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ASSOCIATIONS BETWEEN HABITAT CONDITIONS, SOCIALITY, AND
BRAIN ORGANIZATION IN OCTODONTID RODENTS

Por

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ASSOCIATIONS BETWEEN HABITAT CONDITIONS, SOCIALITY, AND BRAIN ORGANIZATION IN OCTODONTID RODENTS

GENERAL INTRODUCTION

Habitat and other ecological conditions may influence social environment, particularly the extent to which individuals exhibit grouping behavior. In particular, attributes of habitat such as vegetation cover may determine differences in predation risk experienced by organisms. Sociality is more expected in organisms using habitats with relatively low vegetation cover that function as refuge, reducing predator detection (Ebensperger 2001). Several studies conducted so far support vegetation cover contributes to maintain group living in current day social mammals. However, how vegetation cover (and associated predation risk) contributed to the origin and subsequent evolution of group living remains a topic of debate. For instance, given that vegetation cover generally decreases prey detection by predators (Ebensperger 2001; Ebensperger & Blumstein 2006), Old World primates, ungulates and rodents of more open, riskier habitats tend to exhibit larger group sizes than species of more vegetated, safer habitats (e.g., Kleiman 1974; Lagory 1986; Dunbar 1989). In contrast, the association between vegetation cover in the habitat and group living remains particularly an open question in caviomorphs. Lacher (1981) and Trillmich et al. (2004) suggested that habitat is a main constraint to the evolution of sociality in Caviidae (cavies, guinea-pigs, and allies). Across caviomorphs, this hypothesis is supported by the observation that group size across caviomorphs is correlated with body size, diurnality, and active burrowing (Ebensperger & Blumstein 2006). Given that large body size and

diurnality increase conspicuousness to visual predators, these findings were interpreted as supporting a link between predation risk, burrow digging, and sociality in these rodents (Ebensperger & Blumstein 2006). However, group size in these extant rodents was unrelated to the use of habitats with different vegetation cover (Ebensperger & Cofré 2001, Ebensperger & Blumstein 2006). Factors involved in the maintenance of group-living in current-day populations may not be the same as those involved in the origin and subsequent evolution (Reeve & Sherman 1993). In particular, a major topic of research in this context is the extent to which sociality in current day species reflect adaptation to ecological conditions, or the legacy from social ancestors (i.e., “phylogenetic inertia”). Thus, in Chapter 1, I examined how group living in hystricognath rodents reflect historical changes in use of habitat with different vegetation cover and ancestor-descendant relationships.

On the other hand, vegetation cover and social living may both independently affect the phenotype of organisms, including neurological attributes linked to habitat use and social relationships (e.g., Kempermann et al. 1997, Safi & Dechmann 2005, Pollen et al. 2007, Shumway 2008). Thus, the use of habitats with higher vegetation cover or with greater diversity of physical characteristics may select for larger size or greater complexity of neurological structures that allow more efficient spatial navigation (e.g., Mace et al. 1981). Similarly, greater sociality may select for larger size or greater complexity of neurological structures that allow individuals to keep track of social interactions and relationships (Dunbar 1998). Some areas of the mammalian brain seem especially sensitive to the effects of ecological and social environments, including hippocampal formation (e.g., Krebs et al. 1989, Sherry et al. 1992, Gheusi et al. 2009, Roth II & Pravosudov 2009). Controversy exists however, with regard to the relative roles of these two environmental

factors (e.g., Fox et al. 2010). Thus, in Chapter 2, I examined how variation group living and habitat characteristics explain differences in the size and anatomy of dentate gyrus in two octodontid rodents. To accomplish this I compared these neuroanatomical structures in one population of moon-toothed degus (*Octodon lunatus*) and two populations of common degus (*O. degus*) that presumably differ in sociality and habitat used. Given that social behavior of moon-toothed degus was virtually unknown (e.g., Gallardo et al. 2007, Ojeda et al. 2013, Woods & Kilpatrick 2005), I dedicated Chapter 3 to quantify this phenotypic aspect in these rodents.

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CAPÍTULO I

PHYLOGENY MODULATES THE EFFECTS OF ECOLOGICAL CONDITIONS ON SOCIALITY ACROSS HYSTRICOGNATH RODENTS

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**PHYLOGENY MODULATES THE EFFECTS OF ECOLOGICAL CONDITIONS
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ABSTRACT

The evolution of group-living in animals has been linked both to ecological and phylogenetic drivers or constraints. However, available evidence supporting each factor remains equivocal. In this study, we evaluated the influence of both scenarios across 98 species of Hystricognath rodents using phylogenetic approaches, combined with a statistical model of trait evolution. We first estimated the hypothetical ancestral forms of several clades within the Hystricognath supertree. Secondly, we examined evolutionary correlations between habitat conditions in terms of vegetation cover and sociality to determine general macroevolutionary trends on social behavior. Given the contrasting modes of life that characterize these rodents, we also examined whether subterranean habits had an effect on sociality. Our results supported the hypothesis that sociality in Old World Phiomorpha and New World Caviomorpha had an early origin. Subsequently, this aspect of social behavior has been generally being lost, giving rise to species that are secondarily asocial (i.e. supporting the social ancestor or reverse evolution hypothesis, SAH). Logistic regression analyses that included phylogenetic relationships revealed significant correlation between habitats used (i.e. vegetation cover) and absence or presence of group-living. Nodes with social ancestors showed major associations with the use of open habitat. The loss of sociality across the phylogeny was associated with the use of closed habitat conditions. No association was found between changes in sociality and subterranean mode of life. We conclude that ancestor-descendent relationships mediate the effect of changes in habitat use on the evolution of sociality across Hystricognath rodents.

Key words: phylogenetic statistical methods, ancestor reconstruction; behavioural drive, ecological constraints.

INTRODUCTION

Ecological conditions are thought to be a major evolutionary driver of group-living, or sociality (Alexander 1974; Ebensperger & Blumstein 2006). This tenet is based on the hypothesis that ecological conditions influence numerous fitness advantages obtained by social animals in relation to solitary living individuals, including decreased predation risk, decreased costs during building dens or refuges, increased access to resources, and enhanced thermoregulation efficiency (Alexander 1974; Bertram 1978; Krebs & Davies 1993; Ebensperger 2001; Ebensperger & Blumstein 2006). In addition, ecological conditions (e.g. population density, resource distribution, vegetation cover) may constrain animals to live in groups (Shultz & Dunbar 2006; Dunbar & Shultz 2007; Ebensperger & Hayes 2008; Chaverri & Kunz 2010). For instance, individuals in groups may increase their ability to detect and escape from predators, gain protection from predators because of simple dilution of per capita risk, locate themselves such that other group members become more vulnerable to attacks, or even repel predators more efficiently (Hamilton 1971; Bertram 1978; Romey 1997). Given that vegetation cover generally decreases prey detection by predators (Caro 2005; Ebensperger & Blumstein 2006; Ebensperger 2011), species inhabiting more open, riskier habitats tend to exhibit larger group sizes than species living in safer habitats due to increased cover (Kleiman 1974; Lagory 1986; Dunbar 1989). Alternatively, sociality can be the consequence of limitations in breeding sites due to high population density, a patchy distribution of critical resources, or a combination of these factors (Emlen 1982; Brown 1987; Waser 1988; Koenig et al. 1992; Arnold & Owens 1998; Johnson et al. 2002).

Regardless of whether ecological conditions provide opportunities for social benefits or act as constraints, the extent to which sociality across living species reflect changes to past or current ecological conditions remain a topic of discussion. Species differences in sociality may reflect a close functional match with differences in current ecological conditions. This hypothesis is supported in birds where colonial nesting is associated with exposure to nest predation (Rolland et al. 1998), and bird flocking (or social foraging) is linked to the use of clumped food items (Beauchamp 2002). The relevance of ecological factors is similarly supported by studies on social mammals (ungulates, cetaceans, primates) where group-living is linked to habitat openness (i.e., predation risk) and to food availability (and its effect on within-group competition) (Janson & Goldsmith 1995, Brashares et al. 2000, Gygas 2002, Caro et al. 2004). However, current species differences in sociality may represent the historical legacy of ancestral forms (Blomberg et al. 2003) and that may have evolved under different ecological conditions. While this hypothesis has been examined infrequently, it is supported in macaque primates where variation in social organization (based on the asymmetry of social interactions) is associated to ancestor-descendent relationships (Thierry et al. 2000). Similarly, current differences in social and spatial organization across equids (feral horses, zebras) and species differences in sociality in cavioids (i.e., cavies, maras, agoutis, capybaras) are more consistent with phylogenetic relationships than with current habitat differences (Linklater 2000; Rowe & Honeycutt 2002). Specifically, social living in cavies may have been inherited from an already social ancestor (Rowe & Honeycutt 1992). Together, these findings support the hypothesis that differences in sociality across living species may not only reflect a close match with ecological conditions (e.g., vegetation cover), but also the effect of ancestor-descendent relationships.

Different historical scenarios may represent the evolutionary trajectories group-living from ancestors to descendant species. First, the no-social ancestor hypothesis (NAH) states that sociality evolved through directional selection from solitary ancestors into group-living states (e.g., Creel & Macdonald 1995). The NAH predicts an asocial ancestor and a higher rate of gain in sociality through the evolutionary history. In contrast, the social ancestor or reverse evolution hypothesis (SAH) states that sociality evolved directionally from a group-living ancestor into nonsocial living forms (e.g. Wcislo & Danforth 1997; Beauchamp 1999). The SAH predicts a social ancestor and higher rates of sociality losses through the evolutionary history. Finally, the flexible ancestor hypothesis, or FAH, states that an ancestor with the ability to express a variety of social organizations gave rise to a full range of currently existing alternatives (Dalerum 2007). This hypothesis predicts that complex behavioral and physiological traits found in some social species (e.g., suppression of breeding) may also be found in solitary or relatively asocial species. As a consequence, social and asocial ancestors, and similar rates of gains and losses of sociality are expected with the same probability in clades of social and solitary species (Dalerum 2007).

Available evidence supports different patterns of social evolution across different organisms. For instance, the evolution of sociality in mongooses and other families of carnivores fits the NAH in that ancestors were solitary living forms that used habitats with high vegetation cover (Veron et al. 2004; Dalerum 2007). In contrast, the evolution of social behavior in other carnivores such as wolverines is more supportive of the FAH (Dalerum et al. 2006). SAH on the other hand, adequately describes the evolution of sociality in insect parasitoids, bees and birds (van Rhijn 1990; Wcislo & Danforth 1997; Danforth 2002; Cardinal & Danforth 2011; Tanner et al. 2011). Thus, macroevolutionary

patterns of social behavior and the relative roles of ecology and phylogeny during this process are far from well established.

Study model

The importance of ecological conditions versus phylogeny has been the focus of debate when it comes to evolution of social behaviour across Hystricognath rodents. These animals include Old and New World forms that vary markedly with regard to patterns of ecological and evolutionary diversification (Mares & Ojeda 1982; Huchon & Douzery 2001). In particular, sociality is present in 72% of families studied so far, yet this condition exhibits a non-uniform distribution throughout the clade (Woods & Kilpatrick 2005). For example, while group-living and some extreme forms of cooperation occurs in bathyergid mole-rats (Burda et al. 2000), caviids (guinea pigs) (Macdonald et al. 2007, Adrian & Sachser 2011), and octodontids (Lacey & Ebensperger 2007), group-living is rare in ctenomyids (Lacey & Ebensperger 2007), or echimids (Santos & Lacey 2011). To what extent extrinsic, ecological factors or species-specific attributes predict this behavioural diversity remains unresolved.

Lacher (1981) and Trillmich et al. (2004) suggested that ecological conditions (e.g., habitat) represent a main constraint to the evolution of sociality in Caviidae (cavies, guinea-pigs, and allies). Across caviomorphs, this hypothesis is supported by the observation that group size across caviomorphs is correlated with body size (larger species are more social), diurnality (diurnal species are more social), and active burrowing (burrowing species are more social) (Ebensperger & Blumstein 2006). Given that large body size and diurnality

increase conspicuousness to visual predators, these findings were interpreted as supporting a link between predation risk, burrow digging, and sociality in these rodents (Ebensperger & Cofré 2001, Ebensperger & Blumstein 2006). Phylogenetic effects have been implied to play a role in caviids (Rowe & Honeycutt 2002).

Among African bathyergids singular cooperative breeding (i.e., societies where a few individuals breed and most non breeders provide care to offspring of breeders) has been related to ecological constraints due to aridity, unpredictable rainfall and a patchy distribution of food (Jarvis et al. 1994). However, Burda et al. (2000) argued against this hypothesis, suggesting that sociality and cooperative breeding in these rodents evolved from a social ancestor exhibiting monogamy and high within group genetic relatedness. Thus, the solitary living lifestyle seen in some African bathyergids would be a derived trait (i.e., SAH), possibly linked to constraints associated with the subterranean environment (Burda et al. 2000).

Overall, our ability to produce generalizations on the relative roles of ecology and phylogeny across hystricognaths may have been limited by studies addressing each hypothesis separately, or by focusing on a rather limited number of species (or subclades). Very likely, the relative importance of these factors (or others) on the evolution of complex behavioral traits such as sociality differs across subclades.

Upon building a composite species-level phylogeny of African and New World Hystricognath rodents, we aim this study to test two of the three evolutionary scenarios discussed previously: (i) sociality evolved from a solitary ancestor into more advanced forms of group-living, i.e. the NAH; and (ii) sociality evolved directionally from a group-

living ancestor into no-social living, i.e. the SAH. The fact that relatively few studies have been conducted to quantify intraspecific variation in sociality across hystricognaths did not allow us to examine the FAH model. We then estimated the evolutionary trajectories and association of sociality and habitat conditions in terms of vegetation cover through the reconstruction of ancestral character state and phylogenetic logistic regression. Finally, we focused on all nodes to simultaneously examine the extent to which phylogenetic (historical) and ecological factors (based on vegetation cover) explain the evolution of sociality through the clade. In particular, an independent role of ecological factors would be supported (i) by an association between sociality and vegetation cover (where social gains are correlated with use of open habitat, or where social losses are associated with more vegetated, covered habitat), and if (ii) vegetation cover does not exhibit phylogenetic signal. A modulating role of phylogenetic relationships would be supported by a similar association between sociality and vegetation cover and (iii) if vegetation cover exhibits phylogenetic signal.

