



## Research

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**Author for correspondence:**

Pavel Němec

e-mail: [pgnemecc@natur.cuni.cz](mailto:pgnemecc@natur.cuni.cz)

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# Absolute, not relative brain size correlates with sociality in ground squirrels

Jan Matějů<sup>1</sup>, Lukáš Kratochvíl<sup>2</sup>, Zuzana Pavelková<sup>2</sup>, Věra Pavelková Řičánková<sup>3</sup>, Vladimír Vohralík<sup>2</sup> and Pavel Němec<sup>2</sup>

<sup>1</sup>Museum Karlovy Vary, Pod Jelením skokem 30, Karlovy Vary 360 01, Czech Republic

<sup>2</sup>Faculty of Science, Charles University in Prague, Viničná 7, Praha 2 128 44, Czech Republic

<sup>3</sup>Faculty of Science, University of South Bohemia, Branišovská 31, České Budějovice 370 05, Czech Republic

The social brain hypothesis (SBH) contends that cognitive demands associated with living in cohesive social groups favour the evolution of large brains. Although the correlation between relative brain size and sociality reported in various groups of birds and mammals provides broad empirical support for this hypothesis, it has never been tested in rodents, the largest mammalian order. Here, we test the predictions of the SBH in the ground squirrels from the tribe Marmotini. These rodents exhibit levels of sociality ranging from solitary and single-family female kin groups to egalitarian polygynous harems but feature similar ecologies and life-history traits. We found little support for the association between increase in sociality and increase in relative brain size. Thus, sociality does not drive the evolution of encephalization in this group of rodents, a finding inconsistent with the SBH. However, body mass and absolute brain size increase with sociality. These findings suggest that increased social complexity in the ground squirrels goes hand in hand with larger body mass and brain size, which are tightly coupled to each other.

## 1. Introduction

The social brain hypothesis (SBH) [1,2] postulates that the cognitive demands imposed on individuals by living in complex social groups constitute a driving force for the evolution of large brains. Individuals living in stable groups face information processing demands associated with dyadic and polyadic social interactions needed to negotiate conflicts over the communal use of resources. Because the SBH was developed to explain the extraordinary enlargement of brain size in primates, including humans, it is not surprising that the strongest empirical support for this hypothesis came from studies correlating relative (and absolute) primate brain size with various indexes of social complexity, including social group size, grooming clique size, number of females in a group, male mating strategies, deception rates and the frequency of coalitions (for a review, see [3]). A correlation between relative brain size and the size of a social group probably appears also in cetaceans [4]. In carnivores, ungulates, bats and birds, by contrast, relative brain size is associated with bonded social organization (i.e. based on stable pair bonds or female bonds) rather than large social groups [5–10]. Thus, primate sociality seems to be different from that of other vertebrates. It has been argued that bonded relationships have been generalized to all social partners in the anthropoid primates [3,9]. In line with this notion, it has recently been suggested that bonded sociality imposes a selective pressure favouring evolutionary encephalization (i.e. increase in relative brain size over evolutionary time) across mammals [11]. Interestingly, to our knowledge, the SBH has never been tested in rodents, the most speciose mammalian order.

Among rodents, the ground squirrels (tribe Marmotini) provide an ideal model for testing the SBH in an explicit phylogenetic framework. They feature very similar ecologies and share many life-history traits, e.g. they are all diurnal and semi-fossorial, feed on omnivorous diet, occupy mostly open habitats and

reproduce usually once a year [12,13]. On the other hand, the ground squirrels display levels of sociality which range from solitary and single-family female kin groups to large groups including both males and females [14,15]. The most complex social systems probably evolved through several steps, including the retention of daughters within the mother's range, relaxation of distinction between adjacent litters and superposition of male territories, maintained beyond the breeding season, over female ranges [15]. Solitary lifestyle is considered ancestral for ground squirrels [15,16] and sociality evolved repeatedly among them, e.g. twice just within marmots [17]. The repeated evolution of different levels of sociality allows statistical testing of the effect of sociality on brain size.

In asocial ground squirrels (hereafter referred to as social grade 1), juveniles disperse shortly after weaning and social interactions, even between kin, are mainly agonistic [15]. Asocial ground squirrels do not display complex social relationships or social bonding (e.g. [12,18]) and, although they can form aggregate associations under high population densities, the rates of social interactions are very low [18]. Species living in single-family female kin groups (grade 2) develop long-term social relationships among females, which cooperate in territorial defence and anti-predator vigilance [19]. Animals occupy individual burrows, but related females from neighbouring burrows closely interact and defend a common territory, which can be held over several generations [20]. In favourable habitat patches, female kin clusters form large colonies counting several dozen individuals [12]. Members of a colony interact and recognize each other by individually recognizable vocalization [21]. In more social species (grades 3–5), males are incorporated in family groups, i.e. long-term social relationships are not limited to females and bonded association of males and females also occurs [15,22,23]. Typically, a dominant male and several related females and their offspring form a cohesive group, the members of which are engaged in amicable contacts, the communal use and maintenance of burrows, and defence of a common territory from conspecifics from other groups [15]. The social complexity of the egalitarian polygynous harems (grade 5) may be further augmented by the presence of an additional adult male(s) and non-reproductive helpers, and by a complex dominance hierarchy within family groups [15,22]. In species where both sexes disperse and groups consist of related and unrelated individuals, social bonds develop early in the ontogeny and greatly influence dominance rank, dispersal decision and reproductive success in adults of both sexes (e.g. [24,25]). Some species are monogamous because males are not able to monopolize more than one female [26,27]. Taken together, along a continuum of sociality (social grades 1–5; for further details, see Material and Methods and electronic supplementary material), there are trends towards increasing social complexity and bonded social organization [28], and therefore increasing relative brain size would be expected according to the SBH.

