Original Paper

Brain, Behavior and Evolution

Brain Behav Evol
DOI: 10.1159/000444741

Received: April 1, 2015
Returned for revision: May 4, 2015
Accepted after second revision: February 17, 2016
Published online: April 6, 2016

Effects of Habitat and Social Complexity on Brain Size, Brain Asymmetry and Dentate Gyrus Morphology in Two Octodontid Rodents

Raúl Sobrero[a, b] Pedro Fernández-Aburto[b] Álvaro Ly-Prieto[c]
Scarlett E. Delgado[b] Jorge Mpodozis[b] Luis A. Ebensperger[c]

[a]Instituto de Ciencias Veterinarias del Litoral (ICiVet-Litoral), Universidad Nacional del Litoral (UNL) – Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET), Esperanza, Argentina; [b]Departamento de Biología, Facultad de Ciencias, Universidad de Chile, and [c]Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

Key Words

Brain asymmetry · Dentate gyrus anatomy · Habitat complexity · *Octodon* · Sexual dimorphisms · Social brain · Sociality

Abstract

Navigational and social challenges due to habitat conditions and sociality are known to influence dentate gyrus (DG) morphology, yet the relative importance of these factors remains unclear. Thus, we studied three natural populations of *O. lunatus* (Los Molles) and *Octodon degus* (El Salitre and Rinconada), two caviomorph species that differ in the extent of sociality and with contrasting vegetation cover of habitat used. The brains and DG of male and female breeding degus with simultaneous information on their physical and social environments were examined. The extent of sociality was quantified from total group size and range area overlap. *O. degus* at El Salitre was more social than at Rinconada and than *O. lunatus* from Los Molles. The use of transects to quantify cover of vegetation (and other physical objects in the habitat) and measures of the spatial behavior of animals indicated animal navigation based on unique cues or global landmarks is more cognitively challenging to *O. lunatus*. During lactation, female *O. lunatus* had larger brains than males. Relative DG volume was similar across sexes and populations. The right hemisphere of male and female *O. lunatus* had more cells than the left hemisphere, with DG directional asymmetry not found in *O. degus*. Degu population differences in brain size and DG cell number seemed more responsive to differences in habitat than to differences in sociality. Yet, large-sized *O. degus* (but not *O. lunatus*) that ranged over larger areas and were members of larger social groups had more DG cells per hemisphere. Thus, within-population variation in DG cell number by hemisphere was consistent with a joint influence of habitat and sociality in *O. degus* at El Salitre.

Introduction

Environmental complexity is thought to be an important selective factor of cognitive abilities and associated neuroanatomical components [Kempermann et al., 1997; Nilsson et al., 1999; van Praag et al., 1999; Roth and Pravosudov, 2009]. Two major components of this complexity are especially relevant. First, individuals need to man-

KARGER

E-Mail karger@karger.com
www.karger.com/bbe

0006–8977/16/0000–0000$39.50/0

Raúl Sobrero
Laboratorio de Ecología de Enfermedades, ICiVet-Litoral, UNL – CONICET
R.P. Kreder 2805
Esperanza, Santa Fe S3080HOF (Argentina)
E-Mail raulesobrero@gmail.com

age and process spatial and temporal information on resource availability during spatial navigation and to construct physical or cognitive topological reference maps [O'Keefe and Nadel, 1978; Jacobs, 2006]. Second, individuals need to keep track of social conditions and be able to respond appropriately during interactions with conspecifics [Dunbar, 1998].

Available evidence indicates that the same brain regions may be linked to both environmental inputs. In particular, the dentate gyrus (DG), a main region of the hippocampus, is known to be essential for integrating environmental sensory cues into a geometric coordinate system, i.e. the building of cognitive maps of physical and social space [Jacobs, 2003; Eichenbaum, 2015; Tavares et al., 2015]. For instance, adult laboratory rats *(Rattus norvegicus)* housed in larger boxes containing various toys, wooden blocks, climbing platforms, plastic tubes and small houses show an increase in newly generated cells in the DG and enhancement of recognition memory [Bruel-Jungerman et al., 2005]. Evidence from field studies shows how nonbreeding female meadow voles *(Microtus pennsylvanicus)* exhibit a higher rate of DG cell proliferation and cell death than breeding females, a difference presumably linked to differences in the size of female range areas [Galea and McEwen, 1999]. Nonbreeding male Richardson's ground squirrels *(Urocitellus richardsonii)* exhibit significantly larger hippocampal volumes than breeding males or females from either season, a variation that was linked to the male-only food caching behavior during the nonbreeding season [Burger et al., 2013].

On the other hand, evidence also supports that the DG plays a role in integrating social cues. Animal subjects exposed to varying social group sizes [Fowler et al., 2002; Hoshaw et al., 2006; Gheusi et al., 2009], social isolation of adults from their mates [Fowler et al., 2002], social separation of offspring from their parents [Lu et al., 2003] and varying dominance relationships [Kozorovitskiy and Gould, 2004] exhibit changes in the structure and volume of the DG. In humans, changes in social relationships (linked to power and affiliation) predict adult hippocampal activity, implying this brain area is simultaneously involved in processing spatial and social information [Tavares et al., 2015]. Most importantly, social behavior may act as a potent stressor or can buffer the response to an external stressor [Silk, 2007; Beery and Kaufer, 2015], actions that in some wild social rodents *(Octodon* and *Ctenomys)* are linked to the density of oxytocin receptors in the forebrain, including areas of the hippocampus [Beery et al., 2016]. Thus, the processing of social cues derived from group living may be in part mediated by components of the stress response and the brain areas associated with it. Taken together, laboratory studies on traditional animal models and comparative approaches have independently been able to demonstrate a connection between habitat, social conditions and changes in the volume of the DG or structures associated with it. However, the few field studies focused on testing the effects of both sex and season on DG anatomy and they have yielded inconsistent results [Burger et al., 2013, 2014].

Physical and social environmental conditions may also result in differential effects on brain asymmetry, a condition reported in birds, rodents and primates [Vallortigara and Rogers, 2005]. Research on these vertebrates indicates how brain asymmetry is linked to social recognition or social position relative to other group members, a phenomenon associated with right-hemispheric dominance [Rogers et al., 2013; Rogers and Vallortigara, 2015]. However, specialization of the right hemisphere may extend to other sensory modalities, including spatial novelty and intense emotions (i.e., fear or predator attack) [Rogers et al., 2013]. Again, the potential effects of spatial and social complexity on DG asymmetry in free-ranging adult rodents remain virtually unexplored.

Model Species and Hypothesis Predictions

The aim of this study was to examine two natural populations of *Octodon degus* and one population of *O. lunatus*, two phylogenetically related species of rodents that face contrasting conditions of physical complexity and differ in sociality (or group living). *O. degus* uses relatively open savannas or open scrub environments in central Chile, but more closed scrub patches and ravines in northern populations [Quispe et al., 2009; Ebensperger et al., 2012]. In these environments, *O. degus* excavate and use burrow systems connected aboveground by runways or trails used during foraging [Fulk, 1976; Lagos et al., 1995; Vásquez et al., 2002]. In contrast, *O. lunatus* is preferably associated with coastal shrubland, characterized by moist and high vegetative cover [Sobrero et al., 2014]. Compared with *O. degus*, *O. lunatus* seems to rely more on vegetation cover to hide from predators instead of building extensive burrow systems or using interconnected runways [Sobrero et al., 2014].

When navigating, small mammals employ global landmarks (e.g. forest edge or mountain outline), which serve as more distant cues, and local landmarks (e.g. shrub and rock cover, or logs), which are spatially closer to the goal [Jacobs and Schenk, 2003; Nesterova, 2007; Bruck and Mateo, 2010]. Global landmarks may provide more reliable indicators of a goal's location because they are observ-

able from greater distances, stable and more likely to be unique [Biegler and Morris, 1996]. Instead, local landmarks are often not unique, where the presence of other similar and continuous objects (i.e. shrub cover or logs) may challenge animal navigation. Moreover, local landmarks such as vegetation cover may preclude the use of global landmarks. For instance, a study showed how the upper portion of the horizon or visible global landmarks is more important for orientation during food searching than local landmarks in Columbian ground squirrels *(Spermophilus columbianus)* [Vlasak, 2006]. Thus, if higher vegetation cover is associated with greater cognitive demands during navigation, we predicted (i) *O. lunatus* and *O. degus* from populations with higher vegetation cover to exhibit a larger DG volume and density of cells than *O. degus* from populations in habitats with less cover.

O. degus live in relatively large groups ranging from 1 to 12 adult individuals [Hayes et al., 2009], and females of this species exhibit communal care of offspring [Ebensperger et al., 2004]. These characteristics have been documented in at least four populations of this species [Ebensperger et al., 2004, 2012; Jesseau, 2004; Sobrero et al., unpubl. data], implying a high frequency of social interactions and probably a need for cognitive skills underlying these interactions. In contrast, the social behavior of *O. lunatus* is less well known, yet a recent study revealed how these rodents live in small social groups that range from 2 to 4 adults [Sobrero et al., 2014]. Therefore, if greater sociality is associated with greater cognitive demands to keep track of individual relationships, we predicted (ii) more social *O. degus* to exhibit a larger DG volume and density of cells than *O. lunatus*.