METHODS

Data collection

We used the available literature and unpublished data to collect information on sociality and habitat of living Hystricognath rodents. A complete list of the species included in the analysis can be found in electronic supplementary material. We chose robust phylogenetic methods (i.e., based on explicit models of evolutionary change) to examine evolutionary transitions between ancestral and derived character states (see below) based on discrete

variables. We opted to examine discrete variables because data on hystricognath sociality (particularly New World species) do not typically include quantitative estimates of group size (or typical group size), which limit the number of species or subclades represented in the analysis should we have based our approach on group size as a continuous variable. Thus, species were considered “social” when available evidence supported that two or more adults were reported as sharing a den or burrow system (most cases) or a territory (e.g., capybaras) (Ebensperger & Blumstein 2006). Non social species were those in which individuals are typically recorded to perform their activities solitarily, including nesting. Thus, sociality was categorized as a binary character, 0 = non-social and 1 = social. The use of these mutually exclusive social categories is supported by the observation that intraspecific variation reported in caviomorphs typically involves differences in group size rather than extreme differences between solitary and social living (Maher & Burger 2011).

We categorized vegetation cover of habitat as: “Open” for species whose main habitat were grasslands, open shrublands, rocky areas with extensive bare ground, and salt basins habitats, i.e. environments with minimal vegetation cover (Shultz & Dunbar 2006). A “Mixed” habitat category included riparian, swampy, and mangrove conditions; “Closed” habitat conditions included canebrakes, dense shrublands, and forest patches, i.e. environments with relatively high vegetation cover (Shultz & Dunbar 2006). The analysis of discrete and continuous variables is complementary and both types of variables are needed to discern qualitative or quantitative shifts in behavior as an animal evolves into new habitats (Shumway 2008). Therefore, we also ranked vegetation cover of the habitat of each species from totally open (consisting of mostly bare ground, ranks 1 to < 3.5), mixed (ranks 3.5 to 4.9), to closed forest patches (ranks ≥ 5 to 7) (Ebensperger & Blumstein 2006).

Hystricognath rodents include subterranean species whose social behavior may be less sensitive to vegetation cover above ground. To quantify the potential effect of this mode of life on sociality, we further categorized species as subterranean or not. Species were categorized as subterranean when evidence supported they conduct the vast majority of their life underground, foraging excursions are limited to the vicinity of burrow openings, and perform regular digging activities (Lessa et al. 2008, Smorkatcheva & Lukhtanov in press).

Phylogeny of African and New World Hystricognath rodents

The phylogeny available for Hystricognath rodents is well resolved. We used a composite phylogeny or supertree based primarily on Upham & Patterson (2012) to which we added species of *Ctenomys* (Parada et al. 2011), and *Phyllomys* (Loss & Leite 2011). The composite phylogeny was built in Mesquite v2.75 (Maddison & Maddison 2011). We then calibrated the supertree to obtain branch lengths of proportional to times using the BLADJ function in Phylocom v4.0.1b software (Webb et al. 2008). BLADJ constrained the internal nodes of the phylogeny to age estimates which were obtained from previously published studies (Loss & Leite 2011; Parada et al. 2011; Upham & Patterson 2012). This algorithm then interpolated the other nodes of the tree for which direct age estimates were not available (Webb et al. 2008).

Ancestral character states and evolutionary transition rates

We first evaluated the extent to which the phylogeny correctly predicts patterns of similarity in sociality, habitat type (vegetation cover) and mode of life (subterranean or not) of Hystricognath rodents (i.e. phylogenetic signal) using the D (Fritz & Purvis 2010) and AI (Parker et al. 2008) statistics (details on these methods are provided in our electronic supplementary material). Given that these analyses indicated that all variables have strong phylogenetic signal (results in electronic supplementary material), we used APE and GEIGER packages (Paradis et al. 2004; Harmon et al. 2008) written in the R language to evaluate how the origin and evolutionary transitions between categories of sociality were associated with the use of different categories of habitat in terms of vegetation cover across the evolutionary history of Hystricognath rodents. Social behaviour was analyzed with a Maximum Likelihood approach, using a continuous time Markov model (Pagel 1994). We then compared two models: equal rate or one-parameter (ER) and all rate different (ARD) models. The best fit model was determined based on the Akaike Information Criterion (AIC) (Akaike 1974). In particular, the model selected had the lowest AIC value, and $\Delta AIC < 3$ (Burnham & Anderson 2002). We used the same approach to examine habitat conditions in terms of vegetation cover (Open, Mixed, Closed). We then compared ER and ARD models, adding a symmetrical model rate (SYM), i.e. forwards and reverse evolutionary transitions between habitat states were constrained to be equal.

Estimation of phylogenetic logistic regression

We performed phylogenetic logistic regression to evaluate the extent to which sociality was predicted by the rank of vegetation cover (independent ordinal predictor) and subterranean

mode of life (independent discrete predictor) on all nodes of the evolutionary history of Hystricognath rodents. This method is based on an evolutionary model of binary traits in which trait values switch between 0 and 1 as species evolve throughout the phylogenetic tree (Ives & Garland 2010). This analysis was performed using a variance-covariance matrix of the species trait constructed using the composite phylogeny in the module PDAP (Midford et al. 2005) of Mesquite v2.75 (Maddison & Maddison 2011). The phylogenetic logistic regression was run using the PloGReg.m function written by Ives & Garland (2010). The ranks of vegetation cover were log10 transformed and standardized to have mean equal to zero and standard deviation equal to one. Under this standardization the regression coefficients represent effect sizes of the independent variables (Ives & Garland 2010). A bootstrapping procedure involving 2500 simulations was used to generate the confidence intervals and test for statistical significance of the slope of the regression model. Convergence of model parameters was achieved in all cases after these simulations.

RESULTS

The ancestral character estimation for the phylogeny nodes indicated that the most likely common ancestor of the Hystricognath rodents was social (Log-lik = -41.03, proportional likelihood 96 %, Fig. 1) and used open habitat (i.e., low vegetative cover) (Log-lik = -60.92, proportional likelihood 74 %, Fig. 2). The best fit and well-supported model of evolution of social behaviour was the ER, or Equal Rate Model (evolutionary transition rate = 0.014, Table 1). Regarding evolutionary changes in habitat conditions, the best fit of the 3

possible models examined was the ER model (evolutionary transition rate = 0.009, Table 1).

Sociality, vegetation cover, and subterranean mode of life exhibited strong and statistically significant phylogenetic signal (results in electronic supplementary material). The phylogenetic logistic regression analysis revealed that the effect of vegetation cover on sociality is significantly different from zero when the evolutionary relationships of species were included in the model. In particular, group-living across Hystriognathids was predicted significantly by lower values of vegetation cover (Table 2). In contrast, sociality across Hystriognathids was not predicted by whether species are subterranean or not (Table 2).

DISCUSSION

This study supported that the hypothesis that ancestor of Hystriognath rodents was social, and that subsequently, sociality was more frequently lost than re-gained. This evolutionary pattern is more consistent with the social ancestor hypothesis (SAH), where sociality generally evolved from a group-living ancestor into nonsocial living forms. An important implication of this scenario is that extant solitary living species are likely to represent a derived condition in these rodents. Similar patterns have been recorded in other animal taxa, including halictine bees (Weislo & Danforth 1997), communally roosting birds (Beauchamp 1999), and some mammalian taxa such as canids, pinnipeds, or phocids (Dalerum 2007). Intriguingly, recent evidence based on the preservation of multiple adult and sub-adult individuals in close proximity support the hypothesis of a social ancestor of

modern marsupial mammals (Ladevèze et al. 2011). Yet, these findings depart from patterns recorded across other mammalian taxa such as mustelids (Dalerum 2007).

We recorded group-living has been lost in association with the use of habitats with greater vegetation cover. The strength and direction of this historical association between sociality and habitat conditions in terms of vegetation cover was strongly supported by the phylogenetic statistical methods used. However, group-living and habitat in terms of vegetation cover exhibited strong phylogenetic signal, implying an effect of ancestor-descendent relationships throughout the *Hystriognath* lineage. Such ancestor-descendent effects might reflect stabilizing selection as suggested by rates of equal change found for sociality and habitat. However, these findings remain to some extent limited by the relatively low number of species with unknown sociality (i.e., most New World *hystriognath*s), and by the extent to which species has been studied and intraspecific variation examined. Both of these factors may affect character states of terminal taxa (Dalerum 2007).

We did not find an effect of subterranean life on sociality, implying that social and solitary species may have been predisposed to respond differently to habitats with similar vegetation cover because of their subterranean habits. Numerous reports show that some African bathyergids and many ctenomyids and octodontids feed on vegetation at the ground surface (e.g., Bush et al. 2000, Faulkes & Bennett 2000), a behavior that exposes these animals to aerial and terrestrial predators, implying vegetation cover may affect predation risk to these animals. However, the extent to which vegetation cover influences predation risk of subterranean and non subterranean rodents is not well understood.

Results from this study supported previous conclusions on a subset of Hystricognaths according to which the ancestor of guinea-pigs and allies was likely more social than extant species (Rowe & Honeycutt 2002). The social condition of guinea-pig ancestors likely allowed these animals to occupy relatively open habitats characterized by high predation risk, patchily distributed resources, or both (Rowe & Honeycutt 2002). Afterwards, derived species evolved less sociality and this may have been associated with the colonization of habitats with greater vegetation cover. We hypothesize that this evolutionary transition is the consequence of advantages of group-living that materialize when using open or mixed habitat, but that disappear when using habitats with high vegetation cover. In particular, habitats with relatively high vegetation cover may provide solitary animals with adequate shelters and escape routes against predators, or energy savings in terms that the construction or defense of large and complex burrow systems are less critical (Ebensperger & Blumstein 2006; Shultz & Finlayson 2010).

Group-living and cooperative care of offspring characterizes several species of African bathyergids, or mole-rats (Burda et al. 2000; Faulkes & Bennett 2013). Burda et al. (2000) suggested that this complex form of sociality would have originated in these subterranean rodents from an ancestor already exhibiting sociality and cooperative brood care. Thus, solitary living recorded in some species would be a derived trait, possibly as a consequence of constraints linked to a subterranean mode of life. Our findings that sociality was likely the ancestral condition to all hystricognaths and that solitary living represents a more derived condition provide support for the overall scenario suggested by Burda et al. (2000). Yet, we did not find an overall association between subterranean life and sociality across the clade. A recent study specifically aimed to test the importance of subterranean

life across all rodents showed this mode of life is more likely to evolve from ancestors exhibiting sociality (Smorkatcheva & Lukhtanov in press). Together, these findings are consistent with that sociality in African mole-rats represent an ancestral condition and that subterranean life is more likely a consequence rather than a cause of this trait (Burda et al. 2002).

Ancestral Hystricognath rodents are hypothesized to have arrived in the New World from Africa in the Eocene, circa 40-50 mya (Antoine et al. 2011; Ojeda et al. 2012). This arrival was followed by two main events of radiation, one during the Oligocene, and during the middle late Miocene boundary (Vucetich et al. 1999; Huchon & Douzery 2001; Opazo 2005). It has been hypothesized that behavior may drive or inhibit adaptive ecological change (Mayr 1960; Wcislo 1989; West-Eberhard 1989; Duckworth 2009). However, the roles of different behavioral traits, including social behavior, remain unclear (Duckworth 2009). Evolution of renal morphology and particular modes of life such as arboreality have been suggested to contribute to radiation of New World hystricognaths (Galewski et al. 2005; Diaz et al. 2006). The extent to which social behaviour preceded or promoted subsequent adaptive change in Hystricognath rodents needs to be determined.

To summarize, our study based on a large taxonomic sample and a probabilistic framework supported an association between evolutionary changes in sociality, changes in habitat use, and the history of ancestor-descendent relationships across Hystricognath rodents. Although the importance of vegetation cover in the habitat on the evolution of sociality has been examined previously (Veron et al. 2004; Ebensperger & Blumstein 2006), no previous studies reconstructed ancestral and derived states of this factor. Our

results linked both factors together, and suggest both ecological conditions (i.e. vegetation cover) and the phylogenetic relationships of these rodents may drive sociality.

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Table 1. Comparison of model fit to sociality and vegetation cover in the habitat of Hystricognath rodents. Bold typing is used to identify the best fitting model; k = Number of model parameters; Log-Lh = Logarithm of Likelihood; ER = Equal Rate Model; SYM= Symmetric Model; ARD = All Rate Model.

Sociality				Habitat			
Model	K	Log-Lh	AIC	Model	k	Log-Lh	AIC
ER	1	-41.28	84.57	ER	1	-61.40	124.80
SYM	-	-	-	SYM	3	-60.59	127.18
ARD	2	-40.61	85.22	ARD	6	-59.70	131.40

Table 2. Phylogenetic logistic regression parameter estimates for the effect of vegetation cover and subterranean mode of life on the evolution of the social behaviour in Hystricognath rodents. (a) Parameters of logistic regression and standard errors of the estimates were obtained using the generalized estimating equations (see Ives & Garland 2010). (b) Parametric bootstrapping was performed by simulating 2500 data sets to obtain confidence intervals. Parametric bootstrapping was also used to test the null that the regression coefficients equal 0 ($H_0: b_i = 0$, 2-tailed tests).

Parameters	Estimate ^a	Standard Error ^a	Bootstrap mean ^b	Bootstrap CI ^b	<i>p</i> -value
b0 (intercept)	1.475	0.880	-0.071	1.457; 3.702	0.067
b1 (Vegetation cover)	-0.824	0.425	-2.145	-0.999; -0.235	0.002
b2 (Subterranean life)	-1.877	0.904	-3.999	-1.493; 0.354	0.105

FIGURE LEGENDS

Fig. 1. Reconstruction of the ancestral state of the social behaviour in Hystricognath rodents. The squares next to tips of the phylogeny represent the presence (white) or absence (black) of social behaviour. The pie chart in the nodes of phylogeny show the proportional likelihood of each state estimated. The letter C refers to at calibration point using for the BLADJ function: C1 (61.3 Ma), C2 (45.5 Ma), C3 (41.7 Ma), C4 (38 Ma) (Huchon et al. 2007); C5 (34.1 Ma), C6 (30.6 Ma), C7 (7.5 Ma), C8 (32.7 Ma), C9 (19.0 Ma), C10 (26.8 Ma), C11 (25.3 Ma), C12 (19.1 Ma), C14 (9 Ma), 15 (18.8 Ma) (Upham & Patterson 2012); C13 (9.22 Ma) (Parada et al. 2011); and C16 (4.84 Ma) (Loss & Leite 2011).

Fig. 2. Reconstruction of the ancestral state of the habitat in Hystricognath rodents. White = open; gray = mixed; and black = closed habitat. The squares next to tips of the phylogeny represent the habitat in which they living. The pie chart in the nodes of phylogeny show the proportional likelihood of each state estimated. The letter C refers to at calibration point using for the BLADJ function: C1 (61.3 Ma), C2 (45.5 Ma), C3 (41.7 Ma), C4 (38 Ma) (Huchon et al. 2007); C5 (34.1 Ma), C6 (30.6 Ma), C7 (7.5 Ma), C8 (32.7 Ma), C9 (19.0 Ma), C10 (26.8 Ma), C11 (25.3 Ma), C12 (19.1 Ma), C14 (9 Ma), 15 (18.8 Ma) (Upham & Patterson 2012); C13 (9.22 Ma) (Parada et al. 2011); and C16 (4.84 Ma) (Loss & Leite 2011).