In this study, we utilized ground squirrels as a model to test the predictions of the social brain hypothesis by examining the relationship between brain size and social system complexity. Most species of ground squirrels exhibit male-biased sexual dimorphism in body mass [29] and their sociality is primarily based on social bonds among females [14,15]. Because earlier reports have shown that social challenges may exert different selection pressures on males and females [30–33], we assessed

sexual dimorphism in brain size and tested its potential association with sociality and performed all analyses for males and females separately. We assumed that female brain size would be more tightly associated with social system complexity than male brain size.

## 2. Material and methods

The ground squirrels (tribe Marmotini Pocock, 1923; *sensu* [34]) form a monophyletic group within the family Sciuridae. They are widely distributed in the Northern Hemisphere, inhabiting grass-dominated biomes such as montane grasslands, temperate grasslands (steppes, prairies), semi-deserts and tundras.

Endocranial volume was taken as a proxy for assessing brain volume. In total, the endocranial volume was measured in 1526 museum specimens of 63 species (the mode 15 specimens per sex-species category) from the tribe Marmotini. The museums visited to collect this material are specified in the electronic supplementary material (table S1); museum identification numbers of the examined skulls are available on request. Only adult (dental wear pattern was used for skull ageing), undamaged and located specimens were examined. According to a standardized procedure described earlier [35], the endocranial cavity of the skull was filled via the foramen magnum with lead shot (diameter < 1 mm). Once the skull was filled, the lead shot was decanted and weighed, and the weight subsequently transformed to volume using a calibration line. All measurements were taken by a single person (J.M.).

Mean body mass and the hind foot length were taken as proxies for body size. Body mass is a composite measure of body size integrating many aspects, and as such it is the most often used measure in comparative studies of brain size [36]. However, at the same time, body mass varies in many ground squirrels seasonally and it reflects the current individual body condition. Therefore, we primarily used species mean body mass taken from the literature (for references, see electronic supplementary material, table S1). In 10 species, for which mean body mass are not available we averaged the individual body masses obtained from museum tags; data on body mass were missing for six species (electronic supplementary material, table S1). On the other hand, the hind foot in rodents stops growth relatively early in ontogeny [37,38] and, as a measure of structural growth, it is much less environment dependent. Hind foot length may be affected by selective pressures on different locomotion styles, although we expect this effect to be relatively less important in ground squirrels, a group sharing the same primary way of locomotion and a predominantly terrestrial way of life. The data on hind foot length were obtained from museum tags for all studied species (electronic supplementary material, table S1).

The data on social organization were collated from the literature (for references, see electronic supplementary material, table S1). The species were classified into five categories representing different grades of sociality as defined in [15]: 1 – asocial, 2 – single-family female kin clusters, 3 – female kin clusters with a territorial male, 4 – polygynous harems with male dominance, 5 – egalitarian polygynous harems. Descriptions of these grades are provided in the electronic supplementary material. Importantly, it was shown that these social grades are highly correlated with the social complexity index [28], a continuous metric which increases with the number of age–sex ‘roles’ interacting in a social group. The social grades are thus an appropriate measure to describe social complexity, as required for testing the SBH. It has to be stressed, however, that although the species are classified into discrete grades, the sociality scale forms a continuum from the least social (grade 1) to the most social (grade 5) organization [15]. As an alternative way of classifying social systems, we also coded sociality as a variable with two levels.

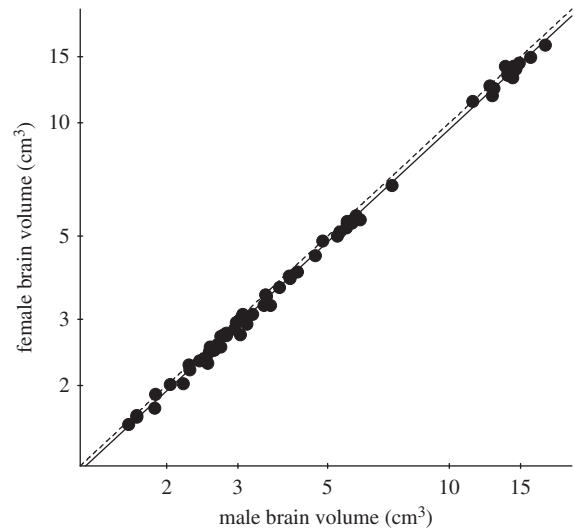
In this approach, we coded sociality grades 1 and 2 as 0, and grades 3, 4 and 5 as 1. This division is based on the expectation that different social organization should be associated with different potential for brain size increase due to the stability of social relationships among individuals [3,8–10]. The social grades 1–2 and 3–5 differ in the presence of stable, bonded associations of males and females. In total, data on body size, brain volume and sociality were available for 44 species (electronic supplementary material, table S1).

