strategies to cope with seasonal fluctuations in resources and temperature, using a combination of changes in morphology, physiology and behavior (Demas et al., 2010). During winter, vertebrates use two main strategies: migration or hibernation. These are usually combined with morphological adaptations such as improving insulating tissues, or changes in behavior including food storing or communal thermoregulation (Merritt and Zegers, 2014). This can be associated with seasonal changes in certain cognitive capacities and the brain structures responsible for those skills (Sherry, 2006).

Seasonally food-storing birds and mammals such as black-capped chickadees (Smulders et al., 1995), Richardson's ground squirrels (Burger et al., 2013) and grey squirrels (Jacobs and Liman, 1991; MacDonald, 1997) exhibit elevated spatial cognitive capacities during the caching season along with a reversible increase of hippocampus size, a brain region responsible for spatial memory and learning (Burger et al., 2013; Lavenex et al., 2000a; Sherry et al., 1992). Similarly, voles and mice exhibit improved spatial learning

capacities along with an increase in hippocampal size during the mating season, when their home ranges increase as they search for mates (Galea et al., 1994; Jacobs et al., 1990; Pyter, 2005; Pyter et al., 2006; Workman et al., 2009; Yaskin, 2013). In birds, the increased ability to cache and find food coincides with higher rates of adult neurogenesis and increased hippocampal cell numbers (Smulders et al., 2000; Tramontin et al., 1998). In contrast, in the mammals studied to date, hippocampus size changes are not reflected in cell numbers (Barker et al., 2003; Lavenex et al., 2000b).

In rare cases, plastic seasonal morphological and behavioral adaptations can be even more pronounced, i.e. in species that are unable to migrate or hibernate, such as some red-toothed shrews (*Sorex* spp.) and small mustelids (*Mustela* spp.; Dechmann et al., 2017; LaPoint et al., 2017). The red-toothed shrews, where this has been most intensively studied, occur in some of the most variable environments, including the Arctic (Mackiewicz et al., 2017), despite their extremely small body size and high metabolic rate (Ochocińska and Taylor, 2005). Their remarkable strategy to cope with harsh winter conditions is to reduce overall body size, including the brain, several other organs, as well as skeletal elements and spine length. Presumably this minimizes absolute metabolic demands when conditions are harsh and thus increases their chance of survival (Pucek, 1965, 1970; Saure and Hyvärinen, 1965; Taylor et al., 2013). They then regrow in spring as they become sexually mature just before their single lifetime reproductive period. In our study species, the common shrew (*Sorex araneus* Linnaeus 1758), winter decrease in skull size and correlated decrease in brain mass is up to 20%, followed by partial regrowth of 15%, a process known as Dehnel's phenomenon (Bielak and Pucek, 1960; Dehnel, 1949; Lázaro et al., 2017). To our knowledge, this is the most extreme individual reversible change of total brain size reported in a vertebrate, but whether it is linked to changes in cognitive abilities is unknown.

Shrews are efficient hunters and seem to remember previous foraging paths (Barnard and Brown, 1985; Pierce, 1987; Saarikko, 1989). However, the seasonal change in brain size has never been considered in these experiments, and in fact, summer shrews performed poorly in an associative learning task (Page et al., 2012). Smaller winter territories coincide with reduced brain size, and in spring both their territories and their brains expand in size (Stockley and Searle, 1998). As reduced home ranges have been associated with lower spatial capacities during winter in other species (see above), we predicted the same in shrews (Yaskin, 2011). The reduced spatial cognition demands of winter may allow individuals to reduce the size of their energetically demanding brain. Several brain regions that may be linked to integrative information, especially the neocortex and the thalamus, show pronounced winter decrease (27% each; Yaskin, 1994). There is also winter decrease followed by spring regrowth in the hippocampus (Yaskin, 1994). This has been hypothesized as a link between spatial cognition and home range size (Yaskin, 2005, 2011).