Figure 1

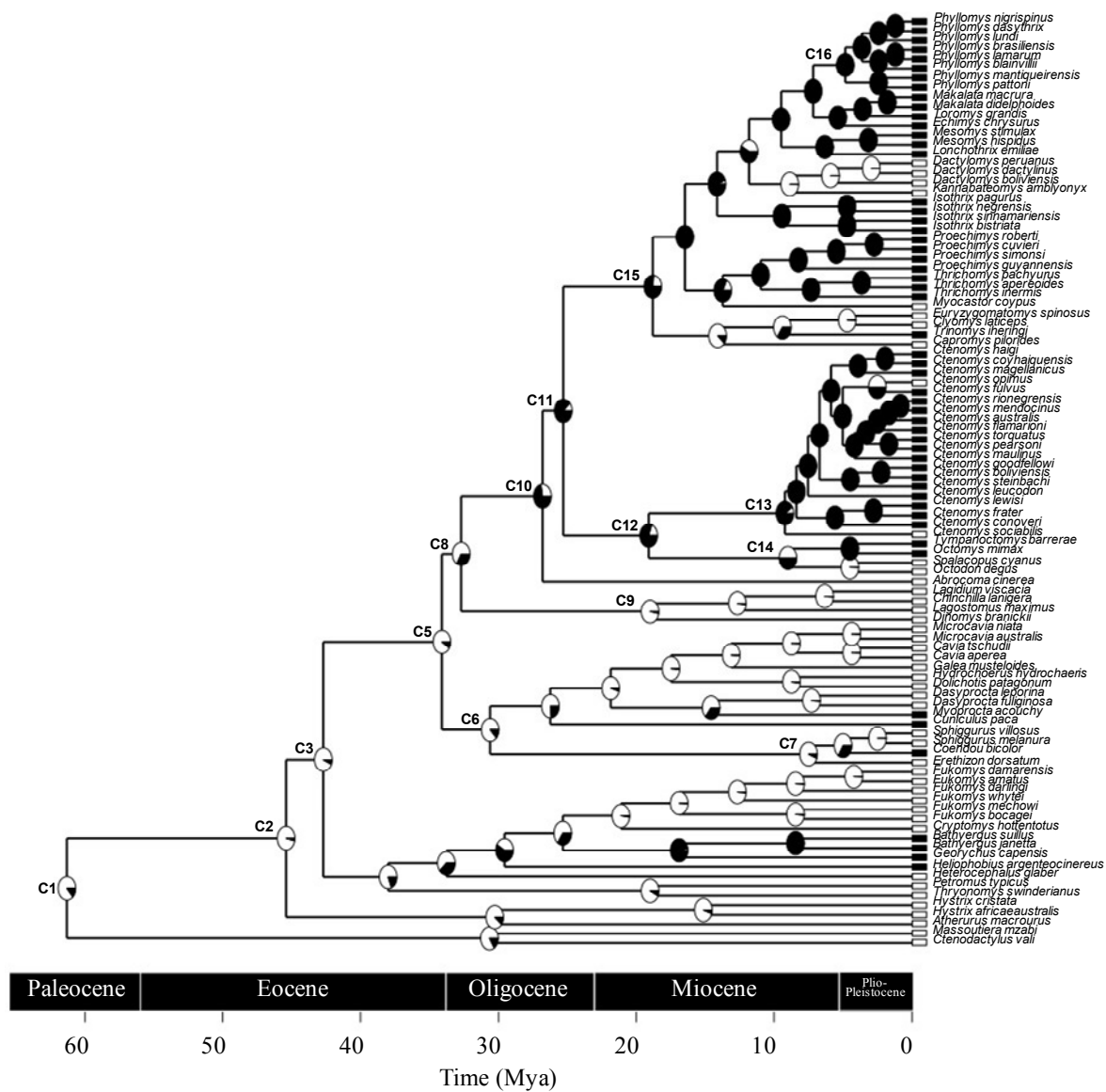
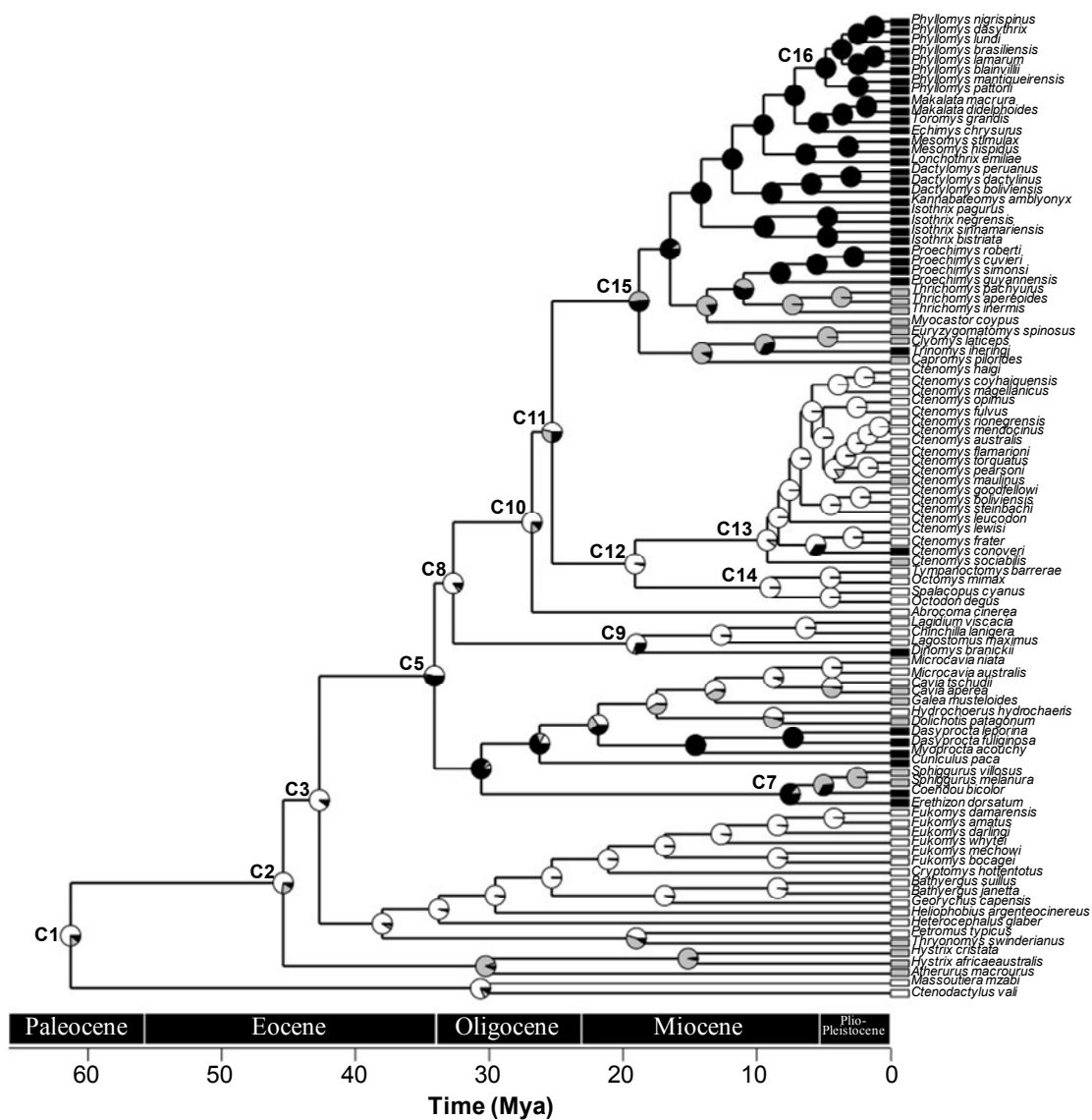


Figure 2



APPENDIX I

SUPPLEMENTARY MATERIAL FOR SOBRERO ET AL., PHYLOGENY MODULATES THE EFFECTS OF ECOLOGICAL CONDITIONS ON SOCIALITY ACROSS HYSTRICOGNATH RODENTS.

Species	SOCIALITY	Sources
<i>Ctenodactylus vali</i>	social	Novak 1999; Nutt 2005; Nutt 2007
<i>Massoutiera mzabi</i>	social	Novak 1999; Nutt 2005; Nutt 2007
<i>Atherurus macrourus</i>	social	Novak 1999
<i>Hystrix africaeaustralis</i>	social	Niall & van Aarde 1996; Novak 1999; Barthelmess 2006
<i>Hystrix cristata</i>	social	Santini 1980; Novak 1999; F.M. Angelici, pers. comm.
<i>Thryonomys swinderianus</i>	social	Novak 1999
<i>Petromus typicus</i>	social	Nutt 2007
<i>Heterocephalus glaber</i>	social	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Faulkes et al. 2004; Lacey & Ebensperger 2007; Lacey & Sherman, 2007; Sichilima et al. 2008
<i>Heliophobius argenteocinereus</i>	no social	Novak 1999; Faulkes et al. 2004; Weisbecker & Schmid, 2007; Sichilima et al. 2008
<i>Georychus capensis</i>	no social	Novak 1999; Jarvis & Sherman 2002; Lacey et al. 2000; Faulkes et al. 2004; Romañach 2005; Bennett et al. 2006; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Sichilima et al. 2008
<i>Bathyergus janetta</i>	no social	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Faulkes et al. 2004; Romañach 2005; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Sichilima et al. 2008
<i>Bathyergus suillus</i>	no social	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Faulkes et al. 2004; Romañach 2005; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Sichilima et al. 2008
<i>Cryptomys hottentotus</i>	social	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Faulkes et al. 2004; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Sichilima et al., 2008; C.G. Faulkes, pers. comm.
<i>Fukomys bocagei</i>	social	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Lacey & Ebensperger 2007; C.G. Faulkes, pers. comm.
<i>Fukomys mechowii</i>	social	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Lacey & Ebensperger 2007; Lacey & Sherman 2007; Sichilima et al. 2008; C.G. Faulkes, pers. comm.

<i>Fukomys whytei</i>	social	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Burda et al. 2005; Sichilima et al. 2008; Lacey & Ebensperger 2007; C.G. Faulkes, pers. comm.
<i>Fukomys darlingi</i>	social	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Lacey & Ebensperger 2007; Sichilima et al. 2008; C.G. Faulkes, pers. comm.
<i>Fukomys amatus</i>	social	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Lacey & Ebensperger 2007; Sichilima et al. 2008; C.G. Faulkes, pers. comm.
<i>Fukomys damarensis</i>	social	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Faulkes et al. 2004; Lacey & Ebensperger 2007; Lacey & Sherman 2007; Sichilima et al. 2008; C.G. Faulkes, pers. comm.
<i>Erethizon dorsatum</i>	social	Struthers 1928; Novak 1999; Nutt 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009
<i>Coendou bicolor</i>	no social	Mares & Ojeda 1982; Roberts et al. 1985; Emmons 1997; Novak 1999; Barquez et al. 2006; Lessa et al. 2008; Morgan 2009
<i>Sphiggurus melanura</i>	social	Novak 1999; Morgan 2009
<i>Sphiggurus villosus</i>	social	Novak 1999; Morgan 2009
<i>Cuniculus paca</i>	no social	Mares & Ojeda, 1982; Pérez 1992; Novak 1999; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Dubost et al. 2005; Ebensperger & Blumstein 2006; Barquez et al. 2006; Weisbecker & Schmid 2007
<i>Myoprocta acouchy</i>	no social	Mares & Ojeda 1982; Emmons 1997; Novak 1999; Ebensperger & Cofré 2001; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007
<i>Dasyprocta fuliginosa</i>	social	Emmons 1997; Novak 1999; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Ebensperger & Blumstein 2006; Morgan 2009
<i>Dasyprocta leporina</i>	social	Emmons 1997; Novak 1999; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Dubost et al. 2005; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009
<i>Dolichotis patagonum</i>	social	Mares & Ojeda 1982; Novak 1999; Campos et al. 2001; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Barquez et al. 2006; Ebensperger & Blumstein 2006; Macdonald et al. 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009; Ojeda & Tabeni 2009
<i>Hydrochoerus hydrochaeris</i>	social	Mares & Ojeda 1982; Mones & Ojasti 1986; Emmons 1997; Novak 1999; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Ebensperger & Blumstein 2006; Macdonald et al. 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009
<i>Galea musteloides</i>	social	Mares & Ojeda 1982; Novak 1999; Pacheco 2002; Rowe & Honeycutt 2002; Trillmich et al. 2004; Barquez et al. 2006; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007; Morgan 2009; Ojeda & Tabeni 2009

<i>Cavia aperea</i>	social	Mares & Ojeda 1982; Novak 1999; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Honeycutt et al. 2003; Asher et al. 2004; Trillmich et al. 2004; Barquez et al. 2006; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007; Asher et al. 2008; Morgan 2009
<i>Cavia tschudii</i>	social	Novak 1999; Rowe & Honeycutt 2002; Barquez et al. 2006; Nutt 2007
<i>Microcavia australis</i>	social	Novak 1999; Ebensperger & Cofré 2001; Tognelli et al. 2001; Barquez et al. 2006; Ebensperger & Blumstein 2006; Morgan 2009; Taraborelli & Moreno 2009
<i>Microcavia niata</i>	social	Mares & Ojeda 1982; Novak 1999; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Ebensperger & Blumstein 2006
<i>Dinomys branickii</i>	social	Mares & Ojeda 1982; White & Alberico 1992; Emmons 1997; Novak 1999; Ebensperger & Cofré 2001; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007
<i>Lagostomus maximus</i>	social	Novak 1999; Ebensperger & Cofré 2001; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007; Morgan 2009; Ojeda & Tabeni 2009
<i>Chinchilla lanigera</i>	social	Novak 1999; Ebensperger & Cofré 2001; Ebensperger & Blumstein 2006; Nutt 2007; Weisbecker & Schmid 2007; Morgan 2009
<i>Lagidium viscacia</i>	social	Novak 1999; Ebensperger & Cofré 2001; Barquez et al. 2006; Ebensperger & Blumstein 2006; Nutt 2007; Weisbecker & Schmid 2007; Morgan 2009
<i>Abrocoma cinerea</i>	social	Mares & Ojeda 1982; Novak 1999; Honeycutt et al. 2003; Barquez et al. 2006; Nutt 2007
<i>Octodon degus</i>	social	Mares & Ojeda 1982; Novak 1999; Ebensperger & Cofré 2001; Honeycutt et al. 2003; Ebensperger et al. 2004; Ebensperger & Blumstein 2006; Cofre et al. 2007; Gallardo et al. 2007; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009; Vassallo & Echeverría 2009
<i>Spalacopus cyanus</i>	social	Mares & Ojeda 1982; Novak 1999; Lacey et al. 2000; Honeycutt et al. 2003; Cofre et al. 2007; Lacey & Ebensperger 2007; Lacey & Sherman 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009; Vassallo & Echeverría 2009
<i>Octomys mimax</i>	no social	Mares & Ojeda 1982; Novak 1999; Ebensperger & Cofré 2001; Emmons et al. 2002; Barquez et al. 2006; Gallardo et al. 2007; Lacey & Ebensperger 2007; Ebensperger et al. 2008; Lessa et al. 2008; Ojeda & Tabeni 2009; Morgan 2009; Sobrero et al. 2010
<i>Tympanoctomys barrerae</i>	no social	Diaz et al. 2000; Ebensperger & Cofré 2001; Honeycutt et al. 2003; Barquez et al. 2006; Ebensperger & Blumstein 2006; Gallardo et al. 2007; Lacey & Ebensperger 2007; Lessa et al. 2008; Morgan 2009; Ojeda & Tabeni 2009
<i>Ctenomys sociabilis</i>	social	Lacey et al. 1987; Gardner & Duszynski 1990; Hadly et al. 2003; Lacey 2004; Lacey & Ebensperger 2007; Lacey & Sherman 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; Barquez et al. 2006; E. Lacey, pers. comm.