Finally, we tested the prediction that (iii) the factor with the strongest effect on brain size and DG morphology would be associated with the most asymmetrical DG volume and cell number. Given that social recognition and other aspects of social behavior are processed primarily in the right hemisphere [Rogers and Vallortigara, 2015], we further predicted (iv) population DG asymmetries or right-hemispheric dominance to be more frequent in the relatively more social *O. degus*.

Materials and Methods

The original research reported herein was performed under guidelines established by the Pontificia Universidad Católica de Chile Bioethical Committee (CBB-042/2011) and adhered to Chilean laws [permits 1-154.2010 (7989), 1-109.2011 (6749), 1-90.2011 (4731) and 1-95-2012 (4486) by the Servicio Agrícola y Ganadero and 013/2011 by the Corporación Nacional Forestal].

Study Populations, Degu Trapping and Marking

We contrasted the volume and total number of DG cells of two *O. degus* and one *O. lunatus* populations across north-central Chile. In particular, we examined *O. degus* from El Salitre (ES; 30°38′S, 71°35′W, altitude 275 m) and Rinconada (RI; 33°23′S, 70°31′W, altitude 495 m), and *O. lunatus* from Los Molles (LM; 32°13′S, 71°31′W, altitude 36 m). The study sites in these populations reached an area of ~3 ha. During 2010 and 2012, adult animals were captured using 14 × 14 × 40 cm Tomahawk traps (model 201; Tomahawk Live Trap Company, Hazelhurst, Wis., USA). Based on previous studies [Ebensperger et al., 2004, 2012], we placed traps near burrow openings and inside patches with high shrub cover and baited them with rolled oats, fruity cereals and sunflower seeds. During each capture, we recorded sex, body mass (to 0.1 g) and reproductive status (whether a female had a perforated vagina, was pregnant or lactating) of all degus, and each animal was marked with an ear tag (Monel 1005-1; National Band and Tag Co., Newport, Ky., USA). While we were not able to determine the exact age of the subjects, we could attain approximate estimates based on body mass and condition. Trapping of *O. degus* included females during early and late gestation (July to August 2012), and *O. lunatus* during lactation (November to December 2010, 2011) [Bauer et al., 2014; Sobrero et al., 2014]. Adult-aged degus were fitted with a radio collar weighing 7–9 g (RI-2D; Holohil Systems Limited, Carp, Ont., Canada; SOM-2190A, and BR radio collars; AVM Instrument Co., Colfax, Calif., USA). At the end of our study, all radio-collared animals were recaptured and radio collars were removed [Ebensperger et al., 2004, 2012].

Habitat Complexity

We first quantified habitat complexity from the overall amount of vegetation cover in the habitat used by the degus. We used 5 randomly placed 50-meter transects to quantify habitat complexity in terms of the percentage of ground surface that included herbaceous cover, shrub cover, rocks or that had no cover [Sobrero et al., 2014]. We also inferred habitat complexity faced by degus from the spatial behavior of these animals. In particular, we quantified the size of range areas and attributes of spatial trajectories. To calculate range areas, we recorded locations of all radio-collared animals each hour during their activity period (i.e. between 09.00 and 17.00 h for *O. degus*; between 21.00 and 07.00 and between 07.00 and 21.00 h for *O. lunatus*). We radio tracked *O. degus* during 5 days and *O. lunatus* during 3 days and 4 nights. The spatial location of animals during activity was determined using triangulation [Kenward, 2001]. To do so, we used 2 LA 12-Q receivers, each connected to a null-peak antenna system (AVM Instrument Co.). Every null-peak system had four 7-element Yagi antennas. The distance between antenna stations was about 120 m. To ensure independence of data points [Swihart and Slade, 1985; Kenward, 1987], intervals between fixes were approximately 1 h. Bearings from both antenna stations were then transformed into x-y locations with the software Locate II [Nams, 1990]. Data points for each degu were then mapped using the 95% minimum convex polygon algorithm of the software Ranges VI [Kenward et al., 2003].

We also quantified habitat complexity from the spatial behavior of animals. We used fluorescent pigments (Radiant Color Co., Richmond, Calif., USA) to trace the movement of *O. degus* at a smaller spatial scale. To do so, non-radio-collared adult-size degus were introduced into a plastic bag containing a unique powder color pigment, gently shaken during a few seconds and released

Table 1. Body mass, brain size, volume and number of DG cells (means ± SE) in *O. degus* and *O. lunatus* from north-central Chile

Species	Population	Sex	n	Body mass, g	Brain size, g	DG volume, mm^3	Relative DG volume	DG cell number, $\times 10^7$
O. degus	ES	F	4	203.35±24.34	2.16±0.06	5.639±0.726	0.0028±0.0003	1.58±0.69
O. degus	ES	M	3	201.23±4.57	2.39±0.10	5.661±0.022	0.0026±0.0002	1.33±0.37
O. degus	RI	F	2	209.50±3.50	2.08±0.03	4.073±0.404	0.0027±0.0002	0.91±0.36
O. degus	RI	M	2	185.90±23.10	2.43±0.05	5.937±1.439	0.0020±0.0005	1.26±0.56
O. lunatus	LM	F	3	156.87±17.23	3.17±0.07	6.890±1.445	0.0024±0.0006	1.84±0.54
O. lunatus	LM	M	3	165.20±18.71	2.68±0.19	6.865±0.359	0.0022±0.0001	2.26±1.17

Both left and right hemispheres were measured to estimate DG volume and number.

back immediately to their original site of capture [Lemen and Freeman, 1985]. Pigment-dusted animals were tracked during night time with a hand-held, long-wave ultraviolet lamp (Ultra-Violet Products Inc., San Gabriel, Calif., USA) [Lemen and Freeman, 1985]. During tracking, we used flagging markers to record the angle of turns along the total trail, and the trail length associated with different vegetation cover (i.e. 'shrub', 'bare ground' or 'grass'). This information was used to create a detailed map of the habitat and movement of every subject studied from RI and ES. Powder marking does not significantly alter spatial behavior [Ebensperger and Tamarin, 1997; Kalcounis-Ruppell et al., 2001].

Social Complexity

We quantified social complexity from the extent of sociality. Differences in sociality were based mainly on group size, an estimate of social tolerance and potential for social interactions [Rubenstein, 2011]. Group size in turn was quantified from (i) the number of male and female adults sharing nesting sites and from (ii) the extent to which range areas of these adults overlap (a measure of social cohesion during activity). A previous study indicated that degus from the same social group (based on the sharing of nesting sites) also share their foraging areas [Ebensperger et al., 2004]. Thus, populations where a larger number of adults shared same burrow systems and showed greater spatial overlap were considered relatively more 'social' [Sobrero et al., 2014]. To this end, all radio-collared animals were radio tracked to their putative resting locations at the time they were inactive [*O. degus*; Ebensperger et al., 2004] or less active [*O. lunatus;* Sobrero et al., 2014]. We determined resting locations with an LA 12-Q receiver (for radio collars tuned to 150.000–151.999 MHz frequency; AVM Instrument Co., Auburn, Calif., USA) and a hand-held, 3-element Yagi antenna (AVM Instrument Co., Colfax, Calif., USA). Once located, the position of each animal was marked with flagging material coded for individual animals. Each radio-fix location was georeferenced twice with a Garmin portable GPS (Garmin International Inc., Olathe, Kans., USA). The precision of GPS readings was always within 5 m. The determination of group size and composition required the compilation of a symmetric similarity matrix of pairwise association of the resting locations of all adult degus during trapping and telemetry [Whitehead, 2008]. We determined the association (overlap) between any 2 individuals by dividing the number of nights *(O. degus)* or evenings *(O. lunatus)* that these individuals were captured at or tracked with telemetry to the same nesting area by the number of nights *(O. degus)* or evenings *(O. lunatus)* that both individuals were trapped or tracked with telemetry on the same night *(O. degus)* or evening *(O. lunatus)* [Ebensperger et al., 2004; Sobrero et al., 2014]. To determine social group composition, we conducted hierarchical cluster analysis of the association matrix in SOCPROG software [Whitehead, 2009]. To determine whether individuals assigned to a same resting location were also socially cohesive when active, we quantified the percent spatial overlap of range areas between individuals assigned to the same resting locations. Pairwise estimates of the percent overlap between polygons for different females were also calculated using Ranges VI.