We designed a spatial learning test to quantify seasonal changes in shrew cognitive abilities as determined from their ability to use a reference cue to find food. We aimed to (1) confirm the seasonal pattern reported in previous studies in skull size and brain mass in our population of common shrews from Southern Germany; and (2) compare the spatial cognitive skills between summer juveniles, wintering individuals and spring adults. We predicted that brain size in shrews is linked to cognitive ability. Seasonal changes in brain size should lead to decreased cognitive abilities in the winter. This study is a first step towards understanding the cognitive consequences of Dehnel's phenomenon.

MATERIALS AND METHODS
Trapping and processing of specimens
All handling and sampling methods were approved by the Regierungspräsidium Freiburg, Baden-Württemberg (35-9185.81/ G-11/21, 35-9185.81/G-14/28). We trapped shrews in Möggingen, Germany (47°46′04.70″N, 8°59′47.11″E), between August 2013 and October 2015 with wooden live-traps (PPUH A. Marcinkiewicz, Rajgród, Poland) baited with mealworms (*Tenebrio molitor*) and checked at ≤2 h intervals. To extract the skulls and brains, we anesthetized shrews with isoflurane and then increased the flow rate to lethal levels (N=58 males, 35 females, 13 undetermined sex). We placed euthanized shrews in a laboratory colony of *Dermestes maculatus* to obtain clean skeletons. We captured shrews for the behavioral test from the same study area using the same capture methods. We also used these experimental animals for a parallel mark-recapture study, as this experiment is part of a larger project (Lázaro et al., 2017). Therefore, immediately after completion of the behavioral tests, we marked individuals with subcutaneous passive integrated transponders (7×1.5 mm, UNO PICO) and released them at the site of capture. For this study we caught new individuals during each season.

For age determination, we classified the individuals as immature juveniles or adults based on the development of testes or mammary glands, tooth wear and fur appearance (Churchfield, 1990; Pankakoski, 1989). In immature shrews we determined the sex using a PCR-based gonosomal sexing method (C. Roos, DPZ Göttingen, unpublished data). DNA was extracted from tail tip samples using Qiagen's DNAeasy kit (Qiagen, GmbH, Hilden). We lacked sufficient material to sex all immature individuals.

Skull and brain measurements
We recorded the following measurements from cleaned skulls: skull length (SKL), from the anteriormost projection of incisor 1 to the occipital condyle; braincase width (BCW), the greatest lateral diameter of the braincase; and braincase height (BCH), from the tympanic rings to the dorsal surface of the braincase (Table S3). All linear measurements were taken with digital calipers to the nearest 0.01 mm, except tooth row length (see below). To obtain brain mass, we weighed the fresh extracted brains with an electronic scale (Kern & Son, AES 200-4 cm, Balingen, Germany) to the nearest 0.001 g (Table S3). We size-corrected all skull measurements and brain mass by the non-changing maxillary tooth row length (i.e. BCH_{cor}, BCW_{cor}, SKL_{cor} and brain $mass_{cor}$) (Lázaro et al., 2017). The tooth row length is defined as the distance from the uppermost edge between the premaxilla and incisor 1 to the basal junction of molars 2 and 3 and was measured via digital X-ray images of the skulls in lateral view using ImageJ (Schneider et al., 2012). To obtain the X-ray images, the skulls were placed on a wooden base, which allowed us to obtain a standardized position for all individuals in lateral view. We obtained the X-ray images with a

Faxitron MX 20 cabinet (26 kV, 6 s), an OPG Imaging Plate (Gendex) and a scanner (DenOptix/Gendex). All measurements were taken by a single observer (J.L.).

Skull measurement error
We estimated the technical error of measurement (Harris and Smith, 2009) based on repeated measurements of 10 extracted skulls. The same observer re-measured each individual in five independent sessions. We quantified the technical error of measurement as the within-subject standard deviation based on these repeated measurements. This gives 95% confidence intervals for repeatability error in normally distributed data (Harris and Smith, 2009) (Table S1).