<i>Ctenomys conoveri</i>	no social	Mares & Ojeda 1982; Ruedas et al. 1983; Gardner & Duszynski 1990; Wilkins & Cunningham 1993; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys frater</i>	no social	Mares & Ojeda 1982; Gardner & Duszynski 1990; Wilkins & Cunningham 1993; Barquez et al. 2006; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys lewisi</i>	no social	Mares & Ojeda 1982; Gardner & Duszynski 1990; Wilkins & Cunningham 1993; Novak 1999; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys leucodon</i>	no social	Mares & Ojeda 1982; Gardner & Duszynski 1990; Wilkins & Cunningham 1993; Pacheco 2002; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys steinbachi</i>	no social	Gardner & Duszynski 1990; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys boliviensis</i>	no social	Mares & Ojeda 1982; Gardner & Duszynski 1990; Wilkins & Cunningham 1993; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys goodfellowi</i>	no social	Wilkins & Cunningham 1993; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys maulinus</i>	no social	Mares & Ojeda 1982; Lacey et al. 1987; Wilkins & Cunningham 1993; Hadly et al. 2003; Barquez et al. 2006; Cofre et al. 2007; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys pearsoni</i>	no social	Wilkins & Cunningham 1993; Barquez et al. 2006; Cofre et al. 2007; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys torquatus</i>	no social	Wilkins & Cunningham 1993; Barquez et al. 2006; Cofre et al. 2007; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys flamarioni</i>	no social	Wilkins & Cunningham 1993; Barquez et al. 2006; Cofre et al. 2007; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys australis</i>	no social	Mares & Ojeda 1982; Wilkins & Cunningham 1993; Lacey et al. 2000; Barquez et al. 2006; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys mendocinus</i>	no social	Mares & Ojeda 1982; Wilkins & Cunningham 1993; Lacey et al. 2000; Barquez et al. 2006; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Ojeda & Tabeni 2009; Vassallo & Echeverría 2009; Albanese et al. 2010; E. Lacey, pers. comm.
<i>Ctenomys rionegrensis</i>	no social	Wilkins & Cunningham 1993; Barquez et al. 2006; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys fulvus</i>	no social	Lacey & Ebensperger 2007; Weisbecker & Schmid, 2007; Mares & Ojeda, 1982; Lessa et al., 2008;

		Wilkins & Cunningham, 1993; Ojeda et al., 2000; Vassallo & Echeverría, 2009; E. Lacey, pers. comm.
<i>Ctenomys opimus</i>	social	Mares & Ojeda 1982; Ruedas et al. 1983; Wilkins & Cunningham 1993; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys magellanicus</i>	no social	Mares & Ojeda 1982; Wilkins & Cunningham 1993; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys coyhaiquensis</i>	no social	Wilkins & Cunningham 1993; Figueroa Rojas et al. 2001; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys haigi</i>	no social	Wilkins & Cunningham 1993; Hadly et al. 2003; Lacey & Ebensperger 2007; Weisbecker & Schmid, 2007; Lessa et al., 2008; Vassallo & Echeverría 2009; Barquez et al. 2006; E. Lacey, pers. comm.
<i>Capromys pilorides</i>	social	Mares & Ojeda 1982; Emmons 1997; Ebensperger & Cofré 2001; Tognelli et al. 2001; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007; C.G. Faulkes, pers. comm.
<i>Trinomys iheringi</i>	no social	Pessôa & dos Reis 1996; Emmons 1997; Novak 1999; Galewski et al. 2005; Ebensperger & Blumstein 2006; Freitas et al. 2008
<i>Clyomys laticeps</i>	social	Mares & Ojeda 1982; Novak 1999; Braggio & Bonvicino 2004; Galewski et al. 2005
<i>Euryzygomatomys spinosus</i>	social	Mares & Ojeda 1982; Novak 1999; Leite 2003; Galewski et al. 2005; Gonçalves et al. 2007; G.L. Gonçalves, pers. comm.
<i>Myocastor coypus</i>	social	Mares & Ojeda 1982; Honeycutt et al. 2003; Galewski et al. 2005; Weisbecker & Schmid 2007; Morgan 2009
<i>Thrichomys inermis</i>	no social	Braggio & Bonvicino 2004; Freitas et al. 2008
<i>Thrichomys apereoides</i>	no social	Mares & Ojeda 1982; Novak 1999; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007; Lessa et al. 2008; Freitas et al. 2008; Morgan 2009; Vassallo & Echeverría 2009
<i>Thrichomys pachyurus</i>	no social	Braggio & Bonvicino 2004; Freitas et al. 2008
<i>Proechimys guyannensis</i>	no social	Emmons 1997; Novak 1999; Galewski et al. 2005; Weisbecker & Schmid 2007
<i>Proechimys simonsi</i>	no social	Emmons 1997; Novak 1999; Galewski et al. 2005; Lessa et al. 2008
<i>Proechimys cuvieri</i>	no social	Emmons 1997; Galewski et al. 2005; Weisbecker & Schmid 2007; Freitas et al. 2008
<i>Proechimys roberti</i>	no social	Emmons 1997; Johnson et al. 2004; Galewski et al. 2005; Freitas et al. 2008
<i>Isothrix bistrata</i>	no social	Mares & Ojeda 1982; Galewski et al. 2005; Witmer & Lowney 2007; J.L. Patton, pers. comm.
<i>Isothrix sinnamariensis</i>	no social	Vié et al. 1996; Galewski et al. 2005; Patterson & Velazco 2008; J.L. Patton, pers. comm.
<i>Isothrix negrensis</i>	no social	Patterson & Velazco 2008; J.L. Patton, pers. comm.

<i>Isothrix pagurus</i>	no social	Emmons 1997; Galewski et al. 2005; Patterson & Velazco 2008; J.L. Patton, pers. comm.
<i>Kannabateomys amblyonyx</i>	social	Mares & Ojeda 1982; Emmons 1997; Novak 1999; Galewski et al. 2005; Románach 2005; Silva et al. 2008
<i>Dactylomys boliviensis</i>	social	Mares & Ojeda 1982; Novak 1999; Galewski et al. 2005; Lessa et al. 2008; J.L. Patton, pers. comm.
<i>Dactylomys dactylinus</i>	social	Mares & Ojeda 1982; Emmons 1997; Novak 1999; Galewski et al. 2005; Lessa et al. 2008; J.L. Patton, pers. comm.
<i>Dactylomys peruanus</i>	social	Novak 1999; Lessa et al. 2008; J.L. Patton, pers. comm.
<i>Lonchothrix emiliae</i>	no social	Emmons 1997; Novak 1999; Galewski et al. 2005; Patterson & Velazco 2008
<i>Mesomys hispidus</i>	no social	Emmons 1997; Novak 1999; Galewski et al. 2005
<i>Mesomys stimulax</i>	no social	Emmons 1997; Novak 1999
<i>Echimys chrysurus</i>	no social	Emmons 1997; Galewski et al. 2005; Weisbecker & Schmid 2007; J.L. Patton, pers. comm.
<i>Toromys grandis</i>	no social	Emmons 1997; Novak 1999; J.L. Patton, pers. comm.
<i>Makalata didelphoides</i>	no social	Mares & Ojeda 1982; Emmons 1997; Novak 1999; Galewski et al. 2005; J.L. Patton, pers. comm.
<i>Makalata macrura</i>	no social	Novak 1999; Galewski et al. 2005; J.L. Patton, pers. comm.
<i>Phyllomys pattoni</i>	no social	Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys mantiqueirensis</i>	no social	Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys blainvillii</i>	no social	Novak 1999; Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys lamarum</i>	no social	Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys brasiliensis</i>	no social	Novak 1999; Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys lundii</i>	no social	Novak 1999; Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys dasythrix</i>	no social	Novak 1999; Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys nigrispinus</i>	no social	Novak 1999; Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.

APPENDIX II

SUPPLEMENTARY MATERIAL FOR SOBRERO ET AL., PHYLOGENY MODULATES THE EFFECTS OF ECOLOGICAL CONDITIONS ON SOCIALITY ACROSS HYSTRICOGNATH RODENTS.

Species	HABITAT					
	Description	Rank	Values used in analyses	Subterranean life	Discrete	Sources
<i>Ctenodactylus vali</i>	Rocky areas	1-3	2	NO	Open	Novak 1999; Nutt 2005; Nutt 2007
<i>Massoutiera mzabi</i>	Rocky areas	1-3	2	NO	Open	Novak 1999; Nutt 2005; Nutt 2007
<i>Atherurus macrourus</i>	Rocky areas. Riparian areas. Forests areas	1-7	4	NO	Mixed	Novak 1999
<i>Hystrix africaeaustralis</i>	Sandy soils. Grasslands. Rocky areas. Open shrubland. Forests areas	1-7	4	NO	Mixed	Niall & van Aarde 1996; Novak 1999; Barthelmess 2006
<i>Hystrix cristata</i>	Sandy soils. Grasslands. Rocky areas. Open shrubland. Forests areas	1-7	4	NO	Mixed	Santini 1980; Novak 1999; F.M. Angelici, pers. comm.

<i>Thryonomys swinderianus</i>	Riparian areas.	3-4	3,5	NO	Mixed	Novak 1999
<i>Petromus typicus</i>	Rocky areas	1-3	2	NO	Open	Nutt 2007
<i>Heterocephalus glaber</i>	Sandy soils	1	1	YES	Open	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Faulkes et al. 2004; Lacey & Ebensperger 2007; Lacey & Sherman, 2007; Sichilima et al. 2008
<i>Heliophobius argenteocinereus</i>	Sandy soils	1	1	YES	Open	Novak 1999; Faulkes et al. 2004; Weisbecker & Schmid, 2007; Sichilima et al. 2008
<i>Georychus capensis</i>	Sandy soils	1	1	YES	Open	Novak 1999; Jarvis & Sherman 2002; Lacey et al. 2000; Faulkes et al. 2004; Romañach 2005; Bennett et al. 2006; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Sichilima et al. 2008
<i>Bathyergus janetta</i>	Sandy soils	1	1	YES	Open	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Faulkes et al. 2004; Romañach 2005; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Sichilima et al. 2008
<i>Bathyergus suillus</i>	Sandy soils	1	1	YES	Open	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Faulkes et al. 2004; Romañach 2005; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Sichilima et al. 2008
<i>Cryptomys hottentotus</i>	Sandy soils	1	1	YES	Open	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Faulkes et al. 2004; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Sichilima et al., 2008; C.G. Faulkes, pers. comm.
<i>Fukomys bocagei</i>	Sandy soils	1	1	YES	Open	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Lacey & Ebensperger 2007; C.G. Faulkes, pers. comm.
<i>Fukomys mehowi</i>	Sandy soils	1	1	YES	Open	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Lacey & Ebensperger 2007; Lacey & Sherman 2007; Sichilima et al. 2008; C.G. Faulkes, pers. comm.
<i>Fukomys whytei</i>	Sandy soils	1	1	YES	Open	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Burda et al. 2005; Sichilima et al. 2008; Lacey & Ebensperger 2007; C.G. Faulkes, pers. comm.
<i>Fukomys darlingi</i>	Sandy soils	1	1	YES	Open	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Lacey & Ebensperger 2007; Sichilima et al. 2008; C.G. Faulkes, pers. comm.
<i>Fukomys amatus</i>	Sandy soils	1	1	YES	Open	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Lacey & Ebensperger 2007; Sichilima et al. 2008; C.G. Faulkes, pers.

						comm.
<i>Fukomys damarensis</i>	Sandy soils	1	1	YES	Open	Novak 1999; Lacey et al. 2000; Jarvis & Sherman 2002; Faulkes et al. 2004; Lacey & Ebensperger 2007; Lacey & Sherman 2007; Sichilima et al. 2008; C.G. Faulkes, pers. comm.
<i>Erethizon dorsatum</i>	Forest areas	7	7	NO	Closed	Struthers 1928; Novak 1999; Nutt 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009
<i>Coendou bicolor</i>	Canebrakes. Forests areas	3-7	5	NO	Closed	Mares & Ojeda 1982; Roberts et al. 1985; Emmons 1997; Novak 1999; Barquez et al. 2006; Lessa et al. 2008; Morgan 2009
<i>Sphiggurus melanura</i>	Rocky areas. Forests areas	1-7	4	NO	Mixed	Novak 1999; Morgan 2009
<i>Sphiggurus villosus</i>	Rocky areas. Forests areas	1-7	4	NO	Mixed	Novak 1999; Morgan 2009
<i>Cuniculus paca</i>	Open and dense forests	6-7	6,5	NO	Closed	Mares & Ojeda, 1982; Pérez 1992; Novak 1999; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Dubost et al. 2005; Ebensperger & Blumstein 2006; Barquez et al. 2006; Weisbecker & Schmid 2007
<i>Myoprocta acouchy</i>	Forests areas	7	7	NO	Closed	Mares & Ojeda 1982; Emmons 1997; Novak 1999; Ebensperger & Cofré 2001; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007
<i>Dasyprocta fuliginosa</i>	Forests areas	7	7	NO	Closed	Emmons 1997; Novak 1999; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Ebensperger & Blumstein 2006; Morgan 2009
<i>Dasyprocta leporina</i>	Riparian areas. Forests areas	6	6	NO	Closed	Emmons 1997; Novak 1999; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Dubost et al. 2005; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009
<i>Dolichotis patagonum</i>	Grasslands and shrublands	3-4	3,5	NO	Mixed	Mares & Ojeda 1982; Novak 1999; Campos et al. 2001; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Barquez et al. 2006; Ebensperger & Blumstein 2006; Macdonald et al. 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009;