Most species exhibit male-biased sexual dimorphism in body mass [29]. The SBH predicts different selection pressures on males and females in species where sociality differs between the sexes [30–33]. Therefore, we tested for an association of sexual dimorphism in brain volume with sociality across species and subsequently performed all analyses for males and females separately. We used means of body mass, hind foot length and brain volume for each species–sex category as an expression of these variables. Brain volume, hind foot length and body mass were log-transformed before the subsequent statistical analyses.

Because species data are not independent, we performed phylogenetically informed analyses using phylogenetic generalized least-squares (PGLS) models [39,40]. We used a time-calibrated phylogeny published recently in [41] that was pruned to include only the species in our brain volume dataset (electronic supplementary material, figure S1). Four species (*Ammospermophilus nelsoni*, *Ictidomys parvidens*, *Urocitellus caninus* and *Urocitellus mollis*) from our dataset were missing in the phylogeny and were excluded from the analyses.

We used the PGLS models to test for association of sexual dimorphism in brain size with sociality and association of brain volume with body size and/or sociality. In PGLS, the  $\lambda$  parameter is found by maximum likelihood [42,43]. This parameter potentially varies between 0, indicating no effect of phylogenetic signal, and 1, corresponding to a strong dependence on underlying phylogenetic relationships among species. In the PGLS models testing the effect of sociality, we coded this variable as either a series of dummy variables representing the aforementioned five grades of sociality or as a 0–1 dummy variable. In models with sociality coded as five grades, in addition to testing the main effect of sociality, we also made four planned contrasts by changing which factor level was the reference level in the model. The planned contrasts were (i) social grades 1 (asociality) versus 2 (single-family female kin clusters) contrasting asociality with exclusively female sociality, (ii) grades 1 versus 3 (female kin clusters with a territorial male) contrasting asociality with a female sociality in combination with bonded relationships among females and a single male, (iii) grades 1 versus 5 (egalitarian polygynous harems) contrasting the least and the most social grades, and (iv) grades 2 versus 5 contrasting species with exclusively female sociality with the most complex bonded social relationships among males and females.

We tested the association of brain volumes between the sexes and scaling of sexual dimorphism in brain volume among ground squirrels with a PGLS model with mean female brain volume as the continuous dependent variable and mean male brain volume as the continuous predictor. Subsequently, we tested the association between sexual dimorphism in brain volume and sociality by testing whether the addition of sociality as a predictor into the PGLS bivariate regression model would significantly improve the model fit in the subset of species with known sociality. Further, we tested the relationship between mean brain volume (dependent variable) and body mass or hind limb length (continuous predictor). This model in a subset of species with known sociality served as the null model for testing the association of relative brain volume with sociality by testing the significance of the addition of sociality. Finally, we tested for an association of absolute measures of brain volume and body size with sociality using analogous PGLS models with just sociality



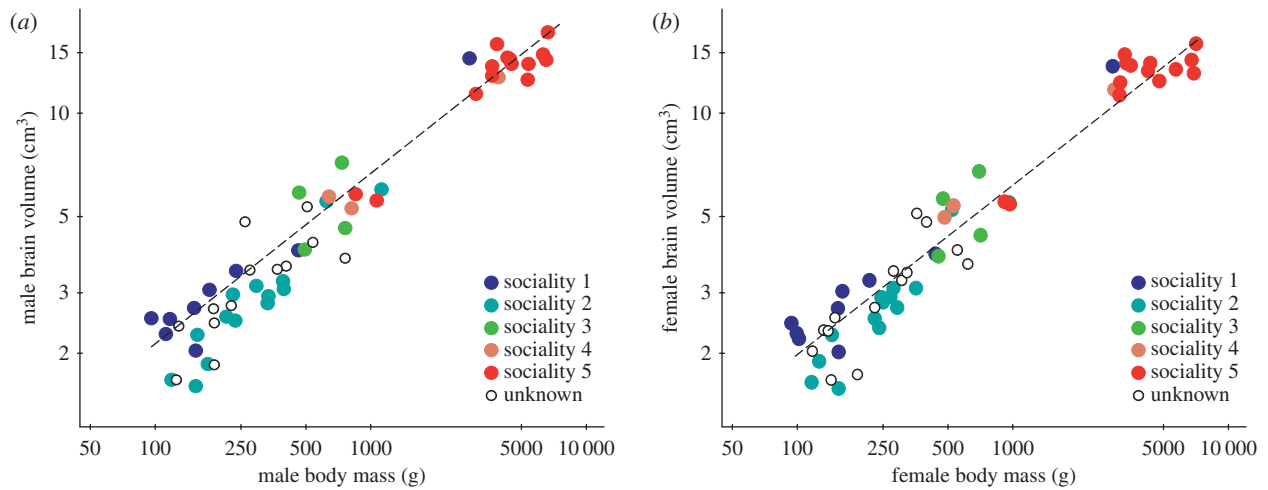
**Figure 1.** Regression of mean female brain volume on mean male brain volume across ground squirrels. Note the extremely tight correlation between these two variables. Although brain volumes in females are generally smaller than in males, brain volumes in both sexes increase nearly perfectly isometrically. The solid line represents the phylogenetic least-squares regression; the dashed line indicates the 1:1 relationship.

as a predictor, and brain volume and body size variables as response variables, respectively. Interactions between the continuous predictor and sociality levels were not significant in any case. We compared the fit of the models using Akaike information criterion (AIC) values and ANOVA. When  $\Delta\text{AIC} < 2$ , the models were considered equivalent, while the more complex model was considered supported when  $\Delta\text{AIC} > 2$  [44,45]. Models with  $\Delta\text{AIC} > 10$  were considered substantially better than the null model [44,45]. We also compared the null models and the models after addition of a predictor using the sequential sum of squares with the `anova.pgl`s function in Caper. All these analyses were performed in the Caper package for R [46].