Behavior test
For the behavior tests, we trapped different individuals during the seasons of peak sizes as follows: large summer juveniles in August 2015 (N=8, undetermined); size-decreased winter subadults in January–February 2015 (N=2 males, 2 females, 4 undetermined); and regrown spring adults in April–May 2015 (N=1 female, 6 males). Shrews used in behavior tests were allowed to recover from capture and habituate to captivity in a double-cage system for 1 day. One cage (38×25×30 cm) contained natural soil, a running wheel, hay for bedding, an inverted terracotta flowerpot and water *ad libitum*. This cage was connected via a plastic tube to a second, equally sized cage that contained a food dish and a thin layer of sand as substrate to familiarize the shrews with the substrate of the experimental arena. The experimental room was illuminated with the natural light:dark regime; the temperature was 18°C. Although temperature might have an effect on the test performance, carrying out all tests at the same temperature allowed for standardized conditions for all animals. The food was a mixture of meat, earthworms and mealworms (Searle, 1984). Pregnant females were not included.

We deprived shrews of food for 2 h prior to testing. The tests started at 17:00 h for all individuals and then lasted varying amounts of time depending on each individual's performance. The experimental setup was a square arena (110×110 cm; Fig. 1). The
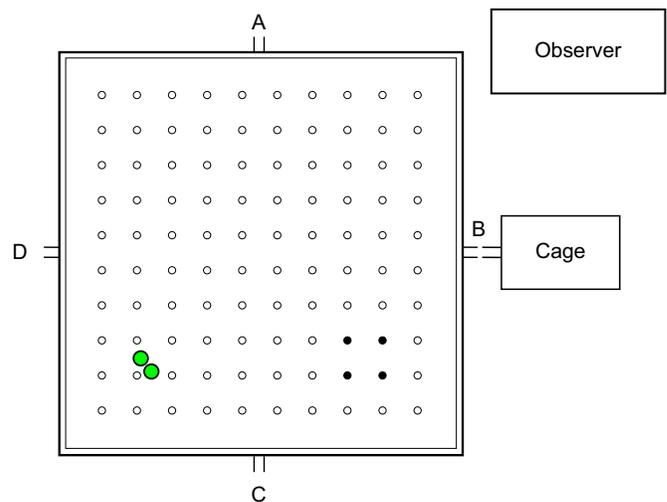

Fig. 1. Experimental setting for behavioral tests. Open circles represent empty wells, green circles the location of the light cue and black circles the wells with food items. The four entrances are located at the cardinal points (A, B, C and D). The cage was connected to a randomly chosen entrance during each trial. See Materials and methods for details.

floor of the arena was a flat surface covered with compressed sand into which 100 wells (diameter 18 mm, depth 15 mm) were pressed with a convex template. The arena was symmetrical except for the placement of the food and cues. Four adjacent wells, located at the southeast corner, each contained one immobile mealworm pupa. The arena sand was sprinkled with mealworm bedding material to ensure mealworm odor was distributed evenly. We used a pair of small, green glow sticks (35 mm long; Suxxes-Fisherman's Partner, Germany) near the southwest corner as reference cues. This spatial arrangement remained unaltered throughout all trials. The arena was covered by a transparent acrylic glass plate ceiling, creating a 2.4 cm high space between the sand surface and the transparent ceiling. It was surrounded by 65-cm-high uniformly painted oriented strand board walls on each side, as sight barriers. Thus, shrews could move around the arena freely, but remained in constant contact with the ceiling or walls as they avoid open spaces in natural habitat. The arena had four entrances, one at the center of each of the four sides (for reference, henceforth called A, B, C and D; Fig. 1). At the beginning of each trial we attached the habituation cage to an entrance, allowing the shrew to freely enter the arena through a connecting tube. The remaining entrances were blocked. We generated a random sequence of entrances for the 10 trials and then always used this sequence. The sequence was: D, B, A, B, D, C, B, A, C, A. The trial ended when the shrew found the first food item. Each individual was subjected to 10 consecutive trials at 20 min intervals. If the shrew had not found the food within 3 h after a trial had started, we would have cancelled the trial to avoid risk of starvation, but that limit was never reached. Before and between trials we rinsed all parts of the arena with an alcohol-based window cleaner and mixed the sand to break up olfactory trails. We used fresh cues and food items in each trial. We replaced the sand between individuals.