						Ojeda & Tabeni 2009
<i>Hydrochoerus hydrochaeris</i>	Open savanna	2-3	2,5	NO	Open	Mares & Ojeda 1982; Mones & Ojasti 1986; Emmons 1997; Novak 1999; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Ebensperger & Blumstein 2006; Macdonald et al. 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009
<i>Galea musteloides</i>	Grasslands and shrublands	3-4	3,5	NO	Mixed	Mares & Ojeda 1982; Novak 1999; Pacheco 2002; Rowe & Honeycutt 2002; Trillmich et al. 2004; Barquez et al. 2006; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007; Morgan 2009; Ojeda & Tabeni 2009
<i>Cavia aperea</i>	Wet savannas and grasslands.	3-4	3,5	NO	Mixed	Mares & Ojeda 1982; Novak 1999; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Honeycutt et al. 2003; Asher et al. 2004; Trillmich et al. 2004; Barquez et al. 2006; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007; Asher et al. 2008; Morgan 2009
<i>Cavia tschudii</i>	Grasslands. Rocky areas. Open shrubland	1-3	2	NO	Open	Novak 1999; Rowe & Honeycutt 2002; Barquez et al. 2006; Nutt 2007
<i>Microcavia australis</i>	Arid puna and scrub	2-3	2,5	NO	Open	Novak 1999; Ebensperger & Cofré 2001; Tognelli et al. 2001; Barquez et al. 2006; Ebensperger & Blumstein 2006; Morgan 2009; Taraborelli & Moreno 2009
<i>Microcavia niata</i>	Altiplano boags	1-2	1,5	NO	Open	Mares & Ojeda 1982; Novak 1999; Ebensperger & Cofré 2001; Rowe & Honeycutt 2002; Ebensperger & Blumstein 2006
<i>Dinomys branickii</i>	Forests areas	7	7	NO	Closed	Mares & Ojeda 1982; White & Alberico 1992; Emmons 1997; Novak 1999; Ebensperger & Cofré 2001; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007
<i>Lagostomus maximus</i>	Open steppe and thorn scrub	2-3	2,5	NO	Open	Novak 1999; Ebensperger & Cofré 2001; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007; Morgan 2009; Ojeda & Tabeni 2009
<i>Chinchilla lanigera</i>	Desert scrub	2-3	2,5	NO	Open	Novak 1999; Ebensperger & Cofré 2001; Ebensperger & Blumstein 2006; Nutt 2007; Weisbecker & Schmid 2007; Morgan 2009
<i>Lagidium viscacia</i>	Rock outcrops,	1-3	2	NO	Open	Novak 1999; Ebensperger & Cofré 2001; Barquez et al. 2006; Ebensperger & Blumstein 2006; Nutt 2007; Weisbecker &

	arid scrub, open steppe					Schmid 2007; Morgan 2009
<i>Abrocoma cinerea</i>	Rocky areas. Open shrubland	1-3	2	NO	Open	Mares & Ojeda 1982; Novak 1999; Honeycutt et al. 2003; Barquez et al. 2006; Nutt 2007
<i>Octodon degus</i>	Rocky areas. Open shrubland.	2-3	2,5	NO	Open	Mares & Ojeda 1982; Novak 1999; Ebensperger & Cofré 2001; Honeycutt et al. 2003; Ebensperger et al. 2004; Ebensperger & Blumstein 2006; Cofre et al. 2007; Gallardo et al. 2007; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009; Vassallo & Echeverría 2009
<i>Spalacopus cyanus</i>	Sandy soils. Rocky areas. Grasslands. Open shrubland	1-3	2	YES	Open	Mares & Ojeda 1982; Novak 1999; Lacey et al. 2000; Honeycutt et al. 2003; Cofre et al. 2007; Lacey & Ebensperger 2007; Lacey & Sherman 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009; Vassallo & Echeverría 2009
<i>Octomys mimax</i>	Rocky areas. Open shrubland.	1-3	2	NO	Open	Mares & Ojeda 1982; Novak 1999; Ebensperger & Cofré 2001; Emmons et al. 2002; Barquez et al. 2006; Gallardo et al. 2007; Lacey & Ebensperger 2007; Ebensperger et al. 2008; Lessa et al. 2008; Ojeda & Tabeni 2009; Morgan 2009; Sobrero et al. 2010
<i>Tympanoctomys barrerae</i>	Sandy soils. Salt basins. Open shrubland	1-2	1,5	NO	Open	Diaz et al. 2000; Ebensperger & Cofré 2001; Honeycutt et al. 2003; Barquez et al. 2006; Ebensperger & Blumstein 2006; Gallardo et al. 2007; Lacey & Ebensperger 2007; Lessa et al. 2008; Morgan 2009; Ojeda & Tabeni 2009
<i>Ctenomys sociabilis</i>	Grasslands. Open shrubland. Swampy areas	1-6	3,5	YES	Mixed	Lacey et al. 1987; Gardner & Duszynski 1990; Hadly et al. 2003; Lacey 2004; Lacey & Ebensperger 2007; Lacey & Sherman 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; Barquez et al. 2006; E. Lacey, pers. comm.
<i>Ctenomys conoveri</i>	Dense shrubland	5-6	5,5	YES	Closed	Mares & Ojeda 1982; Ruedas et al. 1983; Gardner & Duszynski 1990; Wilkins & Cunningham 1993; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm
<i>Ctenomys frater</i>	Grasslands.	1-3	2	YES	Open	Mares & Ojeda 1982; Gardner & Duszynski 1990; Wilkins &

	Open shrubland.					Cunningham 1993; Barquez et al. 2006; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys lewisi</i>	Open shrubland. Riparian areas	1-4	2,5	YES	Open	Mares & Ojeda 1982; Gardner & Duszynski 1990; Wilkins & Cunningham 1993; Novak 1999; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys leucodon</i>	Open shrubland.	2-3	2,5	YES	Open	Mares & Ojeda 1982; Gardner & Duszynski 1990; Wilkins & Cunningham 1993; Pacheco 2002; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys steinbachi</i>	Grasslands. Open shrubland.	1-3	2	YES	Open	Gardner & Duszynski 1990; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys boliviensis</i>	Open shrubland.	2-3	2,5	YES	Open	Mares & Ojeda 1982; Gardner & Duszynski 1990; Wilkins & Cunningham 1993; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys goodfellowi</i>	Open shrubland.	2-3	2,5	YES	Open	Wilkins & Cunningham 1993; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys maulinus</i>	Grasslands. Forests areas	1-7	4	YES	Mixed	Mares & Ojeda 1982; Lacey et al. 1987; Wilkins & Cunningham 1993; Hadly et al. 2003; Barquez et al. 2006; Cofre et al. 2007; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys pearsoni</i>	Sandy soils. Grasslands.	1	1	YES	Open	Wilkins & Cunningham 1993; Barquez et al. 2006; Cofre et al. 2007; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys torquatus</i>	Grasslands. Open shrubland.	1-3	2	YES	Open	Wilkins & Cunningham 1993; Barquez et al. 2006; Cofre et al. 2007; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys flamarioni</i>	Sandy soils	1	1	YES	Open	Wilkins & Cunningham 1993; Barquez et al. 2006; Cofre et al. 2007; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers.

						comm.
<i>Ctenomys australis</i>	Sandy soils. Grasslands. Open shrubland.	1-3	2	YES	Open	Mares & Ojeda 1982; Wilkins & Cunningham 1993; Lacey et al. 2000; Barquez et al. 2006; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys mendocinus</i>	Grasslands. Open shrubland.	1-3	2	YES	Open	Mares & Ojeda 1982; Wilkins & Cunningham 1993; Lacey et al. 2000; Barquez et al. 2006; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Ojeda & Tabeni 2009; Vassallo & Echeverría 2009; Albanese et al. 2010; E. Lacey, pers. comm.
<i>Ctenomys rionegrensis</i>	Sandy soils. Grasslands.	1	1	YES	Open	Wilkins & Cunningham 1993; Barquez et al. 2006; Lacey & Ebensperger 2007; Weisbecker & Schmid 2007; Lessa et al. 2008; Morgan 2009; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys fulvus</i>	Sandy soils. Open shrubland.	1-3	2	YES	Open	Lacey & Ebensperger 2007; Weisbecker & Schmid, 2007; Mares & Ojeda, 1982; Lessa et al., 2008; Wilkins & Cunningham, 1993; Ojeda et al., 2000; Vassallo & Echeverría, 2009; E. Lacey, pers. comm.
<i>Ctenomys opimus</i>	Sandy soils. Open shrubland.	1-3	2	YES	Open	Mares & Ojeda 1982; Ruedas et al. 1983; Wilkins & Cunningham 1993; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys magellanicus</i>	Grasslands. Open shrubland.	1-3	2	YES	Open	Mares & Ojeda 1982; Wilkins & Cunningham 1993; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys coihaiquensis</i>	Sandy soils. Grasslands. Open shrubland	1-3	2	YES	Open	Wilkins & Cunningham 1993; Figueroa Rojas et al. 2001; Weisbecker & Schmid 2007; Lessa et al. 2008; Vassallo & Echeverría 2009; E. Lacey, pers. comm.
<i>Ctenomys haigi</i>	Grasslands. Open shrubland.	1-3	2	YES	Open	Wilkins & Cunningham 1993; Hadly et al. 2003; Lacey & Ebensperger 2007; Weisbecker & Schmid, 2007; Lessa et al., 2008; Vassallo & Echeverría 2009; Barquez et al. 2006; E. Lacey, pers. comm.
<i>Capromys pilorides</i>	Rocky areas.	1-7	4	NO	Mixed	Mares & Ojeda 1982; Emmons 1997; Ebensperger & Cofré 2001; Tognelli et al. 2001; Ebensperger & Blumstein 2006; Weisbecker

	Mangroves. Forests areas					& Schmid 2007; C.G. Faulkes, pers. comm.
<i>Trinomys iheringi</i>	Riparian areas. Forests areas	6-7	6,5	NO	Closed	Pessôa & dos Reis 1996; Emmons 1997; Novak 1999; Galewski et al. 2005; Ebensperger & Blumstein 2006; Freitas et al. 2008
<i>Clyomys laticeps</i>	Grasslands. Dense shrubland. Forests	1-7	4	NO	Mixed	Mares & Ojeda 1982; Novak 1999; Braggio & Bonvicino 2004; Galewski et al. 2005
<i>Euryzygomatomy s spinosus</i>	Grassland. Riparian areas. Dense shrubland.	1-6	3,5	NO	Mixed	Mares & Ojeda 1982; Novak 1999; Leite 2003; Galewski et al. 2005; Gonçalves et al. 2007; G.L. Gonçalves, pers. comm.
<i>Myocastor coypus</i>	Grassland. Open shrubland. Riparian areas. Forests areas	1-7	4	NO	Mixed	Mares & Ojeda 1982; Honeycutt et al. 2003; Galewski et al. 2005; Weisbecker & Schmid 2007; Morgan 2009
<i>Thrichomys inermis</i>	Rocky areas. Open shrubland. Dense shrubland.	1-6	3,5	NO	Mixed	Braggio & Bonvicino 2004; Freitas et al. 2008
<i>Thrichomys apereoides</i>	Sandy soils. Rocky areas. Swampy areas. Dense shrubland. Forest	3-4	3,5	NO	Mixed	Mares & Ojeda 1982; Novak 1999; Ebensperger & Blumstein 2006; Weisbecker & Schmid 2007; Lessa et al. 2008; Freitas et al. 2008; Morgan 2009; Vassallo & Echeverría 2009

<i>Thrichomys pachyurus</i>	Grasslands. Rocky areas. Swampy areas. Dense shrubland. Forest	1-7	4	NO	Mixed	Braggio & Bonvicino 2004; Freitas et al. 2008
<i>Proechimys guyannensis</i>	Riparian areas. Forests areas	3-7	5	NO	Closed	Emmons 1997; Novak 1999; Galewski et al. 2005; Weisbecker & Schmid 2007
<i>Proechimys simonsi</i>	Riparian areas. Forests areas	3-7	5	NO	Closed	Emmons 1997; Novak 1999; Galewski et al. 2005; Lessa et al. 2008
<i>Proechimys cuvieri</i>	Riparian areas. Forests areas	3-7	5	NO	Closed	Emmons 1997; Galewski et al. 2005; Weisbecker & Schmid 2007; Freitas et al. 2008
<i>Proechimys roberti</i>	Riparian areas. Forests areas	3-7	5	NO	Closed	Emmons 1997; Johnson et al. 2004; Galewski et al. 2005; Freitas et al. 2008
<i>Isothrix bistrata</i>	Riparian areas. Forests areas	3-7	5	NO	Closed	Mares & Ojeda 1982; Galewski et al. 2005; Witmer & Lowney 2007; J.L. Patton, pers. comm.
<i>Isothrix sinnamariensis</i>	Forests areas	7	7	NO	Closed	Vié et al. 1996; Galewski et al. 2005; Patterson & Velazco 2008; J.L. Patton, pers. comm.
<i>Isothrix negrensis</i>	Forests areas	7	7	NO	Closed	Patterson & Velazco 2008; J.L. Patton, pers. comm.
<i>Isothrix pagurus</i>	Forests areas	7	7	NO	Closed	Emmons 1997; Galewski et al. 2005; Patterson & Velazco 2008; J.L. Patton, pers. comm.
<i>Kannabateomys</i>	Riparian	3-7	5	NO	Closed	Mares & Ojeda 1982; Emmons 1997; Novak 1999; Galewski et

<i>amblyonyx</i>	areas. Canebrakes. Forests areas					al. 2005; Romañach 2005; Silva et al. 2008
<i>Dactylomys boliviensis</i>	Riparian areas. Canebrakes. Forests areas	3-7	5	NO	Closed	Mares & Ojeda 1982; Novak 1999; Galewski et al. 2005; Lessa et al. 2008; J.L. Patton, pers. comm.
<i>Dactylomys dactylinus</i>	Riparian areas. Canebrakes. Forests areas	3-7	5	NO	Closed	Mares & Ojeda 1982; Emmons 1997; Novak 1999; Galewski et al. 2005; Lessa et al. 2008; J.L. Patton, pers. comm.
<i>Dactylomys peruanus</i>	Riparian areas. Canebrakes. Forests areas	3-7	5	NO	Closed	Novak 1999; Lessa et al. 2008; J.L. Patton, pers. comm.
<i>Lonchothrix emiliae</i>	Forests areas	7	7	NO	Closed	Emmons 1997; Novak 1999; Galewski et al. 2005; Patterson & Velazco 2008
<i>Mesomys hispidus</i>	Forests areas	7	7	NO	Closed	Emmons 1997; Novak 1999; Galewski et al. 2005
<i>Mesomys stimulax</i>	Forests areas	7	7	NO	Closed	Emmons 1997; Novak 1999
<i>Echimys chrysurus</i>	Forests areas	7	7	NO	Closed	Emmons 1997; Galewski et al. 2005; Weisbecker & Schmid 2007; J.L. Patton, pers. comm.
<i>Toromys grandis</i>	Riparian areas. Forests areas	3-7	5	NO	Closed	Emmons 1997; Novak 1999; J.L. Patton, pers. comm.
<i>Makalata didelphoides</i>	Forests areas	7	7	NO	Closed	Mares & Ojeda 1982; Emmons 1997; Novak 1999; Galewski et al. 2005; J.L. Patton, pers. comm.
<i>Makalata</i>	Riparian	3-7	5	NO	Closed	Novak 1999; Galewski et al. 2005; J.L. Patton, pers. comm.