We used an  $\alpha$  level of significance of 0.05. Standard techniques, i.e. inspection of distributions of residuals and the plot of fitted versus predicted values, were used to evaluate the fit of statistical models. We did not observe any deviation in these diagnostic criteria that would not be compatible with the usage of the reported models.

### 3. Results

Species means of female and male brain volume are highly correlated across the species of ground squirrels (figure 1). Mean female brain volume strongly increased with mean male brain volume across species (whole model  $F_{1,57} = 33\,470.00$ ,  $R^2 = 0.998$ ,  $\lambda < 0.01$ ;  $\Delta\text{AIC} = 280.19$  in comparison against the model without continuous predictor, i.e. mean brain volume). The slope of the phylogenetic regression of female brain volume on mean male brain volume was very close to 1.0 (mean  $\pm$  s.e.m.:  $0.996 \pm 0.005$ ), while the intercept was significantly lower than zero ( $-0.030 \pm 0.009$ ;  $p = 0.002$ ), indicating that female brain volume increases nearly perfectly proportionally with male brain volume across species, but that females have on average smaller absolute brain volumes than males. Differences in sexual dimorphism in brain volume across species with known sociality are not associated with diversity in social systems, as the addition of the sociality factor does not improve the PGLS model fit (sociality coded as



**Figure 2.** Brain–body scaling in ground squirrels. (a,b) Plot of species mean brain volume versus species mean body mass for males (a) and females (b) from the tribe Marmotini; social grades 1–5 are colour-coded. The fitted lines represent the phylogenetic least-squares regressions showing the general relationship across all species with available data.

0–1:  $F_1 = 0.49$ ,  $p = 0.48$ ,  $\Delta\text{AIC} = 1.66$ ; sociality coded as five grades: ANOVA:  $F_4 = 1.75$ ,  $p = 0.16$ ,  $\Delta\text{AIC} = 0.87$ ).

Because of an extremely tight correlation between female and male brain volumes (figure 1) and the lack of association of sexual size dimorphism in brain volume with social systems across species, for brevity, we describe here the results obtained for males only. However, the results for females are shown in graphs and described in the electronic supplementary material.

Brain volume strongly increases with body mass across species of ground squirrels ( $F_{1,51} = 260.30$ ,  $p < 0.0001$ ,  $R^2 = 0.83$ ,  $\lambda = 0.60$ ;  $\Delta\text{AIC} = 93.86$  against the null model) showing the close association between absolute brain size and body size (figure 2). Sociality added into the PGLS model in species with known sociality did not significantly improve the model fit when sociality was coded as a 0–1 variable (ANOVA:  $F_1 = 3.17$ ,  $p = 0.08$ ;  $\Delta\text{AIC} = 1.28$ ; the addition of sociality explained less than 0.5% additional variation), but in the analysis with sociality coded as five grades, the addition of sociality was significant and explained 7.8% additional variation (ANOVA:  $F_4 = 3.61$ ,  $p = 0.014$ ;  $\Delta\text{AIC} = 5.46$ ). However, specific contrasts did not support the SBH, as the asocial grade 1 differs significantly neither from grade 3, characterized by female kin clusters with a territorial male, nor from the most social grade 5 (egalitarian polygynous harems), which in turn did not differ from the social grade 2, characterized by single-family female kin clusters ( $t$ -tests:  $p > 0.12$  in all three cases). In sharp contrast with the prediction of the SBH, the asocial species had significantly larger brain volumes relative to body mass than ground squirrels forming single-family female kin clusters, i.e. species belonging to the social grade 2 ( $t = 4.13$ ,  $p = 0.0002$ ). Moreover, neither sociality coded as a 0–1 variable nor as five grades was significant in the PGLS models with hind foot length as the measure of body size (see the electronic supplementary material). We can thus conclude that there is little evidence for a robust correlation between sociality and relative brain size in ground squirrels, and if any, it is counter to the prediction of the SBH.

In PGLS models, absolute brain volume was significantly associated with sociality across species and more social species tend to have absolutely larger brains. The model including sociality coded as a 0–1 variable was significantly better than

the null model (ANOVA:  $F_1 = 11.30$ ,  $p = 0.002$ ; whole model  $R^2 = 0.24$ ,  $\lambda = 0.95$ ;  $\Delta\text{AIC} = 7.15$  against the null model). The model with sociality coded as five grades (whole model  $R^2 = 0.33$ ,  $\lambda = 1.00$ ) also significantly outperformed the null model (ANOVA:  $F_4 = 4.67$ ,  $p = 0.004$ ;  $\Delta\text{AIC} = 9.18$ ). From the planned contrasts, the difference between sociality grades 1 (asociality) and 3 (female kin clusters with a territorial male) was significant ( $t = 2.78$ ,  $p = 0.008$ ) and the difference between sociality grades 1 and 5 (egalitarian polygynous harems) nearly significant with  $t = 1.90$ ,  $p = 0.06$ , all other specific contrasts were not significant. Body mass and hind foot length showed similarly significant tendencies for larger values in more social species (see the electronic supplementary material). All these results demonstrate a positive association between increasing sociality and absolute brain and body size.