Brain Preparation

A sample of radio-collared degu subjects from each population was transported to the laboratory and euthanized (table 1). All animals were anesthetized (0.5 ml ketamine and 0.1 ml xylazine) and perfused transcardially with 0.1% saline followed by 4% buffered paraformaldehyde. Brains were postfixed, weighed (a measure of absolute brain size), kept at 4°C and then cryoprotected in a 30% sucrose solution for 72 h. Tissue was cut into 60-μm coronal sections on a Leica CM 3050S cryostat at –20°C. Free-floating sections were collected in 0.1 M phosphate-buffered saline, and every 3rd section was mounted and stained with cresyl violet (Fluka: 61123, 0.2% solution, pH 4.3) and coverslipped with Permount.

Histological Measures

Measurements of DG volume and cell number were estimated on cresyl violet-stained sections with the use of StereoInvestigator 8.0 (MBF Bioscience, Williston, Vt., USA) and a Nikon microscope (eclipse E400). Stereotaxic reference data were retrieved from the studies by Wright and Kern [1992] and Kumazawa-Manita et al. [2013] (fig. 1a–c). All sampling schemes were optimized by us (R.S. and S.E.D.) and collaborators (S. Fernández, Pontificia Universidad Católica de Chile, and T. Roth II, Franklin and Marshall College) based on strategies in StereoInvestigator 8.0. The DG of each subject was examined on every 12th section with the use of an optical fractionator workflow and a Cavalieri estimator [Gundersen and Jensen, 1987]. DG volume was measured with a 40-μm square grid on a ×40 lens. Cell counts were performed using an optical fractionator procedure [West et al., 1991] using a ×100 oil immersion lens (fig. 1d). A 200-μm sampling grid was used and all 40 × 40 μm frames were counted with

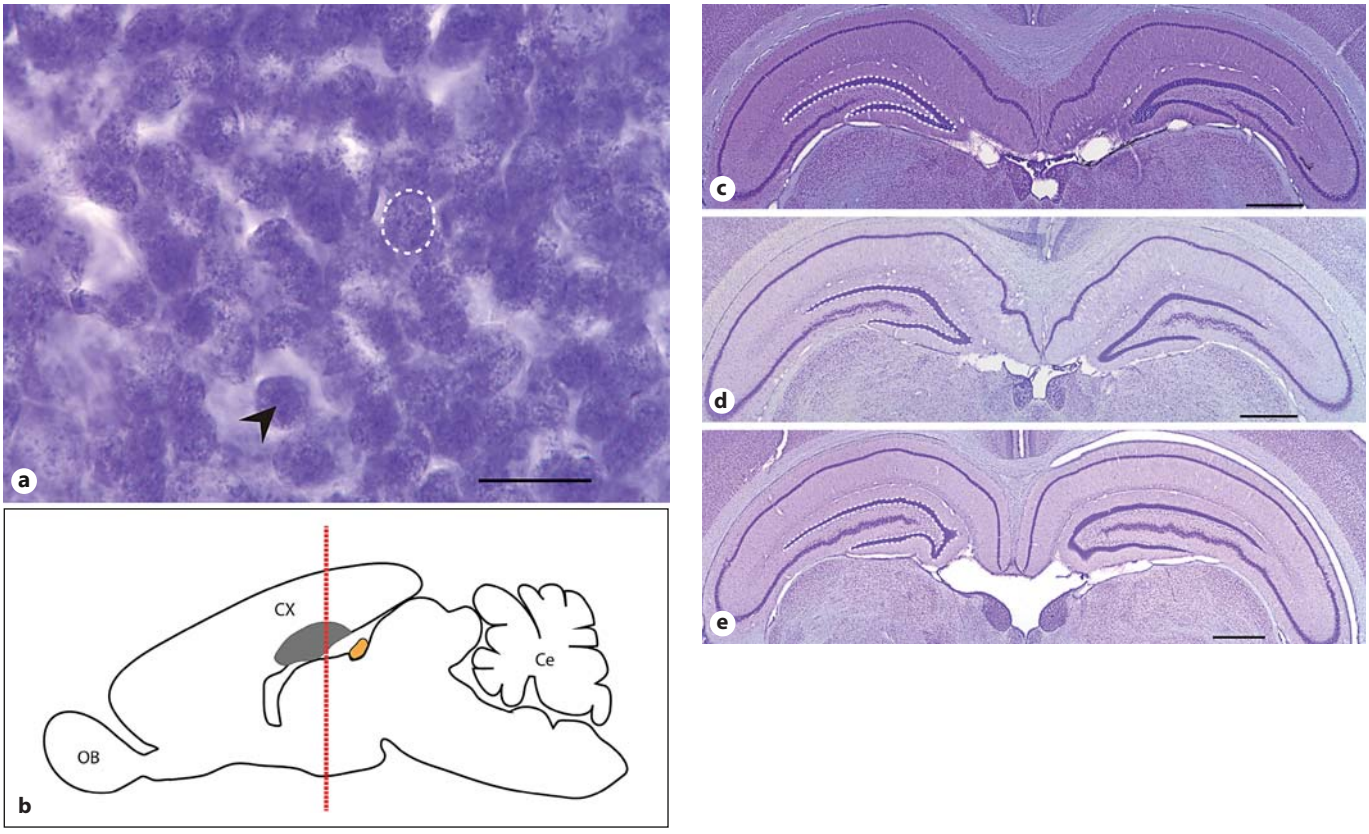

Fig. 1. Cell nuclei (**a**, black arrowhead) can be differentiated into Nissl-stained sections and were used for cell quantification, independent of density and cell overlay (**a**, dashed white line contour). Sagittal sections of the right side of the degu's brain (**b**) showing the location of referential structures in the hippocampus (gray structure): olfactory bulb (OB), cortex (CX), cerebellum (Ce) and pineal gland region (orange structure; see online version for colors). The dashed red line (**b**) indicates the section of the DG where the photomicrographs (**c–e**) were taken. **c–e** Photomicrographs showing the location of the dorsal DG (dashed white line contour) in Nissl-stained coronal sections of octodontid rodents: *O. degus* at RI (**c**) and ES (**d**) and *O. lunatus* (**e**). Scale bars = 20 μm (**a**) and 1 mm (**c–e**). All material has been processed in the laboratory using the same protocols.

a dissector height of 5 μm and 2-μm guard zones. We calculated coefficients of error to estimate precision of estimates [West et al., 1991]. These figures [mean coefficients of error (SE)] were 0.02 (0.001) at LM, 0.03 (0.001) at ES and 0.03 (0.002) at RI. Together, these procedures allowed us to quantify absolute and relative brain sizes, DG total and relative volumes, and the total number of DG cells in the right and left hemispheres.

Statistical Analyses

We first ran χ^2 tests to examine the null hypothesis of equal habitat complexity in terms of vegetation cover among all three populations [Zar, 1999]. To further examine habitat complexity in terms of the spatial behavior of degus, we used ANOVA to compare the percentage of degu trajectories that were recorded in patches with different types of vegetation cover in ES and RI. Given that animal trajectories differed in total length, we examined the number of turns/linear meters of trajectory. This comparison was restricted to the more abundant *O. degus* from ES and RI. Differences in degu range areas across all three populations and sex (males vs. females) were compared with ANCOVA, and where degu subjects' body mass was entered as a covariate. We distinguished males and females in the analyses based on the frequent sex differences in spatial navigation ability reported in other mammalian species, including humans [Jones et al., 2003; Popović et al., 2010]. Range area values were $\log_{10}$ transformed to meet normality and homogeneity of variance assumptions. Student-Newman-Keuls post hoc tests were used to detect significant pairwise differences.

We examined population differences in sociality with generalized linear/nonlinear models. In particular, we assessed the main effect of population on total group size. Total group size was fitted to a Poisson distribution with a log link function. Population differences in the percentage of range area overlap were examined with a general linear model (GLM). Range area overlap values were arcsine squared root transformed to meet normality and homogeneity of variance assumptions.

We also used GLM to examine how population and degu sex explained variation in brain size and DG cell number. In the case

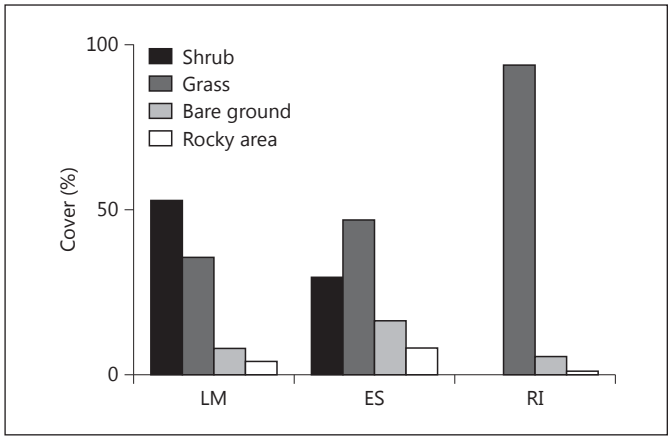

Fig. 2. Habitat variation across the populations studied. It was measured as the distribution (%) of shrub, grass, bare ground and rock cover.