<i>macrura</i>	areas. Forests areas					
<i>Phyllomys pattoni</i>	Mangroves. Forests areas.	3-7	5	NO	Closed	Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys mantiqueirensis</i>	Forests areas	7	7	NO	Closed	Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys blainvillii</i>	Riparian areas. Dense shrubland. Forests areas	3-7	5	NO	Closed	Novak 1999; Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys lamarum</i>	Forests areas	7	7	NO	Closed	Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys brasiliensis</i>	Riparian areas. Dense shrubland. Forests areas	3-7	5	NO	Closed	Novak 1999; Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys lundii</i>	Forests areas	7	7	NO	Closed	Novak 1999; Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys dasythrix</i>	Riparian areas. Forests areas	3-7	5	NO	Closed	Novak 1999; Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.
<i>Phyllomys nigrispinus</i>	Riparian areas. Forests areas	3-7	5	NO	Closed	Novak 1999; Emmons et al. 2002; Leite 2003; Y. Leite, pers. comm.

APPENDIX III

SUPPLEMENTARY MATERIAL REFERENCES

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APPENDIX IV

DETECTING PHYLOGENETIC SIGNAL

(1) We used two methods to determine whether the resemblance between species in sociability, fossorial life style and the habitat type attributes dependent significantly on the phylogenetic relatedness of the species considered (i.e. phylogenetic signal). In first place to evaluate the magnitude of the phylogenetic signal for the binaries variables (i.e. sociability and fossorial life style) we determined the magnitude of the D statistic (Fritz & Purvis 2010) using the R package caper (Orme et al. 2012). Briefly, D varies typically between 0 and 1. A $D = 0$ indicates that a trait evolves on a phylogenetic tree following a Brownian model (strong phylogenetic signal), and $D = 1$ indicates that a trait evolves following a random model (no phylogenetic signal). Additionally, D can be negative, which means that a trait evolves more conserved than predicted by the Brownian model. To assess the significance of the D statistic, we conducted a simulation (1000 permutations) to test whether an estimated D was significantly different from the predictions of a random or a Brownian model of trait evolution.

	Traits	
	Sociability	Fossorial life style
Estimated D	-0.40036	-1.01072
<i>p</i> Random Model	<0.00001	<0.00001
<i>p</i> Brownian Model	0.927	0.9999

(2) Secondly, to assess the phylogenetic signal of habitat type we used another approach due that this variable is multistate. We used the Association index (AI) statics which explicitly takes into account the shape of the phylogeny by measuring the imbalance of internal phylogeny nodes (Wang et al. 2001; see Parker et al. 2008 for details), where low AI values represents strong phylogeny-trait association. A randomization approach was used to generate a null distribution (1000 simulations) for the AI statistic (Wang et al., 2001), evaluating of this way the statistical significance ($p = 0.05$) of AI. This analysis was carry out in BaTS (Bayesian Tip-association Significance testing) software (Parker et al. 2008).

Statistic	Observed mean	Null mean	Lower 95% CI (Null Model)	Upper 95% CI (Null Model)	p -value (BaTS null hypothesis test)
AI	1.203	7.130	5.8245	8.434	<0.0001

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CAPÍTULO II

EFFECTS OF HABITAT AND SOCIAL COMPLEXITY ON BRAIN SIZE AND DENTATE GYRUS MORPHOLOGY IN TWO OCTODONTID RODENTS

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ABSTRACT

Both physical conditions of habitat and social environment are known to influence the size and organization of dentate gyrus (DG), yet the relative importance of these factors remains unclear. This study was aimed to resolve this question in two species of Chilean endemic rodents. We studied *Octodon degus* at two natural populations (Rinconada and El Salitre) and one population of *O. lunatus* that faced contrasting habitat conditions and differed in the extent of sociality. We quantified habitat conditions in terms of plant cover and other habitat features likely to act as visual landmarks during movement in these animals. The extent of sociality was inferred from quantifying group size (based on nesting associations) and range area overlap. The brains and DG of male and female subjects with information on their habitat and social environments were examined. Habitat conditions in terms of vegetation, rock, and bare ground cover, aspects known to be relevant to spatial navigation, differed among populations. The greater shrub cover and the lower abundance of rocks in the habitat indicated spatial navigation based on distant and short-range visual cues is more challenging to *O. lunatus*. Female *O. lunatus* had larger brains than males, but not so in *O. degus*. Relative volume of DG was similar across sexes and populations. The right hemisphere of male and female *O. lunatus* had more cells than the left hemisphere, a DG directional asymmetry not found in *O. degus*. Group size was greater in *O. degus* from El Salitre. All together, degu population differences in brain size and DG cell number seemed more responsive to differences in physical conditions of habitat than to differences in social conditions. Within populations, large sized *O. lunatus* (but not *O. degus* from El Salitre) that ranged over larger areas and that were members of larger social groups had bigger brains. Large sized *O. lunatus* from Los Molles and *O. degus* from El Salitre that ranged

over larger areas and were members of larger social groups had more DG cells. Thus, within population associations are consistent with a joint influence of habitat and sociality on brain size in *O. lunatus*, and on DG cell number in both *O. lunatus* and *O. degus*.

Key words: habitat complexity, social brain, navigation, dentate gyrus, *Octodon*

INTRODUCTION

Environmental conditions are thought to be important selective factors of cognitive abilities and its associated neuroanatomical components in specific brain regions (Kempermann et al., 1997; Nilsson et al., 1999; van Praag et al. 2000; Roth II and Pravosudov, 2009). Two major components of the environment seem important. On the one hand, individuals need to manage and process spatial and temporal information on resource availability during spatial navigation (Mace et al., 1981; van Praag et al., 1999). Second, individuals need to keep track of individual relationships and be able to respond appropriately during social interactions (Dunbar, 1998).

Evidence indicates that same brain structures may be linked to both environmental components. In particular, the dentate gyrus (DG), an integral portion of the brain system known as the hippocampal formation (Amaral and Lavenex, 2007), seems associated with spatial navigation under varying habitat conditions and to species differences in sociality in birds and mammals (Krebs et al., 1989; Sherry et al., 1992; Gheusi et al., 2009; Roth II and Pravosudov, 2009). This structure seems necessary for mapping spatial relationships in physical and social environments and using such relationships for navigation (O'Keefe, 1991). Navigation capacity involves the ability of an organism to orient (choose a heading direction) and navigate (to orient and know their location relative to their destination), a process that involves the use of spatial memory (Holyoak, 2008). Thus, an individual's path of movement is influenced by its navigation capacity, depending on the spatial information available (Revilla and Wiegand, 2008). In particular, DG is essential for integrating environmental sensory cues into a geometric coordinate system, or integrative cognitive map (Jacobs, 2003). Several lines of evidence support an effect of habitat conditions on the

volume and cell number of DG. First, experimental enrichment of housing conditions in terms of stimulation of exploratory behavior with objects such as toys, tunnels, and running wheels contributes to enhance DG cell number in house mice, *Mus musculus* (van Praag et al., 1999). Similarly, adult rats (*Rattus norvegicus*) housed in larger boxes containing various toys, wooden blocks, climbing platforms, plastic tubes and small houses results in an increase in newly generated cells in the DG and enhancement of recognition memory (Bruehl-Jungman et al., 2005). Second, field studies on seasonal variation in DG of wild rodents have provided insights into the effect of habitat conditions. Non-breeding 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). Non-breeding male Richardson's ground squirrels (*Urocitellus richardsonii*) have 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 non-breeding season (Burger et al., 2013). Third, evidence based on phylogenetically controlled comparisons tends to be consistent with that habitat complexity (in terms of the number of diversity of physical elements faced during navigation) is associated with greater size of telencephalon known to be involved in these cognitive tasks such as the hippocampus (Safi and Dechmann, 2005; Pollen et al., 2007; Shumway, 2008). The implication is that habitat conditions have been important drivers of the size and organization of brain structures relevant to spatial and social cognition in vertebrates.

Evidence supporting an effect of social conditions on the structure and volume of DG come mostly from laboratory studies where animal subjects are exposed to varying social conditions (Fowler et al., 2002; Hoshaw et al., 2006; Gheusi et al., 2009). Thus,

postnatal social isolation decreases DG cell number in rats, yet subsequent social interactions can increase cell number attenuated by isolation (Lu et al., 2003). Experimental conditions allowing social interactions and the formation of male-male dominance relationships enhance neurogenesis in the DG of dominant male compared with subordinate male rats (Kozorovitskiy and Gould, 2004). Intriguingly, social interactions involved in the formation of dominance relationships over the access to experimentally enlarged housing conditions decreases the number of DG cells in adult tree shrews (Gould et al., 1997), implying that the nature of neurological effects of social environment may vary across species. The effect of social environment is further supported by studies relying on differences in social group composition. In socially monogamous prairie voles, the number of DG cells decreases in females exposed to periodic isolation from an adult male compared with females not exposed to such social stress (Fowler et al., 2002). In socially monogamous zebra finches (*Taeniopygia guttata*), adults kept in large heterosexual groups exhibit more new cells in three forebrain regions that are involved in vocal communication than birds kept singly or as pairs (Lipkind et al., 2002). However, Fox et al. (2010) failed to report differences between in the number of hippocampal cells associated with heterosexual groups in mountain chickadees (*Poecile gambeli*), again suggesting that species attributes may be important.

Taken together, laboratory studies on traditional animal models and comparative approaches, independently, have been able to demonstrate a connection between habitat and social complexity and changes in the volume of DG or structures associated to it. However, some of these studies have not being able to set apart the relative effects of social and physical environmental conditions. For instance, experimental enrichment of housing conditions to stimulate exploratory behavior (with objects) also enhanced social

interactions in some studies (e.g., van Praag et al., 1999; Bruel-Jungerman et al., 2005). Non experimental studies on wild species on the other hand, have been instrumental to highlight the meaning of habitat-neurological associations. However, the effect of seasonal variation in cognitive abilities on seasonal changes in the anatomy of DG are difficult to separate from the effects of changes in other life history (e.g., breeding activity), ecological (e.g., food abundance, predation risk), or social (e.g., group size) conditions.

On the other hand, it is possible that environmental conditions result in differential effects on brain structure. In particular, brain asymmetry (i.e., lateralization) involves structural and cognitive differences between left or right cerebral hemispheres, a condition reported in birds, frogs, mice, rats, and nonhuman primates (Vallortigara and Rogers 2005). More importantly, lateralization has been hypothesized to enhance capacity for information processing and cognition in several ecological contexts, including escape from predators and foraging (Rogers et al. 2013). Yet, the potential effects of spatial and social complexity on brain asymmetry remain virtually unknown.

Thus, we studied two phylogenetically related species of rodents that live in different habitats and exhibit different social systems as a way to quantify how habitat conditions and sociality influence the volume and cell number of DG. In particular, we studied two natural populations of *Octodon degus* and one population of *O. lunatus*, two species of rodents that face contrasting conditions of physical complexity and with potential differences in sociality. We predicted individuals from populations facing more challenging habitat and social conditions to exhibit larger DG volume and density of cells than individuals from populations and habitats demanding less navigation skills. To our knowledge, this constitutes the first study to examine simultaneously the effects of habitat and social conditions on the DG of free-ganging rodents.

Model species and hypothesis predictions

The habitat used by *O. degus* varies across populations. These rodents use relatively open savannas or open scrub environments in central Chile, but more closed scrub patches and ravines in northern populations (e.g., Quispe et al., 2009; Ebensperger et al., 2012). In contrast, the sister species *Octodon lunatus* (Gallardo and Kirsch, 2001; Honeycutt et al., 2003; Gallardo et al., 2007) is preferably associated to shrublands with an ocean influence and characterized by moist and more abundant vegetative cover than *O. degus* (Sobrero et al., in press). Laboratory studies indicate that spatial navigation in wild rodents is facilitated by distant visual cues or global landmarks (e.g., skyline), and by smaller or more detailed local landmarks (e.g., runways or trails, rocks, burrow openings) (Jacobs, 2003; Vlasak, 2006a,b). Global landmarks would provide reliable indicators of a goal's approximate location because they are observable from greater distances, stable, and unique (Biegler and Morris, 1996). Thus, the greater shrub cover that characterizes the habitat of *O. lunatus* may prevent these rodents from using global landmarks and make spatial navigation more challenging compared with the more open habitats used by *O. degus*. In contrast, habitats with greater abundance of runways and rocks may provide more frequent local landmarks and facilitate spatial navigation. Interestingly, *O. degus* make frequent use of runways or trails, but very little is known about how these habitat features act as landmarks or cues during their movements (Root-Bernstein, 2012).

Octodon degus is known to live in social groups (Ebensperger et al., 2004; Hayes et al., 2009) where females cooperate to excavate and maintain underground burrow systems (Ebensperger and Bozinovic, 2000), as well as to raise their litters communally (Ebensperger et al., 2002; 2004). These characteristics have been documented in at least

four populations of this species (Ebensperger et al., 2004; 2012, Jesseau, 2004; R.S., A.L. and L.A.E. unpublished data), implying a high frequency of social interactions and probably a need for cognitive skills underlying these interactions. Indeed, *O. degus* is able to distinguish individuals based on their genetic relatedness and familiarity (Jesseau et al., 2008; Villavicencio et al., 2009). The social behavior of *O. lunatus* is less well known, yet a recent study indicates these animals exhibit some sociality in terms of sharing their resting locations (Sobrero et al., in press).

Thus, if habitat conditions play a major role in influencing the volume and cell number of DG we predicted: (i) greater brain size and higher DG volume and cell number in degus from populations with higher vegetative cover. If greater sociality is associated with greater cognitive demands to keep track of individual relationships we predicted: (ii) greater DG volume and higher cell number in degus from more social populations. Finally, we tested the prediction that (iii) the factor with the strongest effect on brain size and DG morphology would be associated with asymmetrical DG volume and cell number.