## 4. Discussion

The analyses performed in this study do not indicate a positive association between encephalization (relative brain size deviation from brain–body allometry) and sociality in ground squirrels. Species living in single-family female kin groups that share territory with males only during the mating season (grade 2) tend to have the lowest encephalization; all other species, including solitary ones and those living in complex social systems, have similar relative brain sizes (figure 2). Thus, the complexity of the social system does not drive the evolution of relatively large brains in this group of rodents, a finding consistent with an earlier study based on the restricted dataset [47] but clearly inconsistent with the SBH. However, the degree of sociality is positively correlated with body mass and absolute brain size. These findings raise the intriguing possibility that, among ground squirrels, a certain minimal absolute brain size (c.f., figure 2), rather than high encephalization, is needed to cope with the cognitive demands of living in complex, stable social groups.

When data for females were analysed, one possible link between relative brain size and sociality emerged (see the electronic supplementary material) that was not present in the data for males. Females in species without male–female bonded relationships have significantly lower

encephalization than species exhibiting bonded association of males and females, i.e. the significant positive association between sociality and relative brain volume was found when sociality was coded as a 0–1 variable and body mass was used as a proxy for body size. Because the social system of ground squirrels is matrilineal and primarily based on female bonds [14,15], it is tempting to conclude that, just like in primates and carnivores [30–33], social challenges exert stronger selection pressures on females than on males. However, the addition of sociality into the model explained only a negligibly larger proportion of additional variation (less than 1%) and thus might not be biologically relevant. It is also not robust, as significance was lost when an alternative proxy for body size was used. Moreover, this result is not supported by data on the sexual dimorphism in brain volume, which changes neither with body size (figure 1) nor with social system complexity.

As noted above (see Introduction), in all taxa examined, except for anthropoid primates and perhaps cetaceans, high encephalization seems to be associated with bonded sociality. Decoupling between these two variables appears to be rather rare and has been reported in lemurs [48] and ground squirrels (the present study), and at least in some carnivores [49,50] and ungulates [49]. The absence of a clear link between relative brain size and social system complexity is highly unexpected in ground squirrels, because they display a remarkable interspecific variation in the occurrence and strength of social bonds (see Introduction). One extreme is represented by strictly solitary species that only pair for short periods of time during the breeding season and do not exhibit stable female bonds. At the other extreme there are truly social species that show stable bonds among females as well as between males and females. Assuming that social bonds are cognitively demanding, this raises the question as to why the stark differences in social group coherence are correlated with absolute but not relative brain size in the ground squirrels.

One can argue that encephalization might not be an accurate measure of cognitive capacity. The notion that higher encephalization correlates with improved cognitive abilities [51] has recently been disputed in favour of the absolute number of cortical neurons and connections [52,53] or simply the total number of brain neurons [54]. Indeed, a growing body of evidence suggests that absolute brain size is tightly coupled with its intrinsic complexity, which, in turn, provides the substrate for cognitive abilities [55]. The proportional and absolute sizes of the neocortex, the number of cortical areas and total number of cortical neurons increase with absolute brain size (for reviews, see [55,56]). This is in line with recent findings that absolute brain size is the best predictor of species differences in cognitive capacity [57–59]. Cellular scaling rules strongly suggest that this applies also to rodents, despite a lower neuronal density in larger rodent brains [60–62]. Explicitly speaking, of two rodents with similar encephalization, the one with the larger brain would be expected to have superior cognitive abilities [62]. On the other hand, an extensive body of evidence suggests that high encephalization endows species with improved cognitive abilities and behavioural flexibility [63–65]. This is due to the fact that more encephalized species have larger brains and, therefore, higher total numbers of neurons than expected for their body size [62]. These arguments lend credibility to the inference that information processing demands associated with sociality do not require

increased encephalization, provided that the degree of sociality covaries with body mass and absolute brain size. Thus, a key question to be answered is: why do the ground squirrels respond to social challenges by a concerted increase of body mass and brain size rather than by increased encephalization?

We suggest that two synergic reasons may account for this highly unexpected phenomenon. First, as in strepsirrhine primates [66] and marsupials [67], seasonal shortages in energy supplies may constitute a constraint on relative brain size in ground squirrels. They inhabit environments that are characterized by pronounced seasonal changes in rainfall and temperature. The vast majority of species (approx. 85%) hibernate or aestivate to overcome the inevitable periods of food and/or water scarcity [12,13]. Because the brain is metabolically expensive and requires a sustained supply of energy (for a recent review of the expensive brain hypothesis, see [68]), it seems likely that hibernation, the most extreme adaptation for coping with environmental seasonality, prevents the evolution of relatively large brains. Unfortunately, because there were only two evolutionary transitions between year-long activity and hibernation among the species included into our analysis (data not shown), a broader phylogenetic scope is needed in future studies to test the effect of hibernation on relative brain size in rodents.

Second, fossil evidence and phylogenetic reconstruction of ancestral states strongly suggest that the enlargement of body size in ground squirrels from the tribe Marmotini constitutes an adaptive response to the global cooling that started in the early Miocene, i.e. some 15 million years ago, and resulted in increased aridity, seasonality and expansion of low productivity grassland ecosystems [69,70]. Ecophysiological advantages of large body size include improved thermal efficiency, more effective extracting of usable energy from low-quality foods and enhanced capacity of fat storage. Large body size is associated with slower postnatal development and delayed dispersal. Thus, owing to a short growing season and increased need for social hibernation, the harsh environment selects for increased social tolerance and retention of subadult offspring in family groups [14,22].