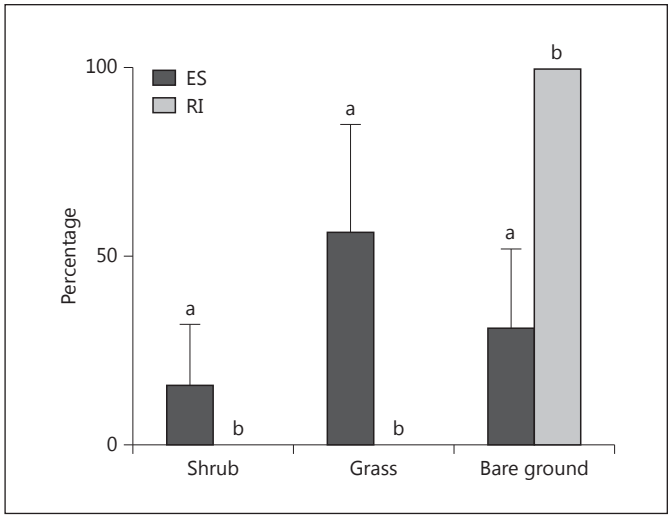

Fig. 3. Habitat complexity across the populations studied. *O. degus* trajectory (%) through a diverse array of habitat patches. Different letters on top of the bars are used to indicate population differences.

of brain size, body mass was added to the effects of population and degu sex. Given that data transformation failed to normalize relative DG volume, we used the Kruskal-Wallis test with the Scheirer-Ray-Hare extension (a nonparametric equivalent of two-way ANOVA) [Sokal and Rohlf, 1995] to determine the effects of population, sex and a population-by-sex interactive effect on relative DG volume. We used repeated-measure ANOVA followed by Student-Newman-Keuls post hoc tests to examine the effects of brain hemispheres (right vs. left), population, sex and factor interactions on DG cell number.

We used GLM followed by best-fit and supported model approaches to examine how degu sex, body mass, total group size and range area within a population predicted variation in brain size, DG cell number and relative volumes of the DG by brain hemisphere.

All data are reported as means ± SE. Analyses were conducted with Statistica 9.0 (StatSoft Inc., Tulsa, Okla., USA), SigmaPlot (Systat Software Inc., San Jose, Calif., USA, www.sigmaplot.com) and the R software 3.0.1 (The R Foundation for Statistical Computing, http://www.rproject. org/foundation/).

Results

Habitat Conditions in Terms of Vegetation Cover

Based on 5 transects per population, we recorded that vegetation cover did vary across populations (contingency table analysis, $\chi^2 = 124.4$, d.f. = 6; $p < 0.0001$; fig. 2). A subsequent subdivision of contingency tables [Zar, 1999] revealed that habitat based on cover was different in all three populations ($\chi^2 = 16.66$, d.f. = 3; $p = 0.0008$). In particular, habitat at LM had more shrubs, followed by bare ground and rock cover (fig. 2). Instead, ES was characterized by higher grass cover, followed by shrubs, bare ground and rock cover (fig. 2). The habitat used by degus at RI was characterized mostly by grass cover and bare ground (fig. 2). Thus, a decreasing gradient of habitat complexity in terms of vegetation cover observed was LM > ES > RI.

Habitat Conditions in Terms of the Spatial Behavior of Animals

Our standardized trajectories ($\overline{X}$ ± SE = 35 ± 15 m) were based on fluorescent marks recorded for 28 adult *O. degus* from RI (1 male, n = 8) and ES (10 males, n = 20). These data indicated that degus from ES moved through a more diverse array of habitat cover compared with RI (ANOVA, $F_{5, 162} = 25.41$, $p = 0.0001$; fig. 3). After controlling for this effect, we found that habitat complexity in terms of the spatial behavior of degus did vary across populations (contingency table analysis, $\chi^2 = 10.43$, d.f. = 2; $p = 0.0054$). Trajectories of degus intersected more patches with shrubs and grass, but less patches with bare ground at ES compared with RI.

Information on range areas was available for 45 radio-collared *O. degus* (n = 15 from RI, n = 30 from ES) and 20 radio-collared *O. lunatus*. The size of range areas (ha) estimated from telemetry was greater at LM than ES (ANCOVA, $F_{2, 56} = 3.72$, $p = 0.030$) when sex and degu body mass were included in the analysis (fig. 4). In contrast, the size of range areas of degus at RI was not different from ES and LM (unequal sample HSD post hoc test, $p > 0.05$). Across populations, males had larger range areas than

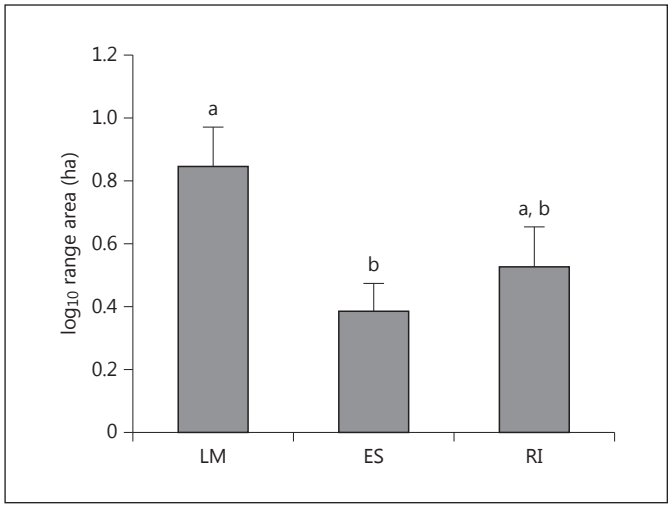

Fig. 4. Habitat differences as revealed from variation in *O. degus* range areas across populations. Means ± SE. Different letters on top of the bars are used to indicate population differences.

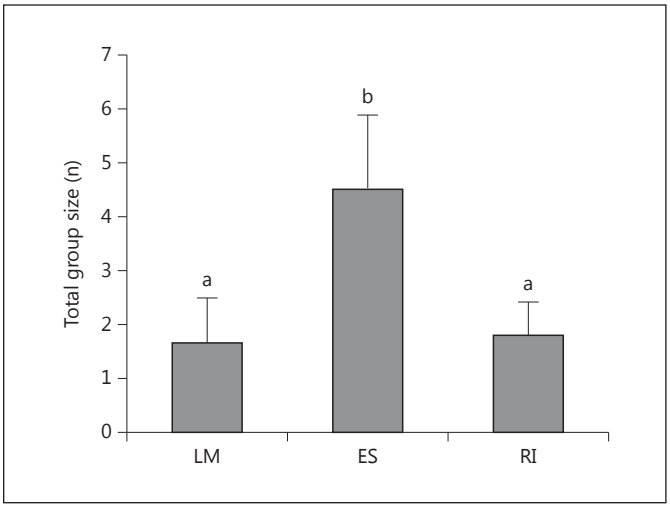

Fig. 5. Variation in total group size (number of adults) across populations of *O. lunatus* (LM) and *O. degus* (ES and RI). Means ± SE. Different letters on top of the bars are used to indicate population differences.

females (ANCOVA, $F_{1, 56} = 9.29$, $p = 0.004$). Thus, a decreasing gradient of habitat complexity in terms of spatial behavior of degus was LM > ES ≥ RI.

Variation in Sociality

The numbers of social groups identified at RI, ES and LM were 11, 8 and 5, respectively. Our examination of social conditions based on total group size (fig. 5) revealed statistically significant differences across populations (Wald = 9.73, $p = 0.008$) and where social groups from ES were larger than social groups from RI and LM. Instead, range area overlap was similar across populations (GLM, $F_{2, 9} = 0.90$, $p = 0.439$) and sex (GLM, $F_{1, 9} = 0.47$, $p = 0.510$) of degus (fig. 6). Thus, a decreasing gradient of social complexity in terms of group size was ES > RI = LM.