MATERIALS AND METHODS

Study populations and degu trapping

We contrasted the volume and total number of DG cells of degus (*Octodon*) at three populations across north-central Chile: *O. degus* (El Salitre, 30°38'S, 71°35'W, altitude 275 m), *O. lunatus* (Los Molles, 32°13'S, 71°31'W, altitude 36 m), and *O. degus* (Rinconada, 33°23'S, 70°31'W, altitude 495 m). During 2010 and 2012, animals were captured using 14 x 14 x 40 cm Tomahawk traps (model 201, Tomahawk Live Trap Company, Hazelhurst, Wisconsin). Based on previous studies (e.g., Ebensperger et al.,

2004; 2012), we placed traps at burrows 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, reproductive condition and each animal was marked with an ear tags (Monel 1005-1, National Band and Tag Co., Newport, Kentucky), and adult-sized individuals were fitted with a radio-collar weighing 7–9 g (RI-2D, Holohil Systems Limited, Carp, Ontario, Canada; SOM-2190A, and BR radio-collars, AVM Instrument Co., Colfax, California). At the end of our study all radio-collared animals were recaptured and radio-collars removed (e.g., Ebensperger et al., 2004; 2012).

Habitat characteristics

We first quantified habitat complexity directly in terms of the percentage of ground surface that included herbaceous cover, shrub cover, rocks, or and had no cover (Sobrero et al., in press). We used 5 randomly placed 50 m transects and determined shrub cover. We also inferred habitat complexity faced by degus from the spatial behaviour 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 in activity period. Patterns of spatial activity were monitored using triangulation (Kenward, 2001). 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. 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 (MCP) algorithm of the software Ranges VI (Kenward et

al., 2003). The range area of each radio-collared degu was determined from locations recorded through triangulation at the time these were active (*O. degus*, Ebensperger et al., 2004) or relatively more active (*O. lunatus*, Sobrero et al., in press). Data points from each individual were mapped using the 95% minimum convex polygon algorithm in Ranges VI (Kenward et al., 2003).

We used fluorescent pigments (Radiant Color Co., Richmond, California) to characterize degu trajectories. To do so, non radiocollared but adult sized degus were introduced into a plastic bag containing a unique powder colour pigment, gently shaken during a few seconds, and released back immediately to their original site of capture. Pigment collared animals were tracked during night time with a long-wave ultraviolet lamp (Ultra-Violet Products, Inc., San Gabriel, California). We mapped the length and shape of trajectories from pigment tracks left by subjects on the ground and vegetation (Lemen and Freeman, 1985). In particular, we recorded the length of each trajectory that was associated with patches with shrubs, herbs, rocks, or bare ground. Powder marking does not significantly alter animal behaviour (e.g., Ebensperger and Tamarin, 1997; Kalcounis-Ruppell et al., 2001).

Social environment

Differences in sociality across degu populations were quantified based on group size (a measure of social tolerance and potential social interactions), which in turn was based on nesting site associations, and total range area overlap (a measure of social cohesion during activity). 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., in press). 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, California) and a hand-held, 3-element Yagi antenna (AVM instrument Co., Colfax, California). Once located, the position of each animal was marked with flagging material coded for individual animals. Each radio-fix location was then referenced twice with a Garmin portable GPS (Garmin International Inc., Olathe, Kansas). The precision of GPS readings was always within 5 m. The determination of group 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 evenings that these individuals were captured at or tracked with telemetry to the same nesting area by the number of evenings that both individuals were trapped or tracked with telemetry on the same day (Ebensperger et al., 2004). 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 spatial overlap of range areas between individuals assigned to same resting locations. Pairwise estimates of the percent overlap between polygons for different females were also calculated using Ranges VI.

Thus, degus in larger social groups (i.e., sharing their nest sites with more conspecifics) and greater range overlap were regarded as more social.

Brain preparation

A sample of wild degu subjects from each population was transported to the laboratory and euthanized. All animals were anesthetized (0.5 ml Ketamina and 0.1 ml Xilacina) and

perfused transcardially with 0.1% saline followed by 4% buffered paraformaldehyde. Brains were postfixed, weighted (a measure of absolute brain size), and 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. Sections were collected in 0.1 M phosphate-buffered saline and every 3th section was mounted and stained with cresyl violet (Fluka: 61123, 0.2% solution, pH 4.3).

Histological measures

Measurements of DG volume and cell number were estimated on Nissl-stained sections with modern stereological methods using StereoInvestigator 8.0 (MBF Bioscience, 2008) and Nikon microscope (eclipse E400). DG was measured entirety. The atlas of Wright and Kern (1992) was used as a stereotaxic reference (Fig. 1a-c). All sampling schemes were optimized by authors (R.S., S.E.D.) and collaborators (S. Fernández, P. Universidad Católica de Chile; T. Roth II, Franklin and Marshall College) based on strategies in StereoInvestigator 8.0 (MBF Bioscience, 2008). The DG was measured on every 4th section. DG volume was estimated using the Cavalieri procedure (Gundersen and Jensen, 1987). DG volume was measured with a 200 µm grid. Cell counts were performed using an optical fractionator procedure (West et al., 1991) at 100x oil immersion lens (Fig.1d). A 200 µm sampling grid was used and all counting frames were 40 x 40 µm, with a dissector height of 5 µm and 2 µm guard zones. We calculated a coefficient of error (CE) to estimate precision with the nugget effect (West et al., 1991), as follows [mean CE (SE)]: El Salitre 0.03 (0.001), Rinconada 0.03 (0.002) and Los Molles 0.02 (0.001). Based on the procedures we estimated absolute and relative brain size, DG total and relative volume, and total number of cells of DG at right and left hemispheres.

Statistical analyses

We ran chi-square tests to examine the null hypothesis of equal habitat conditions in terms of vegetative cover among all populations, namely Los Molles (LM), El Salitre (ES) and Rinconada (RI). To further examine habitat conditions in terms of spatial behaviour of degus, we used Mann–Whitney U-tests to compare the percentage of degu trajectories that were recorded in patches with different types of cover (i.e., “shrub”, “bare ground”, “grass”, “rocky areas”) among populations. 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 versus females) were compared with ANCOVA, and where degu subjects’ body mass was entered as a covariate. 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 (GLZ). In particular, we assessed the main effect of population on total group size. Group size was fitted to a Poisson distribution with a Log link function. Population differences in total range area overlap were examined with General Linear Model (GLM). Total range area overlap values were arcsin squared root transformed to meet normality and homogeneity of variance assumptions.

We used GLM to examine how population and degu sex explained variation in brain size and DG cell number. In the case of brain size (g), body mass (g) was added to the effects of population and degu sex. Data transformation failed to obtain a normal distribution and variance homogeneity for relative DG volume, so we used a Kruskal–Wallis test with the Scheirer–Ray–Hare extension (SRHE Kruskal–Wallis, a non-

parametric equivalent of a two-way ANOVA) to determine the effects of population, sex, and a population by sex interactive effect on relative DG volume. We used repeated-measures ANOVA followed by Student-Newman-Keuls post-hoc tests to examine the effects of brain hemisphere (right versus left), population, sex, and factor interactions on DG cell number. DG cell number of right and left hemispheres were \log_{10} transformed to meet normality and homogeneity of variance assumptions.

Finally, we used GLM approach followed by best fit and supported model approach to examine how degu sex, body mass, group size, and size of range area within population predicted variation in brain size, relative volumes of DG, and right and left hemisphere DG cell number in

All data are reported as means \pm SE. Analyses were conducted with Statistica 9.0 (StatSoft Inc., 1984-2004), SigmaPlot (Systat Software Inc.), and the R software 3.0.1 (The R Foundation for Statistical Computing, 2013).

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-square = 124.4, $df = 6$; $P < 0.0001$; Fig.2). A subsequent subdivision of contingency tables that excluded RI, the population category contributing the most to Chi-square, revealed that habitat based on cover was different in all three populations (Chi-square, $Chi^2 = 16.66$, $df = 3$; $P = 0.0008$). 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 shrub, 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 in terms of vegetation cover observed was $LM > ES > RI$.

Habitat conditions in terms of the spatial behaviour of animals

Our examination of animal movements based on fluorescent marks recorded to *O. degus* from RI ($n = 8$) and ES ($n = 20$) indicated that degus from ES moved through a more diverse array of habitat patches compared with RI (Fig. 3). In particular, degu trajectories at ES included significantly more patches with shrubs ($32.59 \pm 4.25\%$; Mann-Whitney test, $Z = 3.87$, $P < 0.001$), more patches with grass cover ($23.30 \pm 3.65\%$; Mann-Whitney test, $Z = 3.68$, $P < 0.001$), and more patches with rocks ($7.69 \pm 5.01\%$; Mann-Whitney test, $Z = 3.87$, $P < 0.001$). In contrast, degu trajectories at RI intersected patches with more bare ground than trajectories at ES (100%; Mann-Whitney test, $Z = -3.87$, $P < 0.001$).

Information on range areas was available for 35 radiocollared *O. degus* ($n = 15$ from RI, $n = 30$ from ES) and 20 radiocollared *O. lunatus*. We recorded that 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 (g) 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 exhibited greater home ranges than females (ANCOVA, $F_{1,56} = 9.29$, $P = 0.004$).

Sociality

The number 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).

Population and species differences in brain size, DG volume and cell number

The brains of 11 adult-sized *O. degus* (6 females, 5 males) and 6 *O. lunatus* (3 females, 3 males) were examined during this study (Table 1). We found a statistically significant population by sex interaction ($F_{2,10} = 7.92$, $P = 0.009$), where that 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 relative volume of DG (g) indicated no effects of population ($H_{2,11} = 1.79$, $P = 0.212$), sex ($H_{1,11} = 3.10$, $P = 0.106$), or a population by sex interaction ($H_{2,11} = 1.44$, $P = 0.278$) (Fig. 8).

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 (Fig. 9).

Within population predictors of neurological variables

The examination of how body mass (g), range area (ha), and group size predicted brain size (g) of *O. lunatus* at LM revealed that the best fit and well supported model at LM was the full additive model (Table 2). Thus, large sized degus that ranged over larger areas and were members of larger social groups exhibited larger brains. In contrast, the best fit model at ES was not well supported, implying that brain size of *O. degus* at this population was not well predicted by any of these factors (Table 3).

Regarding DG cell number, the best fit and well supported model in both rodent species was the full additive model, meaning of *O. lunatus* at LM (Table 2) and *O. degus* at ES (Table 3) with more cells were larger, ranged over larger areas, and were members of larger social groups.

Lastly, the best fit model explaining DG cell number 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 DG cell number per hemisphere and any of 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 behaviour 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 degus intersected more patches with shrubs, herbs and rocks at ES compared with RI. Greater shrub cover at LM would make the use of distant visual cues or global landmarks more difficult to sight, implying that this habitat is more challenging for spatial navigation compared with RI. The relatively intermediate shrub cover and greater rock cover at ES would make the use of local and global landmarks less difficult to sight compared with LM. The complete absence of shrub cover at RI would make the use of global landmarks an easier task compared with LM and ES. In contrast to physical conditions of habitat, the social environment was more 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 DG morphology to different extents. In particular, female *O. lunatus* had larger brains than males from LM, but not so in *O. degus* from RI or ES. Male and females degus from all three populations exhibited similarly sized DGs in terms of relative volume. 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, 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 DGs of *O. degus* were associated with relatively more social environments in terms of group size at ES. Taken together, population differences in brain size and DG cell number seemed more responsive to differences in physical conditions of habitat than to differences in social conditions.

Effects of habitat conditions

Our population and species comparisons confirmed an association between physical conditions of habitat and DG cell number and brain size. Similarly, brain size and DG cell number in these octodontid rodents were associated to within population variation in habitat conditions. According to the hypothesis of ecological competence, enhanced cognitive ability allows individuals to solve problems involved in managing and processing of spatial information (Clutton-Brock and Harvey, 1980; Sherry et al. 1992). As predicted by Dukas (1998) and Shettleworth (1998), we confirmed an important influence of cognitive constraints derived from physical conditions of habitat on DG organization.

Habitat conditions are well known to influence navigation of scatter hording birds and small mammals, and where species from seasonal environments with unpredictable terrestrial or aerial cover in space and/or time, exhibit greater hippocampal volume and spatial recall accuracy (e.g., Clayton and Krebs, 1994; Jacobs, 1995, 1996; Barkley and Jacobs 1998; Gibss et al., 2007). We lack data about the 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. in press), implying that *O. lunatus* has the ability to search and locate resting sites despite habitat conditions that make the use of distant landmarks more difficult. Recently, *O. lunatus* has been shown to have a low number of retinal ganglion cells, and hence a relatively low visual acuity (Vega-Zuniga et al., in press), a condition matching the partially nocturnal activity of these rodents (Sobrero et al., in press). More importantly, a greater number of brain cells is linked to

greater computational capacity or cognitive ability in rodents and other mammals (Herculano-Houzel, 2006; Herculano-Houzel et al., 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. In addition, navigation based on detailed, short-term landmarks may be similarly limited as these rodents do not burrow or use runways actively (Sobrero et al. in press).

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). It has been shown that males can generate cognitive maps and navigate efficiently based on the use of global references only (Langley 1994). In contrast, females rely more on local references (Langley, 1994; Sandstrom et al., 1998; MacFadden et al., 2003). In addition, female *O. lunatus* studied included pregnant and lactating subjects. Then, it is possible that potential hormonal differences associated with these different breeding stages translated into variation in brain size or structures linked to the construction of cognitive maps for navigation. Previous studies revealed effects of high testosterone and estradiol levels on spatial learning during the breeding in rodents (Pawluski et al., 2009). Subsequent studies are needed to examine relations between seasonal changes in spatial behavior as linked to variation in hormone levels brain structure.

Our study also revealed directional asymmetry (or lateralization) at the population or species level (*sensu* Rogers et al., 2013), and where DG cell number of right hemisphere was consistently higher than DG cell number of left hemisphere of *O. lunatus*.

Lateralization 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 (Vallortigara et al., 2004; LaMendola and Bever, 1997; Maguire et al., 2006). Thus, lateralization in DG cell number of *O. lunatus* is further consistent with more challenging conditions of habitat in terms of spatial navigation.

Effects of sociality

Population differences in sociality were not associated with neurological differences in degus. Relatively more social degus from ES did not exhibit 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* exhibits non clearly diurnal activity, and is restricted to habitat with high shrub cover. In contrast to *O. degus* (Ebensperger et al., 2006; Ebensperger and Wallem, 2002), the use closed habitat conditions coupled to a partially nocturnal activity in *O. lunatus* would reduce opportunities to decrease predation risk through social vigilance or its potential benefit (Ebensperger, 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 same social groups were not simultaneously lactating (R.S., A.L. and L.A.E. unpublished data) further suggest reduced (if any) opportunities for communally rearing their offspring. All together,

these considerations suggest a more challenging environment in terms of sociality in *O. degus* compared with *O. lunatus*. Therefore, and pending additional studies to confirm a general absence of cooperative behavior in *O. lunatus*, we suggest that population differences in brain size and DG cell number are linked to cognitive demands from the physical environment and navigation rather than to social demands in these rodents.