Taken together, environmental seasonality probably constitutes a key factor promoting the evolution of sociality in the ground squirrels and, at the same time, prevents brain enlargement due to energetic constraint associated with hibernation. The present study suggests that the ground squirrels respond to these antagonistic pressures by a concerted increase in body mass and brain size. Owing to a tight correlation between brain volume and body size, it was impossible to disentangle the causal relationships between sociality, absolute brain size and body size. Therefore, it remains unclear whether (i) sociality has directly driven increases in absolute brain size or (ii) enlarged absolute brain size is a by-product of the enlargement of the body associated with the necessity to survive prolonged periods of low food availability. Importantly, both these evolutionary scenarios lead to an increased absolute brain size providing the substrate for cognitive capacities needed for living in stable social groups.

**Ethics.** No human or animal subjects were used in this study, only museum specimens.

**Data accessibility.** The entire dataset used in our analyses can be found in the electronic supplementary material.

**Authors' contributions.** J.M. and P.N. designed the research, J.M. collected the data, L.K. and Z.P. analysed the data and all authors wrote the paper.

**Competing interests.** We have no competing interests.

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## References

- Byrne R, Whiten A. 1988 *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans*. Oxford, UK: Oxford University Press.
- Dunbar RIM. 1998 The social brain hypothesis. *Evol. Anthropol.* **6**, 178–190. (doi:10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8)
- Dunbar RIM, Shultz S. 2007 Evolution in the social brain. *Science* **317**, 1344–1347. (doi:10.1126/science.1145463)
- Marino L. 1996 What can dolphins tell us about primate evolution? *Evol. Anthropol.* **5**, 81–86. (doi:10.1002/(SICI)1520-6505(1996)5:3<81::AID-EVAN3>3.0.CO;2-Z)
- Pérez-Barbería F, Gordon I. 2005 Gregariousness increases brain size in ungulates. *Oecologia* **145**, 41–52. (doi:10.1007/s00442-005-0067-7)
- Shultz S, Dunbar RIM. 2006 Both social and ecological factors predict ungulate brain size. *Proc. R. Soc. B* **273**, 207–215. (doi:10.1098/rspb.2005.3283)
- Pitnick S, Jones KE, Wilkinson GS. 2006 Mating system and brain size in bats. *Proc. R. Soc. B* **273**, 719–724. (doi:10.1098/rspb.2005.3367)
- Shultz S, Dunbar RIM. 2007 The evolution of the social brain: anthropoid primates contrast with other vertebrates. *Proc. R. Soc. B* **274**, 2429–2436. (doi:10.1098/rspb.2007.0693)
- Emery NJ, Seed AM, von Bayern AMP, Clayton NS. 2007 Cognitive adaptations of social bonding in birds. *Phil. Trans. R. Soc. B* **362**, 489–505. (doi:10.1098/rstb.2006.1991)
- Shultz S, Dunbar RIM. 2010 Social bonds in birds are associated with brain size and contingent on the correlated evolution of life-history and increased parental investment. *Biol. J. Linn. Soc.* **100**, 111–123. (doi:10.1111/j.1095-8312.2010.01427.x)
- Shultz S, Dunbar RIM. 2010 Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality. *Proc. Natl Acad. Sci. USA* **107**, 21 582–21 586. (doi:10.1073/pnas.1005246107)
- Thorington RWJr, Koprowski JL, Steele MA, Wharton JF. 2012 *Squirrels of the world*. Baltimore, MD: The Johns Hopkins University Press.
- Nowak RM. 1999 *Walker's mammals of the world*. Baltimore, MD: The Johns Hopkins University Press.
- Armitage KB. 1981 Sociality as a life-history tactic of ground squirrels. *Oecologia* **48**, 36–49. (doi:10.1007/BF00346986)
- Michener GR. 1983 Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In *Advances in the study of mammalian behavior* (eds F Eisenberg, DG Kleiman), pp. 528–572. Shippensburg, PA: American Society of Mammalogists.