The trials were carried out in a room illuminated by a faint red LED light bulb and the arena was directly illuminated with an infrared light. We recorded the complete trials with a consumer video camera sensitive to near-infrared light (Somikon PX8262675, Buggingen, Germany) and one observer was always present, sitting in the same position (Fig. 1). The movement paths were extracted blind to the trial and shrew using the tracking software Tracker V 4.87 (http://www.cabrillo.edu/~dbrown/tracker/) by a single observer (M.S.). Path lengths were calculated with the 'move' package (http://computational-ecology.com/main-move.html) in R version 3.2.3 (R Foundation for Statistical Computing, Vienna, Austria). We also measured the search time as the time from the shrew's entrance to the arena until it finds the first food item.

Statistical analyses

All analyses were performed in R (R Core Team, 2015). To quantify the seasonal patterns in skull dimensions and brain mass we used the seasonal non-linear predictions of the change for our variables of interest (i.e. BCH_{cor}, BCW_{cor}, SKL_{cor} and brain $mass_{cor}$) to formulate our *a priori* expectations. We used generalized additive models (GAM) (Wood, 2006) with sex as a parametric term and an age-corrected Julian capture day of the year (jday) as a non-parametric term to quantify potential nonlinear patterns. To calculate jday for the juveniles, we shifted 1 June of year 1 (the year when the shrew is born) to jday=1 until 31 May of the following year (jday=365). For adults, jday is 365+jday of year 2 (adults are trapped in their year 2). For example, a juvenile captured on 12 October has a jday of 134, whereas an adult captured on 19 July has a jday of 413. We used a Gaussian distribution and added a smoothing function to jday that included five knots in a thin plate regression spline. We

restricted the number of knots to identify the *a priori* pattern while reducing the risk of model overfitting. We ran this initial GAM on both skull measurements and brain mass data for individuals with known sex to verify there was no sexual dimorphism in the patterns. Then, we ran the models again with combined sexes. GAMs were performed using the R package mgcv (Wood, 2015).

To assess seasonal differences in food searching behavior during the tests, we calculated search path length as path efficiency ratio, i.e. path length divided by the straight-line distance between the entrance and the central point between the four food wells in each trial (Table S2). We used linear mixed-effects models to analyze the search path length (log transformed to obtain a Gaussian distribution) and compared these models using ANOVA. In the first model (M1), we treated trial and season as factors and included individual as a random effect. We removed season from the second model (M2) to assess its influence and compared both models using ANOVA. We then ran a third model (M3) with a trial and season interaction term. We analyzed the variation in log-transformed search time using the same method as with search path length. We used the three models and ANOVA comparisons as described above, replacing the response variable with search time, i.e. M4, M5 and M6. Linear mixed-effects models were performed with the R package lme4 (Bates et al., 2014).

RESULTS AND DISCUSSION
Seasonal variation in skull size and brain mass

Our results confirm decreases in skull size and brain mass from summer juveniles to winter subadults and regrowth in spring adults. We found this pattern in the four analyzed metrics (BCH_{cor}, BCW_{cor}, SKL_{cor} and brain $mass_{cor}$), although the pattern in BCW_{cor} and SKL_{cor} was less pronounced than in BCH_{cor} (Figs S1 and S2). The focal region of change is therefore the post-rostral cranium, of which the braincase forms the largest portion. Thus our discussion will focus on brain $mass_{cor}$ and BCH_{cor}, which show the strongest change among skull size parameters (Fig. 2A).

In accordance with previous studies (Bielak and Pucek, 1960; Pucek, 1970) we found no significant difference in BCH_{cor} or brain $mass_{cor}$ between sexes (BCH_{cor}: GAM, $n=85$, male estimate=0.838929, female estimate=0.836018, $P>0.1$; brain $mass_{cor}$: GAM, $n=71$, male estimate=0.0332797, female estimate=0.0329003, $P>0.1$). The sexes also did not differ when we included an interaction between sex and jday [BCH_{cor}: GAM, $n=85$, e.d.f. (females)=2.354, e.d.f. (males)=3.865, P(smooth term)<0.001, deviance explained=67.4%; brain mass: GAM, $n=71$, e.d.f. (females)=2.120, e.d.f. (males)=3.384, P(smooth term)<0.01, deviance explained=44.5%].