Population and Species Differences in Brain Size, DG Volume and Cell Number

The brains of 11 adult-sized *O. degus* (6 females and 5 males) and 6 *O. lunatus* (3 females and 3 males) were examined during this study (table 1). We found a statistically significant population by sex interaction effect on brain size ($F_{2, 10} = 7.92$, $p = 0.009$), where female *O. lunatus* from LM had larger brains than males, but not so in *O. degus* from RI or ES (fig. 7). Body mass of degus did not influence brain size ($F_{1, 10} = 1.82$, $p = 0.207$). Our examination of the relative volume of DG indicated no effects of population ($H_{2, 11} = 3.20$, $p = 0.202$), sex

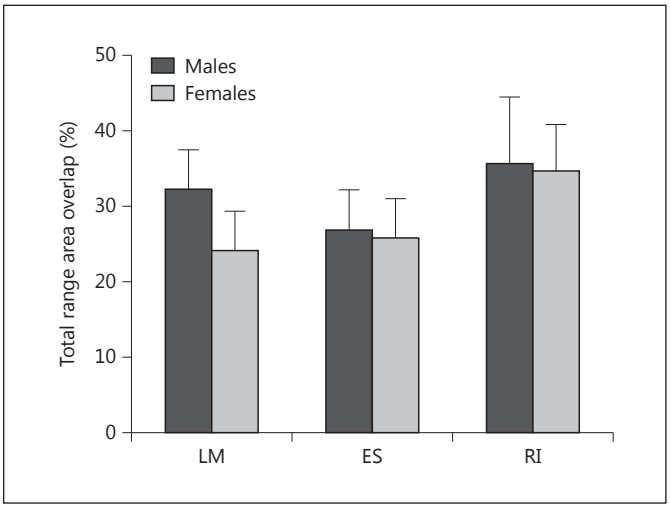

Fig. 6. Variation in total range area overlap across populations of *O. lunatus* (LM) and *O. degus* (ES and RI). Means ± SE.

($H_{1, 11} = 3.20$, $p = 0.074$) or a population by sex interaction ($H_{2, 11} = 3.20$, $p = 0.202$).

When potential differences between hemispheres were considered, we found a statistically significant population by hemisphere interaction ($F_{2, 11} = 4.27$, $p = 0.042$), where the right hemisphere of male and female DG had more cells than the left hemisphere, but only in *O. lunatus* at LM (Student-Newman-Keuls post hoc test, $p = 0.030$; fig. 8).

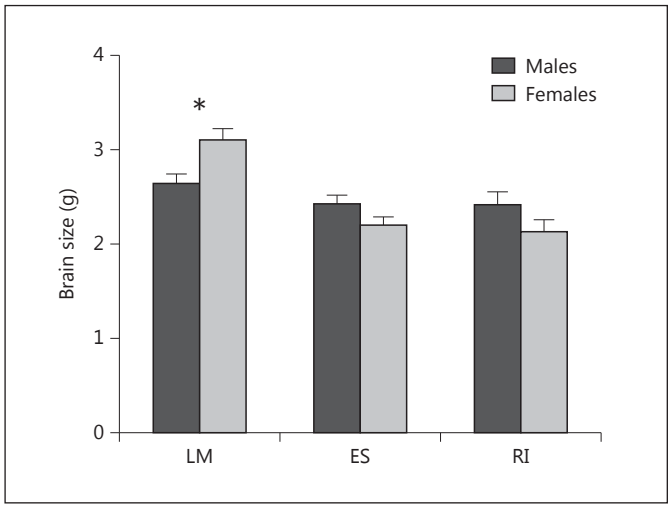

Fig. 7. Female and male relative (to body mass) brain size across populations of *O. lunatus* (LM) and *O. degus* (ES and RI). Means ± SE. * $p < 0.001$.

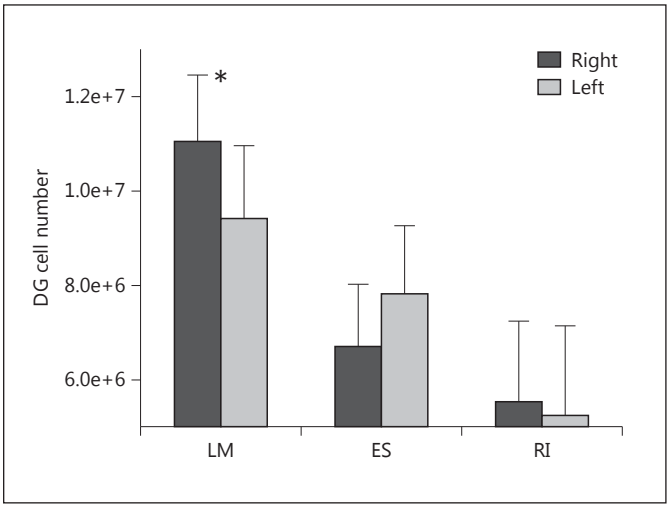

Fig. 8. Female and male total number of DG cells in each brain hemisphere across populations of *O. lunatus* (LM) and *O. degus* (ES and RI). Means ± SE. * $p < 0.001$.

Table 2. Akaike's information criterion (AIC) values associated with five possible best-fit models explaining differences in brain size, DG cell number and relative DG volume per brain hemisphere in *O. lunatus* at LM

Variable examined and model	Parameters, n	AIC	ΔAIC	Akaike weight	Evidence ratio
Brain size					
Additive	3	*–7.511*	*0.000*	*0.000*	*0.001*
Sex	1	4.157	11.668	0.222	0.187
Total group size	1	5.568	13.079	0.320	0.379
Range area	1	6.225	13.736	0.494	0.526
Body mass	1	6.558	14.069	1.000	0.621
Relative DG volume/hemisphere					
Sex	1	*–138.022*	*0.000*	*0.579*	*1.000*
Total group size	1	–137.070	0.952	0.853	1.610
Range area	1	–132.719	5.303	0.658	14.175
Body mass	1	–131.410	6.612	1.000	27.276
Additive	3	–78.40	59.282	1.000	7.46e+15
DG cell number/hemisphere					
Sex	1	*–137.247*	*0.000*	*0.644*	*1.000*
Total group size	1	–135.443	1.804	0.734	2.465
Range area	1	–132.796	4.451	0.735	9.258
Body mass	1	–130.751	6.496	1	25.739
Additive	3	–76.374	60.873	1.000	1.65e+16

Predictors in these models were sex, body mass, range area and total group size. Values in italics indicate the best-fit, yet not well-supported model for each variable. A best-fit model that was well supported had the lowest AIC value, ΔAIC <2, Akaike weight approaching 0.90 or higher and evidence ratios close to 1 [Burnham and Anderson, 2002; Symonds and Moussalli, 2011].

Table 3. AIC values associated with five possible best-fit models explaining differences in brain size, DG cell number and relative DG volume per brain hemisphere in *O. degus* at ES

Variable examined and model	Parameters, n	AIC	ΔAIC	Akaike weight	Evidence ratio
Brain size					
Sex	1	*–1.902*	*0.000*	*0.580*	*1.000*
Body mass	1	0.762	2.664	0.365	3.789
Additive	3	1.517	3.419	0.394	5.53e+03
Range area	1	1.805	3.707	0.564	6.382
Total group size	1	2.318	4.220	1.000	8.248
Relative DG volume/hemisphere					
Sex	1	*–138.022*	*0.000*	*0.579*	*1.000*
Total group size	1	–137.070	0.952	0.853	1.610
Range area	1	–132.719	5.303	0.658	14.175
Body mass	1	–131.410	6.612	1.000	27.276
Additive	3	–78.740	59.282	1.000	7.46e+15
DG cell number/hemisphere					
Additive	**3**	**245.500**	**0.000**	**1.000**	**1.000**
Sex	1	330.300	84.800	0.598	2.60e+21
Total group size	1	331.428	85.928	0.846	4.56e+21
Range area	1	335.593	90.093	0.685	3.66e+22
Body mass	1	337.150	91.650	1.000	7.97e+22

Predictors in these models were sex, body mass, range area and total group size. Bold typing is used to indicate the best-fit, well-supported model in each case. Instead, values in italics indicate the best-fit, yet not well-supported model for each variable. A best-fit model that was well supported had the lowest AIC value, ΔAIC <2, Akaike weight approaching 0.90 or higher and evidence ratios close to 1 [Burnham and Anderson, 2002; Symonds and Moussalli, 2011].

Within-Population Predictors of Neuroanatomical Variables

The examination of how sex, body mass, range area and total group size predicted brain size of *O. lunatus* revealed that the best-fit model at LM was not well supported (table 2). Similarly, the best-fit model at ES was not well supported, implying that brain size of *O. lunatus* and *O. degus* was not well predicted by any of the factors examined (table 3).

Regarding DG cell number by hemisphere, the best-fit model at LM was not well supported, implying that DG cell number of *O. lunatus* was not well predicted by sex, body mass, range area or total group size. In contrast, the best-fit and well-supported model at ES was the full additive model (table 3). Thus, large-sized *O. degus* that ranged over larger areas and were members of larger social groups exhibited a higher number of cells per hemisphere. Instead, the best-fit model explaining relative DG volumes per hemisphere of *O. lunatus* at LM (table 2) and *O. degus* at ES (table 3) were not well supported, implying that there was no association between relative DG volumes per hemisphere and any of the predictors examined.