- Smorkatcheva AV, Lukhtanov VA. 2014 Evolutionary association between subterranean lifestyle and female sociality in rodents. *Mamm. Biol. Z. Säugetierkunde* **79**, 101–109. (doi:10.1016/j.mambio.2013.08.011)
- Kruckenhauser L, Pinsker W, Haring E, Arnold W. 1999 Marmot phylogeny revisited: molecular evidence for a diphyletic origin of sociality. *J. Zool. Syst. Evol. Res.* **37**, 49–56. (doi:10.1046/j.1439-0469.1999.95100.x)
- Munroe KE, Koprowski JL. 2014 Levels of social behaviors and genetic structure in a population of round-tailed ground squirrels (*Xerospermophilus tereticaudus*). *Behav. Ecol. Sociobiol.* **68**, 629–638. (doi:10.1007/s00265-013-1677-4)
- Nunes S. 2014 Juvenile social play and yearling behavior and reproductive success in female Belding's ground squirrels. *J. Ethol.* **32**, 145–153. (doi:10.1007/s10164-014-0403-7)
- Nunes S, Weidenbach JN, Laffler MR, Dever JA. 2015 Sibling relatedness and social play in juvenile ground squirrels. *Behav. Ecol. Sociobiol.* **69**, 357–369. (doi:10.1007/s00265-014-1848-y)
- Pollard KA, Blumstein DT. 2011 Social group size predicts the evolution of individuality. *Curr. Biol.* **21**, 413–417. (doi:10.1016/j.cub.2011.01.051)
- Allainé D. 2000 Sociality mating system and reproductive skew in marmots: evidence and hypotheses. *Behav. Processes.* **51**, 21–34. (doi:10.1016/S0376-6357(00)00116-9)
- Blumstein DT. 2013 Yellow-bellied marmots: insights from an emergent view of sociality. *Phil. Trans. R. Soc. B* **368**, 20120349. (doi:10.1098/rstb.2012.0349)
- Blumstein DT, Wey TW, Tang K. 2009 A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proc. R. Soc. B* **276**, 3007–3012. (doi:10.1098/rspb.2009.0703)
- Blumstein DT, Chung LK, Smith JE. 2013 Early play may predict later dominance relationships in yellow-bellied marmots (*Marmota flaviventris*). *Proc. R. Soc. B* **280**, 20130485. (doi:10.1098/rspb.2013.0485)
- Blumstein DT, Arnold W. 1998 Ecology and social behavior of golden marmots (*Marmota caudata aurea*). *J. Mammal.* **79**, 873–886. (doi:10.2307/1383095)
- Waterman JM. 2007 Male mating strategies in rodents. In *Rodent societies: an ecological and evolutionary perspective*. (eds JO Wolf, PW Sherman), pp. 27–41. Chicago, IL: The University of Chicago Press.
- Blumstein DT, Armitage KB. 1997 Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *Am. Nat.* **150**, 179–200. (doi:10.1086/286062)
- Matějů J, Kratochvíl L. 2013 Sexual size dimorphism in ground squirrels (Rodentia: Sciuridae: Marmotini) does not correlate with body size and sociality. *Front. Zool.* **10**, 27. (doi:10.1186/1742-9994-10-27)
- Gittleman JL. 1994 Female brain size and parental care in carnivores. *Proc. Natl Acad. Sci. USA* **91**, 5495–5497. (doi:10.1073/pnas.91.12.5495)
- Lindenfors P. 2005 Neocortex evolution in primates: the 'social brain' is for females. *Biol. Lett.* **1**, 407–410. (doi:10.1098/rsbl.2005.0362)
- Lindenfors P, Nunn CL, Barton RA. 2007 Primate brain architecture and selection in relation to sex. *BMC Biol.* **5**, 20. (doi:10.1186/1741-7007-5-20)
- Arsznov BM, Sakai ST. 2013 The procyonid social club: comparison of brain volumes in the coatimundi (*Nasua nasua*, *N. narica*), kinkajou (*Potos flavus*), and raccoon (*Procyon lotor*). *Brain Behav. Evol.* **82**, 129–145. (doi:10.1159/000354639)
- McKenna MC, Bell SK. 1997 *Classification of mammals above the species level*. New York, NY: Columbia University Press.
- Iwaniuk AN. 2001 Interspecific variation in sexual dimorphism in brain size in Nearctic ground squirrels (*Spermophilus* spp.). *Can. J. Zool.* **79**, 759–765. (doi:10.1139/z01-037)
- Healy SD, Rowe C. 2007 A critique of comparative studies of brain size. *Proc. R. Soc. B* **274**, 453–464. (doi:10.1073/pnas.0401955101)
- Zimmerman EG. 1972 Growth and age determination in the thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*. *Am. Midl. Nat.* **87**, 314–325. (doi:10.2307/2423564)
- Turner BN, Iverson SL, Severson KL. 1976 Postnatal growth and development of captive Franklin's