The final model for BCH_{cor} (Fig. 2B) indicated a significant non-linear pattern matching our seasonal predictions [GAM, $n=98$, e.d.f. (smooth term)=3.847, $P<0.001$, deviance explained=68.4%]. The average decrease in BCH_{cor} from July juveniles to February subadults was −11.9% and the regrowth to adults (June–August) was +12.9%. A previous study used BCH as a proxy metric for overall braincase capacity and brain mass (Bielak and Pucek, 1960). Our results corroborate this correlation between BCH_{cor} and brain $mass_{cor}$ (Pearson's product-moment correlation, $t=8.0959$, $P<0.001$, $r=0.70$; Fig. 2D). Brain $mass_{cor}$ also exhibited significant non-linearity across seasons [GAM, $n=72$, e.d.f. (smooth term)=3.862, $P<0.001$, deviance explained=44.4%; Fig. 2C], with a mean decrease of −21.4% from July to February and a regrowth of 17.0% to summer (June–August). We thus confirm that our study population exhibits large reversible changes in brain mass. Both BCH_{cor} and brain $mass_{cor}$ showed a second decline in adults during their second autumn, but sample sizes were too low for analyses.
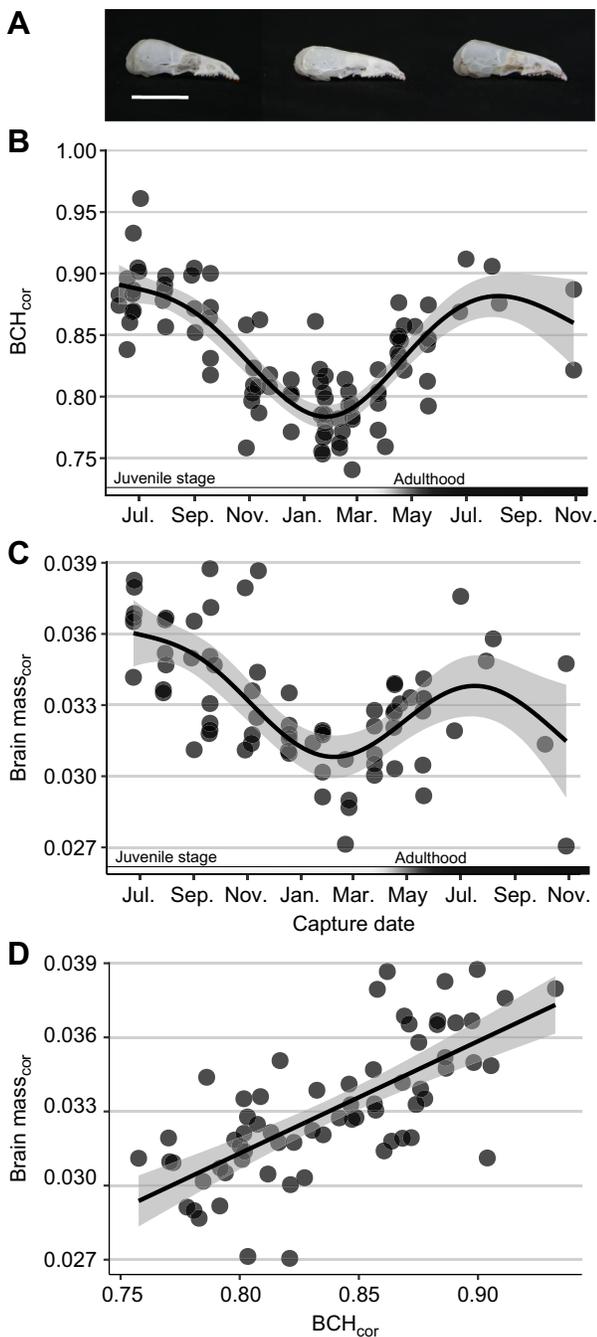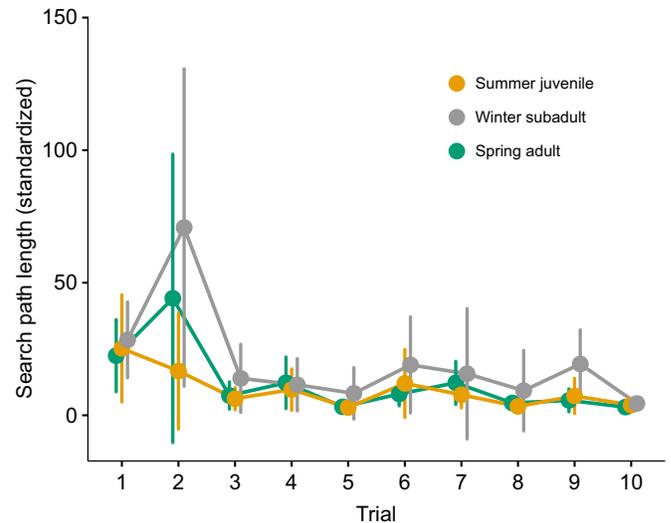
Fig. 3. Learning performance of individuals across three seasons. Small winter subadults (N=8 individuals) used longer search paths than large summer juveniles (N=8) and regrown spring adults (N=7) to find food. Circles and bars represent mean±s.d. search path length. Units of search path length are expressed as path efficiency ratio (see Materials and methods for details).