Discussion

Habitat conditions relevant to animal movements differed across all three populations. Shrub cover was greater at LM, intermediate at ES and minimal at RI. Rock cover was relatively lower at LM and RI compared with ES. Cover of herbaceous vegetation was higher at RI compared with LM and RI. When habitat conditions were examined in terms of the spatial behavior of animals, we found degus from LM to range over larger areas compared with degus at ES. The tracking of fluorescent marks further indicated movement of *O. degus* intersected more patches with shrubs and grass at ES compared with RI. *O. degus* trajectories at RI intersected patches with more bare ground than trajectories at ES. These findings suggest

that greater overhead or total shrub cover at LM makes the use of distant visual cues or global landmarks more difficult to see, implying that this habitat is more cognitively challenging for individual spatial use compared with RI. The relatively intermediate shrub and grass cover at ES would make the use of local and global landmarks less difficult to see compared with LM. The complete absence of shrub and grass cover at RI would make the use of global landmarks an easier task compared with LM and ES. In contrast to vegetation cover of habitat, the social environment was more cognitively challenging at ES compared with LM and RI, as revealed by differences in total group size (a measure of social tolerance and the potential for social interactions), but not total range area overlap (a measure of social cohesion during activity). These differences in habitat and social conditions did co-vary with differences and similarities in brain size and hemisphere DG morphology to different extents. In particular, female *O. lunatus* had larger brains than males from LM, a sex-linked difference not recorded in *O. degus* from RI or ES. Males and females degus from all three populations had similarly sized DG in terms of relative volume. Alternatively, absolute differences in brain size may represent size-scaled, allometric differences. This is supported by the observation that relative brain size was not different among the populations. Mammalian brain evolution has often been studied with the implicit assumption of common scaling rules. However, the relationship between brain size and the number of neurons varies between individuals, among species and among neuroanatomical structures [Herculano-Houzel et al., 2015]. Subsequent studies are needed to determine how this absolute differences associate with brain structures other than DG.

The right hemisphere of male and female *O. lunatus* from LM had more cells than the left hemisphere, a DG asymmetry not found in *O. degus* from ES or RI. Thus, the larger brain size of females and higher DG cell number in male and female *O. lunatus* were associated with the use of habitat with greater shrub cover. Instead, similarly sized right- and left-hemisphere DG of *O. degus* were associated with differences in social conditions based on total group size. Taken together, population differences in brain size and DG cell number seemed more responsive to differences in habitat complexity than to differences in social complexity.

Effects of Habitat

Our population and species comparisons confirmed an association between physical conditions of habitat and DG cell number and brain size. Brain size and DG cell number in *O. degus* from ES were associated to within-population variation in habitat conditions. Individuals need to manage and process spatial information on physical environment during spatial navigation [Clutton-Brock and Harvey, 1980; Sherry et al., 1992]. As predicted by Dukas [1998] and Shettleworth [1998], we confirmed an influence of cognitive constraints derived from physical conditions of habitat on DG organization.

Habitat conditions influence navigation of scatter hoarding birds and small mammals, and species exposed to seasonal variation in terrestrial or aerial cover in space and/or time exhibit greater hippocampal volume and spatial recall accuracy [Clayton and Krebs, 1994; Jacobs, 1995, 1996; Barkley and Jacobs, 1998]. We lack information on handling, transport and storage of food in *O. lunatus*. However, these rodents exhibit high fidelity to their resting locations despite roaming over extensive range areas [Sobrero et al., 2014], implying that *O. lunatus* has the ability to search and locate resting sites despite habitat conditions that make the use of distant landmarks more challenging. Recently, Vega-Zuniga et al. [2013] showed that *O. lunatus* has a small number of retinal ganglion cells and, therefore, low visual acuity, a condition that matches the partially nocturnal activity of these rodents [Sobrero et al., 2014]. More importantly, a greater number of brain cells is linked to greater computational capacity or cognitive ability in rodents and other mammals [Herculano-Houzel et al., 2006, 2007]. Thus, the higher DG cell number recorded in *O. lunatus* compared with *O. degus* may reflect the greater challenges faced by *O. lunatus* in terms of more difficult use of long-range landmarks. Intriguingly, navigation based on local landmarks may be similarly limited as these rodents do not burrow or use runways actively [Sobrero et al., 2014].

The observation that female *O. lunatus* from LM had larger brains than males remained puzzling. These findings might reflect greater cognitive difficulties in the females for spatial learning and navigation compared with males [Cimadevilla, 2001; Jacobs and Schenk, 2003; Barkley and Jacobs, 2007]. Males can generate cognitive maps and navigate efficiently based on the use of global references exclusively [Langley, 1994]. In contrast, females rely more on local references [Langley, 1994; Sandstrom et al., 1998; MacFadden et al., 2003]. Popović et al. [2010] demonstrated gender dimorphism in *O. degus* spatial navigation. *O. degus* males subjected to spatial navigation challenges tend to explore (or look for alternative navigation strategies) the environment earlier and more widely than females. In contrast, the females exhibit initially longer fixation duration, a condition necessary for encoding

specific landmarks [Popović et al., 2010]. While all three degu populations were examined during the breeding season, female subjects were mostly pregnant in *O. degus* populations and lactating in the *O. lunatus* population. Thus, we cannot rule out that differences in the breeding stage within the breeding season further contributed to brain size differences between female and male *O. lunatus* or between species differences. Seasonal and sex differences in overall brain size remain poorly understood, but likely include hippocampal dendritic morphology, cell sizes, numbers of cells and water content [Pucek, 1965; Pyter, 2005; Workman et al., 2009].

Female *O. lunatus* of this study included lactating individuals, a condition characterized by important changes in circulating hormones, hippocampal anatomy and cognition [Roes and Galea, 2016]. Previous studies revealed how low estradiol and high progesterone levels increase spatial ability in pregnant rats [Galea et al., 2000], and Hamilton et al. [1977] demonstrated that lactating rats had increased cortical thickness compared with nonbreeding rats. Thus, potential hormonal differences associated with these different breeding stages may have translated into various volumes in neuroanatomical structures linked to the construction of cognitive maps for navigation [McEwen, 2002]. Subsequent studies are needed to examine how seasonal changes in spatial behavior are linked to variation in hormone levels and brain structure in free-ranging adult degus and other rodents.

Our study also revealed directional asymmetry at the population or species level [Rogers et al., 2013], and where the DG cell number of the right hemisphere was consistently higher than the DG cell number of the left hemisphere of *O. lunatus*. Brain asymmetry has been linked to a greater ability for information processing and cognition in several ecological contexts, including escape from predators and foraging [Rogers et al., 2013]. The right hemisphere of domestic chickens, rats and humans is involved in short-term memory of object location [LaMendola and Bever, 1997; Vallortigara et al., 2004; Maguire et al., 2006]. Thus, asymmetry in the DG cell number of *O. lunatus* is further consistent with more challenging conditions of habitat in terms of navigation ability.

Effects of Sociality

Population differences in sociality were not associated with neuroanatomical differences in degus. Relatively more social degus from ES did not have greater brain size, relative DG volume or DG cell number. On the other hand, *O. lunatus* was less social than *O. degus* from ES yet exhibited greater brain size (females) and DG cell number. Moreover, at least three observations suggest reduced opportunities for cooperative behavior in *O. lunatus*, an additional and relevant aspect of sociality. In particular, *O. lunatus* exhibit locomotor activity during daytime and nighttime, associated with high shrub cover [Sobrero et al., 2014]. The use of closed habitat conditions coupled to a partially nocturnal activity in *O. lunatus* would reduce opportunities to decrease the predation risk through social vigilance or its potential benefit as suggested by species comparisons across caviomorph rodents [Ebensperger and Cofré, 2001; Ebensperger and Blumstein, 2006]. Second, an absence of burrow digging may prevent cooperation in terms of communal burrowing as recorded in *O. degus* [Ebensperger and Bozinovic, 2000]. Third, the observation that female *O. lunatus* from the same social groups were not simultaneously lactating [Sobrero et al., unpubl. data] further indicates reduced (if any) opportunities for communally rearing their offspring. Altogether, these considerations suggest a more challenging environment in terms of sociality in *O. degus* compared with *O. lunatus*. Therefore, population differences in brain size and DG cell number seem more closely associated with cognitive demands from the physical environment and navigation rather than to social demands in these rodents.

Interestingly, neuroanatomical variation was associated with differences in total group size within populations of *O. lunatus* and *O. degus*, suggesting neuroanatomical plasticity to social conditions. Previous laboratory studies have shown how experimental changes in the composition of social groups influence DG cell proliferation in adult female prairie voles *(Microtus ochrogaster)* [Fowler et al., 2002]. Changes in group composition (i.e. a form of social instability) may disrupt adult partnerships reflecting social bonds and potentially affect social interactions, including communal rearing [Champagne and Curley, 2009; Cirulli et al., 2010]. Since permanent changes in group composition are known to occur in *O. degus* during the breeding season [Ebensperger et al., 2009], these animals represent a natural model to determine how changes in brain asymmetry and DG morphology underlie the effect of varying social conditions on social interactions among individuals.