- ground squirrels (*Spermophilus franklinii*). *Am. Midl. Nat.* **95**, 93–102. (doi:10.2307/2424236)
39. Pagel MD. 2002 Modelling the evolution of continuously varying characters on phylogenetic trees. In *Morphology, shape and phylogeny* (eds N MacLeod, PL Foley), pp. 269–286. London, UK: Taylor & Francis.
  40. Revell LJ. 2010 Phylogenetic signal and linear regression on species data. *Methods Ecol. Evol.* **1**, 319–329. (doi:10.1111/j.2041-210X.2010.00044.x)
  41. Zelditch ML, Li JC, Tran LAP, Swiderski DL. 2015 Relationships of diversity, disparity, and their evolutionary rates in squirrels (Sciuridae). *Evolution* **69**, 1284–1300. (doi:10.1111/evo.12642)
  42. Grafen A. 1989 The phylogenetic regression. *Phil. Trans. R. Soc. Lond. B* **326**, 119–157. (doi:10.1098/rstb.1989.0106)
  43. Pagel M. 1997 Inferring evolutionary processes from phylogenies. *Zool. Scr.* **26**, 331–348. (doi:10.1111/j.1463-6409.1997.tb00423.x)
  44. Burnham KP, Anderson DR, Huyvaert KP. 2011 AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* **65**, 23–35. (doi:10.1007/s00265-010-1029-6)
  45. Symonds MRE, Moussalli A. 2011 A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* **65**, 13–21. (doi:10.1007/s00265-010-1037-6)
  46. Orme D. 2012 *The Caper package: comparative analysis of phylogenetics and evolution in R*. <http://cran.r-project.org/web/packages/caper>.
  47. Meier PT. 1983 Relative brain size within the North American Sciuridae. *J. Mammal.* **64**, 642–647. (doi:10.2307/1380520)
  48. MacLean EL, Barrickman NL, Johnson EM, Wall CE. 2009 Sociality, ecology, and relative brain size in lemurs. *J. Hum. Evol.* **56**, 471–478. (doi:10.1016/j.jhevol.2008.12.005)
  49. Pérez-Barbería FJ, Shultz S, Dunbar RIM. 2007 Evidence for coevolution of sociality and relative brain size in three orders of mammals. *Evolution* **61**, 2811–2821. (doi:10.1111/j.1558-5646.2007.00229.x)
  50. Finarelli JA, Flynn JJ. 2009 Brain-size evolution and sociality in Carnivora. *Proc. Natl Acad. Sci. USA* **106**, 9345–9349. (doi:10.1073/pnas.0901780106)
  51. Jerison HJ. 1973 *The evolution of the brain and intelligence*. New York, NY: Academic Press.
  52. Roth G, Dicke U. 2005 Evolution of the brain and intelligence. *Trends Cogn. Sci.* **9**, 250–257. (doi:10.1016/j.tics.2005.03.005)
  53. Dicke U, Roth G. 2016 Neuronal factors determining high intelligence. *Phil. Trans. R. Soc. B* **371**, 20150180. (doi:10.1098/rstb.2015.0180)
  54. Herculano-Houzel S. 2011 Brains matter, bodies maybe not: the case for examining neuron numbers irrespective of body size. *Ann. NY Acad. Sci.* **1225**, 191–199. (doi:10.1111/j.1749-6632.2011.05976.x)
  55. Striedter GF. 2005 *Principles of brain evolution*. Sunderland, MA: Sinauer Associates, Inc.
  56. Finlay BL, Brodsky P. 2007 Cortical evolution as the expression of a program for disproportionate growth and the proliferation of areas. In *Evolution of nervous systems: a comprehensive reference—mammals* (eds JH Kaas, LA Krubitzer), pp. 74–93. Amsterdam, The Netherlands: Elsevier Academic Press.
  57. Deane RO, Isler K, Burkart J, van Schaik C. 2007 Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain Behav. Evol.* **70**, 115–124. (doi:10.1159/000102973)
  58. MacLean EL *et al.* 2014 The evolution of self-control. *Proc. Natl Acad. Sci. USA* **111**, E2140–E2148. (doi:10.1073/pnas.1323533111)
  59. Stevens JR. 2014 Evolutionary pressures on primate intertemporal choice. *Proc. R. Soc. B* **281**, 20140499. (doi:10.1098/rspb.2014.0499)
  60. Herculano-Houzel S, Mota B, Lent R. 2006 Cellular scaling rules for rodent brains. *Proc. Natl Acad. Sci. USA* **103**, 12 138–12 143. (doi:10.1073/pnas.0604911103)
  61. Herculano-Houzel S, Ribeiro P, Campos L, Valotta da Silva A, Torres LB, Catania KC, Kaas JH. 2011 Updated neuronal scaling rules for the brains of Glires (Rodents/Lagomorphs). *Brain Behav. Evol.* **78**, 302–314. (doi:10.1159/000330825)
  62. Herculano-Houzel S. 2007 Encephalization, neuronal excess, and neuronal index in rodents. *Anat. Rec.* **290**, 1280–1287. (doi:10.1002/ar.20598)
  63. Lefebvre L, Reader SM, Sol D. 2004 Brains, innovations and evolution in birds and primates. *Brain Behav. Evol.* **63**, 233–246. (doi:10.1159/000076784)
  64. Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. 2005 Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Natl Acad. Sci. USA* **102**, 5460–5465. (doi:10.1073/pnas.0408145102)
  65. Ratcliffe JM, Fenton MB, Shettleworth SJ. 2006 Behavioral flexibility positively correlated with relative brain volume in predatory bats. *Brain Behav. Evol.* **67**, 165–176. (doi:10.1159/000090980)
  66. van Woerden JT, van Schaik CP, Isler K. 2010 Effects of seasonality on brain size evolution: evidence from strepsirrhine primates. *Am. Nat.* **176**, 758–767. (doi:10.1086/657045)
  67. Weisbecker V, Blomberg S, Goldizen AW, Brown M, Fisher D. 2015 The evolution of relative brain size in marsupials is energetically constrained but not driven by behavioral complexity. *Brain Behav. Evol.* **85**, 125–135. (doi:10.1159/000377666)
  68. Isler K, van Schaik CP. 2009 The expensive brain: a framework for explaining evolutionary changes in brain size. *J. Hum. Evol.* **57**, 392–400. (doi:10.1016/j.jhevol.2009.04.009)
  69. Ge DY, Liu X, Lv XF, Zhang ZQ, Xia L, Yang QS. 2014 Historical biogeography and body form evolution of ground squirrels (Sciuridae: Xerinae). *Evol. Biol.* **41**, 99–114. (doi:10.1007/s11692-013-9250-7)
  70. Edwards EJ, Osborne CP, Strömberg CA, Smith SA. 2010 The origins of C4 grasslands: integrating evolutionary and ecosystem science. *Science* **328**, 587–591. (doi:10.1126/science.1177216)