Fig. 2. Seasonal pattern in relative braincase height (BCH$_{corr}$) and brain mass from post-mortem specimens. (A) Three representative skulls from the main stages of the cycle (from left to right): July juvenile, size-decreased February subadult and regrown May adult. Scale bar, 10 mm. (B) BCH$_{cor}$ over time with fitted GAM. Solid line and shaded area represent fitted values and standard error of the model, respectively. The shaded x-axis indicates the two main life stages. (C) Brain mass over time with fitted model as depicted in B. (D) Correlation between corrected brain mass and BCH$_{cor}$ with fitted regression line and 95% confidence intervals (P<0.001, adj. r^2=0.48).

Differences in behavioral performance

The behavior experiment revealed that most individuals attained and maintained short search paths within the first four trials, but this varied between seasons (Fig. 3). The comparison between the first model [M1, N(individuals)=23, n(observations)=225, s.d.(individual)=0.277, F(trial)=9.831, F(season)=4.856, second-

order Akaike's information criterion (AICc)=659.04] and the second model [M2, s.d.(individual)=0.368, F(trial)=9.839, AICc=660.27] revealed a significant effect of season at the factor level (ANOVA, P<0.05). The comparison of M2 with the third model [M3, s.d.(individual)=0.275, F(trial)=9.873, F(season)=4.897, F(interaction)=1.056, AICc=675.88] revealed no significant effect of season at the interaction level (ANOVA, P=0.07). Large summer juveniles and regrown spring adults showed similar learning curves, while small winter animals exhibited longer search paths. This result matches seasonal variation in brain mass (Fig. 2C).

There was a learning curve for search time for the three seasons, but the high variation between and within trials made between-season differences less clear (Fig. S3). Comparison between the first model for search time [M4, N=23 individuals, n=225 observations, s.d.(individual)=0.076, F(trial)=8.362, F(season)=3.409, AICc=344,97] and the second model for search time [M5, s.d.(individual)=0.109, F(trial)=8.364, AICc=340.30] revealed a significant difference between models (ANOVA, P<0.05), but AICc values indicate M5 (without season) as the preferred model. The comparison of M5 with the third model for search time [M6, s.d.(individual)=0.080, F(trial)=8.488, F(season)=3.414, F(interaction)=1.164, AICc=386.36] revealed no significant effect of the interaction (ANOVA, P=0.08).