Overall, results from this study suggest a greater influence of habitat complexity on population differences in DG anatomy compared with social conditions, but a joint effect of habitat and social environments within populations. Our findings highlight how degus and other nontraditional study species [Burger et al., 2013; Amrein et al., 2014; Burger et al., 2014] are important for a better understanding of adult hippocampal plasticity in an eco-

logically relevant context. Our study also shows how records of habitat, and social and neuroanatomical measures to the same wild study subjects are important to place firmer conclusions on these associations. Yet, statements from this study remain constrained by the relatively small number of subjects studied, an unavoidable compromise between sufficient statistical power and the numbers of animals that could be sacrificed to quantify neuroanatomical measures [Sikes et al., 2011]. This was a particularly important concern in *O. lunatus*, a wild and hardly known species [Sobrero et al., 2014].

Acknowledgements

We are very thankful to our colleagues Verónica Lahoz, Juan Monárdez, Macarena Palma, Cecilia León, Juan Carlos Ramírez, Daniela Rivera, Francisco Vargas, Rachel Chock, Morgan Elfelt, Tina Wey, Valentina Bunster, Nickolas Ulloa and Loren Hayes for field assistance. We are indebted to Roman Andrade (Fundo El Salitre, IV Región) and Marcelo Orellana Reyes (Estación Experimental G. Greve Silva, Región Metropolitana) for providing all necessary facilities to access the field sites. Our thanks og to our colleagues Timothy C. Roth II, Sara Fernández, Elisa Sentis and Alfonso Deichler for advice and assistance in obtaining histological data. Timothy C. Roth II provided constructive and useful comments that improved an earlier version of this article. We also thank Loreto Correa for her insightful suggestions during the discussion of results. Valeria Campos kindly helped with analyses in R. This study was partially supported by FONDECYT (grant 3150306 to R.S. and grant 1090302 to L.A.E.) and Program 1 of the Centro de Estudios Avanzados en Ecología and Biodiversidad (FONDAP 1501-001).

References

Amrein I, Becker AS, Engler S, Huang S, Müller J, Slomianka L, Oosthuizen MK (2014): Adult neurogenesis and its anatomical context in the hippocampus of three mole-rat species. Front Neuroanat 8:39.

Barkley CL, Jacobs LF (1998): Visual environment and delay affect cache retrieval accuracy in a food-storing rodent. Anim Learn Behav 26:439–447.

Barkley CL, Jacobs LF (2007): Sex and species differences in spatial memory in food storing kangaroo rats. Anim Behav 73:321–329.

Bauer CM, Hayes LD, Ebensperger LA, Romero LM (2014): Seasonal variation in the degu *(Octodon degus)* endocrine stress response. Gen Comp Endocrinol 197:26–32.

Beery A, Kamal Y, Sobrero R, Hayes LD (2016): Comparative neurobiology and genetics of mammalian social behavior; in Ebensperger LA, Hayes LD (eds): Sociobiology of Caviomorph Rodents. Hoboken, Wiley.

Beery AK, Kaufer D (2015): Stress, social behavior, and resilience: insights from rodents. Neurobiol Stress 1:116–127.

Biegler R, Morris RG (1996): Landmark stability: further studies pointing to a role in spatial learning. QJ Exp Psychol B 49:307–345.

Bruck JN, Mateo JM (2010): How habitat features shape ground squirrel *(Urocitellus beldingi)* navigation. J Comp Psychol 124:176–186.

Bruel-Jungerman E, Laroche S, Rampon C (2005): New neurons in the dentate gyrus are involved in the expression of enhanced long-term memory following environmental enrichment. Eur J Neurosci 21:513–521.

Burger DK, Gulbrandsen T, Saucier DM, Iwaniuk AN (2014): The effects of season and sex on dentate gyrus size and neurogenesis in a wild rodent, Richardson's ground squirrel *(Urocitellus richardsonii)*. Neuroscience 272:240–251.

Burger DK, Saucier JM, Iwaniuk AN, Saucier DM (2013): Seasonal and sex differences in the hippocampus of a wild rodent. Behav Brain Res 1:131–138.

Burnham KP, Anderson DR (2002): Model Selection and Multimodel Inference, ed 2. New York, Springer.

Champagne FA, Curley JP (2009): The trans-generational influence of maternal care on offspring gene expression and behavior in rodents; in Maestripieri D, Mateo JM (eds): Maternal Effects in Mammals. Chicago, University of Chicago Press, pp 182–202.

Cimadevilla JM (2001): Transient sex differences in the between-sessions but not in the within-session memory underlying an active place avoidance task in weanling rats. Behav Neurosci 115:695–703.

Cirulli F, Berry A, Bonsignore LT, Capone F, D'Andrea I, Aloe L, Branchi I, Alleva E (2010): Early life influences on emotional reactivity: evidence that social enrichment has greater effects than handling on anxiety-like behaviors, neuroendocrine responses to stress and central BDNF levels. Neurosci Biobehav Rev 34:808–820.

Clayton NS, Krebs JR (1994): Memory for spatial and object-specific cues in food-storing and non-storing birds. J Comp Physiol A 174: 371–379.

Clutton-Brock TH, Harvey PH (1980): Primates, brains and ecology. J Zool Lond 190:309–323.

Dukas R (1998): Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making. Chicago, University of Chicago Press.

Dunbar RIM (1998): The social brain hypothesis. Evol Anthropol 6:178–190.

Ebensperger LA, Blumstein DT (2006): Sociality in New World hystricognath rodents is linked to predators and burrow digging. Behav Ecol 17:410–418.

Ebensperger LA, Bozinovic F (2000): Communal burrowing in the hystricognath rodent, *Octodon degus*: a benefit of sociality? Behav Ecol Sociobiol 47:365–369.

Ebensperger LA, Chesh AS, Castro RA, Ortiz Tolhuysen L, Quirici Q, Burger JR, Hayes LD (2009): Instability rules social groups in the communal breeder rodent *Octodon degus*. Ethology 115:540–554.

Ebensperger LA, Cofré H (2001): On the evolution of group-living in the New World cursorial hystricognath rodents. Behav Ecol 12: 227–236.

Ebensperger LA, Hurtado MJ, Soto-Gamboa M, Lacey EA, Chang AT (2004): Communal nesting and kinship in degus *(Octodon degus)*. Naturwissenschaften 91:391–395.

Ebensperger LA, Sobrero R, Quirici V, Castro RA, Ortiz Tolhuysen L, Vargas F, Burger JR, Quispe R, Villavicencio C, Vásquez R, Hayes LD (2012): Ecological drivers of group living in two populations of the communally rearing rodent, *Octodon degus*. Behav Ecol Sociobiol 66:261–274.

Ebensperger LA, Tamarin RH (1997): Use of fluorescent powder to infer mating activity of male rodents. J Mammal 78:888–893.

Eichenbaum H (2015): The hippocampus as a cognitive map of social space. Neuron 87:9–11.
Fowler CD, Liu Y, Ouimet C, Wang Z (2002): The effects of social environment on adult neurogenesis in the female prairie vole. J Neurobiol 51:115–128.
Fulk GW (1976): Notes on the activity, reproduction, and social behavior of *Octodon degus*. J Mammal 57:495–505.
Galea LA, McEwen BS (1999): Sex and seasonal differences in the rate of cell proliferation in the dentate gyrus of adult wild meadow voles. *Microtus pennsylvannicus*. Neuroscience 89: 955–964.
Galea LA, Ormerod BK, Sampath S, Kostaras X, Wilkie DM, Phelps MT (2000): Spatial working memory and hippocampal size across pregnancy in rats. Horm Behav 37:86–95.
Gheusi G, Ortega-Perez I, Murray K, Lledo PM (2009): A niche for adult neurogenesis in social behaviour. Behav Brain Res 200:315–322.
Gundersen HJG, Jensen EB (1987): The efficiency of systematic sampling in stereology and its prediction. J Microsc 147:229 –263.
Hamilton WL, Diamond MC, Johnson RE, Ingham CA (1977): Effects of pregnancy and differential environments on rat cerebral cortical depth. Behav Biol 19:333–340.
Hayes LD, Chesh AS, Castro RA, Ortiz Tolhuysen L, Burger JR, Bhattacharjee J, Ebensperger LA (2009): Fitness consequences of group living in the degu *Octodon degus*, a plural breeder rodent with communal care. Anim Behav 78: 131–139.
Herculano-Houzel S, Collins CE, Wong P, Kaas H (2007): Cellular scaling rules for primate brains. Proc Natl Acad Sci USA 104:3562–3567.
Herculano-Houzel S, Messeder DJ, Fonseca-Azevedo K, Pantoja NA (2015): When larger brains do not have more neurons: increased numbers of cells are compensated by decreased average cell size across mouse individuals. Front Neuroanat 9:64.
Herculano-Houzel S, Mota B, Lent R (2006): Cellular scaling rules for rodent brains. Proc Natl Acad Sci USA 103:12138–12143.
Hoshaw BA, Evans JC, Mueller B, Valentino RJ, Lucki I (2006): Social competition in rats: cell proliferation and behaviour. Behav Brain Res 175:343–351.
Jacobs LF (1995): The ecology of spatial cognition: adaptive patterns of hippocampal size and space use in wild rodents; in Alleva E, Fasolo A, Lipp H-P, Nadel L (eds): Studies of the Brain in Naturalistic Settings. Dordrecht, Kluwer, pp 301–322.
Jacobs LF (1996): The economy of winter: phenotypic plasticity in behaviour and brain structure. Biol Bull 191:92–100.
Jacobs LF (2003): The evolution of the cognitive map. Brain Behav Evol 62:128–139.
Jacobs LF (2006): From movement to transitivity: the role of hippocampal parallel maps in configural learning. Rev Neurosci 17:99–109.
Jacobs LF, Schenk F (2003): Unpacking the cognitive map: the parallel map theory of hippocampal function. Psychol Rev 110:285–315.
Jesseau SA (2004): Kin Discrimination and Social Behaviour in Communally Nesting Degus *(Octodon degus)*; PhD dissertation, Univeristy of Michigan.
Jones CM, Braithwaite VA, Healy SD (2003): The evolution of sex differences in spatial ability. Behav Neurosci 117:403–411.
Kalcounis-Ruppell MC, Patrick A, Millar JS (2001): Effect of fluorescent powder marking of females on mate choice by male white-footed mice *(Peromyscus leucopus)*. Am Midl Nat 146:429–433.
Kempermann G, Kuhn HG, Gage FH (1997): More hippocampal neurons in adult mice living in an enriched environment. Nature 386: 493–495.
Kenward RE (1987): Wildlife Radio Tagging: Equipment, Field Techniques and Data Analysis. London, Academic Press.
Kenward RE (2001): A Manual for Wildlife Radio Tagging. San Diego, Academic Press.
Kenward RE, South AB, Walls SS (2003): Ranges 6, Version 1.2: For the Analysis of Tracking and Location Data. Wareham, Anatrack Ltd.
Kozorovitskiy Y, Gould E (2004): Dominance hierarchy influences adult neurogenesis in the dentate gyrus. J Neurosci 24:6755–6759.
Kumazawa-Manita N, Katayama M, Hashikawa T, Iriki A (2013): Three-dimensional reconstruction of brain structures of the rodent *Octodon degus*: a brain atlas constructed by combining histological and magnetic resonance images. Exp Brain Res 231:65–74.
Lagos VO, Contreras LC, Meserve PL, Gutiérrez JR, Jaksic, FM (1995): Effects of predation risk on space use by small mammals: a field experiment with a neotropical rodent. Oikos 74: 259–264.
LaMendola NP, Bever TG (1997): Peripheral and cerebral asymmetries in the rat. Science 278: 483–486.
Langley CM (1994): Spatial memory in the desert kangaroo rat *(Dipodomys deserti)*. J Comp Psychol 108:3–14.
Lemen CA, Freeman PW (1985): Tracking mammals with fluorescent pigments: a new technique. J Mammal 66:134–136.
Lu L, Bao G, Chen H, Xia P, Fan X, Zhang J, Pei G, Ma L (2003): Modification of hippocampal neurogenesis and neuroplasticity by social environments. Exp Neurol 183:600–609.
MacFadden A, Elias L, Saucier D (2003): Males and females scan maps similarly, but give directions differently. Brain Cogn 53:297–300.
Maguire EA, Woollett K, Spiers HJ (2006): London taxi drivers and bus drivers: a structural MRI and neuropsychological analysis. Hippocampus 16:1091–1101.
McEwen B (2002): Estrogen actions throughout the brain. Recent Prog Horm Res 57:357–384.
Nams VO (1990): Locate II User's Guide. Tatamagouche, Pacer Computer Software.
Nesterova AP (2007): Age-dependent use of local and global landmarks during escape: experiments using Columbian ground squirrels. Behav Processes 75:276–282.
Nilsson M, Perfilieva E, Johansson U, Orwar O, Eriksson PS (1999): Enriched environment increases neurogenesis in the adult rat dentate gyrus and improves spatial memory. J Neurobiol 39:569–578.
O'Keefe J, Nadel J (1978): The Hippocampus as a Cognitive Map. Oxford, Clarendon Press.
Popović N, Madrid JA, Rol MA, Caballero-Bleda M, Popović M (2010): Barnes maze performance of *Octodon degus* is gender dependent. Behav Brain Res 212:159–167.
Pucek M (1965): Water contents and seasonal changes of the brain weight in shrews. Acta Theriol 10:353–367.
Pyter LM (2005): Short photoperiods impair spatial learning and alter hippocampal dendritic morphology in adult male white-footed mice *(Peromyscus leucopus)*. J Neurosci 25:4521–4526.
Quispe R, Villavicencio CP, Cortés A, Vásquez RA (2009): Interpopulation variation in hoarding behaviour in degus, *Octodon degus*. Ethology 115:465–474.
Roes M, Galea LAM (2016): The maternal brain: short- and long-term effects of reproductive experience on hippocampus structure and function in adulthood; in Shansky RM (ed): Sex Differences in the Central Nervous System. Amsterdam, Elsevier, pp 197–221.
Rogers LJ, Vallortigara G (2015): When and why did brains break symmetry? Symmetry 7: 2181–2194.
Rogers LJ, Vallortigara G, Andrew RJ (2013): Divided Brains: The Biology and Behaviour of Brain Asymmetries. New York, Cambridge University Press.
Roth TC II, Pravosudov VV (2009): Hippocampal volume and neuron numbers increase along a gradient of environmental harshness: a large-scale comparison. Proc R Soc B 276:401–405.
Rubenstein DR (2011): Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. Proc Natl Acad Sci USA 108:10816–10822.
Sandstrom NJ, Kaufman J, Huettel SA (1998): Males and females use different distal cues in a virtual environment navigation task. Brain Res Cogn Brain Res 6:351–360.
Sherry DF, Jacobs LF, Gaulin SJ (1992): Spatial memory and adaptive specialization of the hippocampus. Trends Neurosci 15:298–302.
Shettleworth SJ (1998): Cognition, Evolution and Behaviour. New York, Oxford University Press.
Sikes RS, Gannon WL, The Animal Care and Use Committee of the American Society of Mammalogists (2011): Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J Mammal 92:235–253.
Silk JB (2007): The adaptive value of sociality in mammalian groups. Phil Trans R Soc B 362: 539–559.

Sobrero R, Ly Prieto A, Ebensperger LE (2014): Activity, overlap of range areas, and sharing of resting locations in the moon-toothed degu, *Octodon lunatus*. J Mammal 95:91–98.
Sokal RR, Rohlf FJ (1995): Biometry: The Principles and Practice of Statistics in Biological Research, ed 3. New York, Freeman.
Swihart RK, Slade NA (1985): Testing for independence of observations in animal movements. Ecology 66:1176–1184.
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.
Tavares RM, Mendelsohn A, Grossman Y, Williams CH, Shapiro M, Trope Y, Schiller D (2015): A map for social navigation in the human brain. Neuron 87:231–243.
Vallortigara G, Pagni P, Sovrano VA (2004): Separate geometric and non-geometric modules for spatial reorientation: evidence from a lopsided animal brain. J Cogn Neurosci 16:390–400.
Vallortigara G, Rogers LJ (2005): Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. Behav Brain Sci 28:574–633.
van Praag H, Kempermann G, Gage FH (1999): Running increases cell proliferation and neurogenesis in the adult mouse dentate gyrus. Nat Neurosci 2:266–270.
Vásquez RA, Ebensperger LA, Bozinovic F (2002): The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. Behav Ecol 13:182–187.
Vega-Zuniga T, Medina FS, Fredes F, Zuniga C, Severín D, Palacios AG, Karten HJ, Mpodozis J (2013): Does nocturnality drive binocular vision? Octodontine rodents as a case study. PLoS One 8:e84199.
Vlasak AN (2006): Global and local spatial landmarks: their role during foraging by Columbian ground squirrels *(Spermophilus columbianus)*. Anim Cogn 9:71–80.
West MJ, Slomianka L, Gundersen HJ (1991): Unbiased stereological estimation of the total number of neurons in the subdivisions of the rat hippocampus using the optical fractionator. Anat Rec 231:482–497.
Whitehead H (2008): Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis. Chicago, University of Chicago Press.
Whitehead H (2009): SOCPROG programs: analysing animal social structures. Behav Ecol Sociobiol 63:765–778.
Workman JL, Bowers SL, Nelson RJ (2009): Enrichment and photoperiod interact to affect spatial learning and hippocampal dendritic morphology in white-footed mice *(Peromyscus leucopus)*. Eur J Neurosci 29:161–170.
Wright JW, Kern MD (1992): Stereotaxic atlas of the brain of *Octodon degus*. J Morphol 214: 299–320.
Zar JH (1999): Biostatistical Analysis, ed 4. Englewood Cliffs, Prentice Hall.