We postulate that the learning impairment in winter is a direct consequence of the decrease in brain size and changes in internal structure. In particular, it might be linked to the shrinkage observed in the neocortex and hippocampus (Yaskin, 1994), which process cue integration and spatial cognition (Martin et al., 2017; Sherry et al., 1992). A decrease of the hippocampus may affect spatial cognition and the ability to recognize objects, which has been shown to be crucial in a cue-based test (Martin et al., 2017). As our trials were with different animals during each season, this can clearly be distinguished from a memory loss. In contrast, the least shrew, whose brain mass does not change, does not show a seasonal pattern in spatial learning abilities, but rather a steady decline associated with senescence (Punzo and Chavez, 2003). However,

the neurological mechanisms underlying the observed cognitive differences remain unclear (Bartkowska et al., 2008).

Reducing energetically expensive tissue such as the brain (Niven and Laughlin, 2008) might provide a survival advantage during the period of resource scarcity (Kotrschal et al., 2013; Pucek, 1970). In wintering shrews, this need for energy saving may outweigh potential cognitive advantages of a large brain. This trade-off translates into an acceptable cognitive impairment in the small-brained wintering shrews. This might cause an adaptive constraint for demanding spatial tasks such as foraging (but see below). In summer and spring this balance switches, leading to larger body and brain size as food resources increase and shrews are faced with more diverse spatial tasks. During the first summer, juveniles disperse and establish their own territories for wintering. This requires exploration and intraspecific competition, and even displacement of adults (Churchfield, 1990). In spring, after reaching sexual maturity, shrews dramatically enlarge their home ranges again, meeting increased competitive and spatial demands. The expansion of home ranges is especially strong in males, which increase mobility as they search for mates (Stockley and Searle, 1998). This sexual difference in adult spatial behavior would predict higher spatial capacity in adult males than in females (Yaskin, 2005, 2011), as has been observed in polygamous rodents (Galea et al., 1996; Gaulin and Fitzgerald, 1989), but the exclusion of pregnant females from our tests impeded this comparison. Moreover, general activity of all organisms is higher in spring and summer, which leads to a more dynamic environment. Productivity, such as the growth and replacement of plants, as well as products of other animals' activities, such as galleries from burrowers, produce a more dynamic micro-topography. These dynamic habitat structures probably require higher explorative effort and spatial memory than the more steady winter landscape, similar to flying vertebrates in dense versus open habitats (Safi et al., 2005).

Alternatively, we must also consider non-cognitive explanations, especially in these freshly trapped wild animals that were confronted with a new artificial environment during the experiments. The decrease in path length variation along trials could be caused, in part, by an effect of habituation to the experimental setting and a gradual decrease in stress. Also, right after shrews enter the arena for the first time, explorative movements could partially explain the longer paths in the first trials. However, it is important to note that several individuals from the three groups increased their path length from trial 1 to 2 (Fig. S4). This cannot be explained by explorative behavior. In winter, when productivity is lower, prey replenishment would slow down in their natural habitat. This would lead us to predict a more pronounced increase in trial 2 in the winter shrews in our test. However, we found no significant differences in search path between seasons in trial 2 (Kruskal–Wallis, $P>0.05$). In fact, there is no evidence for decline in the populations of active prey in winter according to the literature. Soil cores reveal no reduction of prey abundance in winter (Churchfield et al., 2012), but a possible reduction in prey quality. Earthworms, shrews' main prey in summer (Churchfield et al., 2012; Pernetta, 1976), migrate into deeper soil layers and remain mostly inactive during winter (Nordström, 1975; Rundgren, 1975; but see Churchfield et al., 2012). Thus, shrews switch to other less nutritive but still active prey (e.g. beetles, snails, spiders and opilionids), some of which have autumn and winter activity peaks (Gongal'skii et al., 2003; Hågvar and Hågvar, 2011; Jaskuła and Soszyńska-Maj, 2011; Merriam et al., 1983; Pernetta, 1976).

The seasonal variations we describe illustrate a rarely investigated but highly interesting coping strategy for resource seasonality. This involves processes at the morphological, neuronal and behavioral levels. The common shrew offers a unique opportunity to understand the bidirectional selective forces that shape the size and structure of the mammalian brain, not only in the same population, but within individuals. Apart from its implications in evolutionary biology, such reversible changes in brain mass will be of interest for medical research on neurodegenerative diseases and cognitive disorders related to ageing.

Supplementary information
Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.166595.supplemental

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