Interestingly, neurological variation was associated with differences in group size within populations of *O. lunatus* and *O. degus*. Neurological variation in response to experimental manipulations or to seasonal changes of social conditions might reveal plasticity to social environment during subsequent studies on these species. Previous laboratory studies show that experimental changes to composition of social groups influence DG cell proliferation in adult female prairie voles (*Microtus ochrogaster*) (Fowler et al., 2002). A more direct influence of social interactions in leading to neurological plasticity in adults is supported by studies on rats, and where dominant males exhibit 35–50% higher levels of cell proliferation compared with subordinates (Hoshaw et al., 2006).

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Table 1. Number of animals and means (\pm SE) for body mass (g), brain size (g), volumes (mm^3) and cell estimates of the DG in *Octodon degus* and *O. lunatus* from north-central Chile. The left and right hemispheres were both measured for the DG volumes, and summed to produce the values given in this article.

Species	Population	Sex	<i>n</i>	Body mass (g)	Brain size (g)	DG volume (mm^3)	DG relative volume	DG cells $\times 10^6$
<i>O. degus</i>	El Salitre	F	4	203.35 \pm 24.34	2.16 \pm 0.06	5,266,692 \pm 1,143,879	0.004 \pm 0.0003	5.27 \pm 1.14
<i>O. degus</i>	El Salitre	M	3	201.23 \pm 4.57	2.39 \pm 0.10	4,425,377 \pm 704,245	0.004 \pm 0.0010	4.43 \pm 0.70
<i>O. degus</i>	Rinconada	F	2	209.50 \pm 3.50	2.08 \pm 0.03	3,018,540 \pm 858,730	0.004 \pm 0.0001	3.02 \pm 0.86
<i>O. degus</i>	Rinconada	M	2	185.90 \pm 23.10	2.43 \pm 0.05	4,195,632 \pm 1,325,458	0.002 \pm 0.0002	4.20 \pm 1.33
<i>O. lunatus</i>	Los Molles	F	3	156.87 \pm 17.23	3.17 \pm 0.07	6,121,097 \pm 1,045,170	0.003 \pm 0.0003	6.12 \pm 1.05
<i>O. lunatus</i>	Los Molles	M	3	165.20 \pm 18.71	2.68 \pm 0.19	7,529,599 \pm 2,249,798	0.003 \pm 0.0007	7.53 \pm 2.25

Table 2. AIC values associated with five possible best-fit models explaining differences in brain size (g), DG cell number, and DG cell number per brain hemisphere in *O. lunatus* at Los Molles. Predictors in these models were sex, body mass (g), range area (ha), and group size, and range area. Bold typing is used to indicate the best-fit and 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, delta AIC<2, Akaike weight approaching 0.90 or higher, and evidence ratios close to 1 (Burnham and Anderson, 2002; Symonds and Moussalli, 2011).

Response variable and model examined	Number of parameters	AIC	Delta AIC	Akaike weight	Evidence ratio
<i>Brain size</i>					
Sex + body mass + group size + range area	3	-7.15	0,00	0.99	1,00
Sex	1	4.16	11.31	0,00	285.72
Group size	1	5.57	12.72	0,00	578.25
Range area	1	6.22	13.37	0,00	800.31
Body mass	1	6.56	13.71	0,00	948.61
<i>DG total cell number</i>					
Sex + body mass + group size + range area	3	236.57	0,00	1,00	1,00
Sex	1	311.63	75.06	0,00	1,99E+16
Group size	1	311.83	75.26	0,00	2,20E+16
Range area	1	316.14	79.57	0,00	1,90E+17
Body mass	1	316.51	79.94	0,00	2,28E+17
<i>DG cell number per brain hemisphere</i>					
<i>Sex</i>	<i>1</i>	<i>-107.93</i>	<i>0,00</i>	<i>0.47</i>	<i>1,00</i>
Range size	1	-106.8	1.13	0.27	1.76
Group size	1	-106.57	1.36	0.24	1.97
Body mass	1	-100.93	7,00	0.01	33.12
Sex + body mass + group size + range area	3	-48.1	59.83	0,00	9,82E+12

Table 3. AIC values associated with five possible best-fit models explaining differences in brain size (g), DG cell number, and DG cell number per brain hemisphere in *O. degus* at El Salitre. Predictors in these models were sex, body mass (g), range area (ha), and group size, and range area. Bold typing is used to indicate the best-fit and 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, delta AIC<2, Akaike weight approaching 0.90 or higher, and evidence ratios close to 1 (Burnham and Anderson, 2002; Symonds and Moussalli, 2011).

Response variable and model examined	Number of parameters	AIC	Delta AIC	Akaike weight	Evidence ratio
<i>Brain size</i>					
<i>Sex</i>	<i>1</i>	<i>-1.90</i>	<i>0.00</i>	<i>0.42</i>	<i>1.00</i>
Sex + body mass + group size + range area	3	-1.52	0.38	0.35	1.21
Body mass	1	0.76	2.66	0.11	3.78
Range area	1	1.80	3.70	0.07	6.36
Group size	1	2.32	4.22	0.05	8.25
<i>DG total cell number</i>					
Sex + body mass + group size + range area	3	230.12	0.00	1.00	1.00
Sex	1	308.32	78.20	0.00	9.57E+16
Social group	1	309.46	79.34	0.00	1.69E+17
Range area	1	313.62	83.50	0.00	1.35E+18
Body mass	1	<i>315.18</i>	85.06	0.00	2.95E+18
<i>DG cell number per brain hemisphere</i>					
<i>Group size</i>	<i>1</i>	<i>-100.32</i>	<i>0.00</i>	<i>0.51</i>	<i>1.00</i>
Sex	1	-99.99	0.33	0.43	1.18
Range area	1	-95.31	5.01	0.04	12.24
Body mass	1	-93.17	7.15	0.01	35.69
Sex + body mass + group size + range area	3	<i>-48.10</i>	52.22	0.00	2.18E+11

FIGURE LEGENDS

Fig.1. Cell nuclei (a, black arrow) can be differentiated in nissl-stained sections and were used for cell quantification, independent of density and cell overlay (a, dashed white line countour). 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). The dashed red line (b) indicates the section of the DG where the photomicrographs (c-e) were taken.

Photomicrographs showing the location of dorsal DG (dashed white line countour) in nissl-stained coronal sections of octodontid rodents: *Octodon degus* at (c) Rinconada and (d) El Salitre; (e) *O. lunatus*. Scale bars, 20 μ m (a); 1 mm (c–e). All material has been processed in the laboratory using the same protocols.

Fig. 2. Habitat complexity across populations, distribution (%) of the cover type.

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

Fig. 4. Habitat complexity across populations. Mean (\pm SE) size of range relative to body mass in *O. degus*. Different letters on top of the bars are used to indicate population differences.

Fig. 5. Social complexity across populations. Mean (\pm SE) total group size. Different letters on top of the bars are used to indicate population differences.

Fig. 6. Social complexity across populations. Mean (\pm SE) total range area overlap size.

Fig. 7. Mean (\pm SE) female and male relative (to body mass) brain sizes across populations.

* $p < 0.001$.

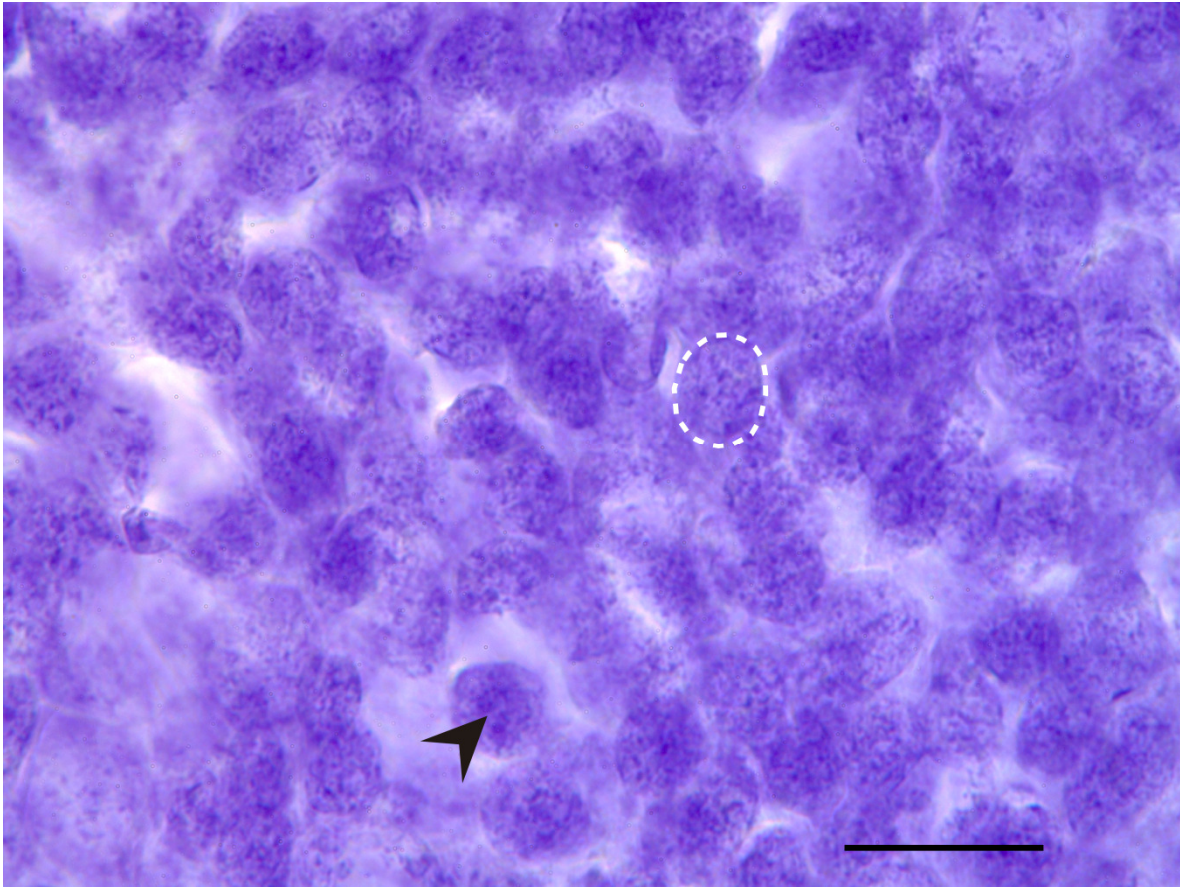
Fig. 8. Mean (\pm SE) relative (to brain size) DG volumes across populations.

Fig. 9. Mean (\pm SE) female (a) and male (b) DG total number of cells in each brain

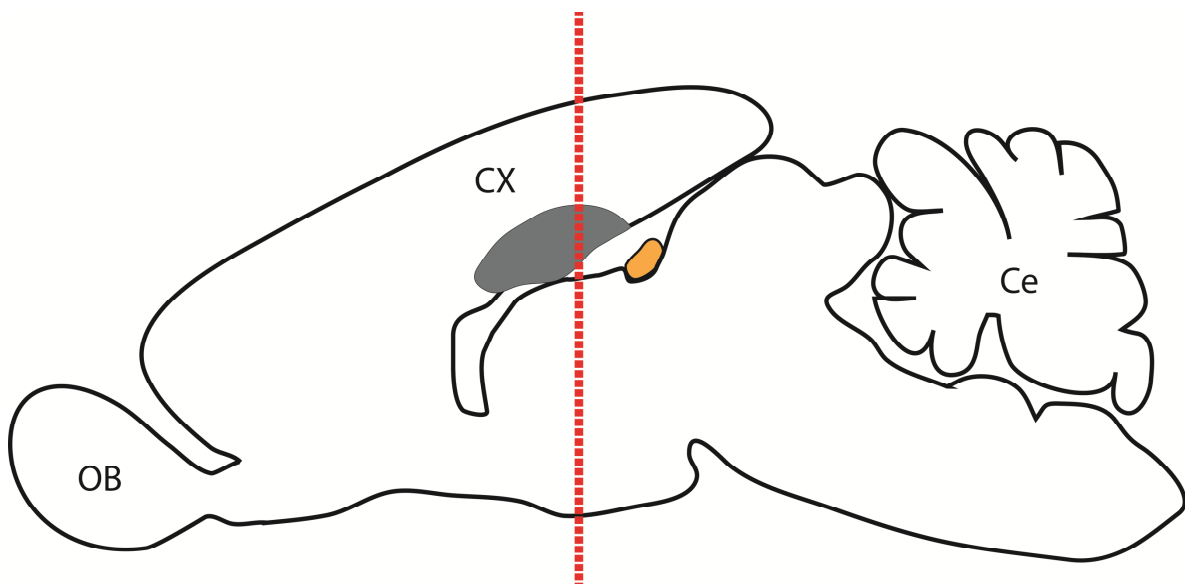
hemisphere, across populations. * $p < 0.001$.

Figure 1

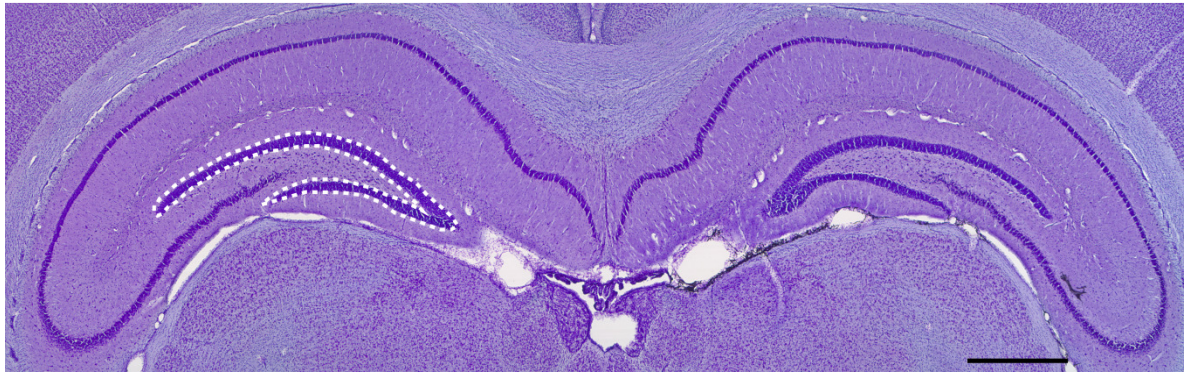
(A)



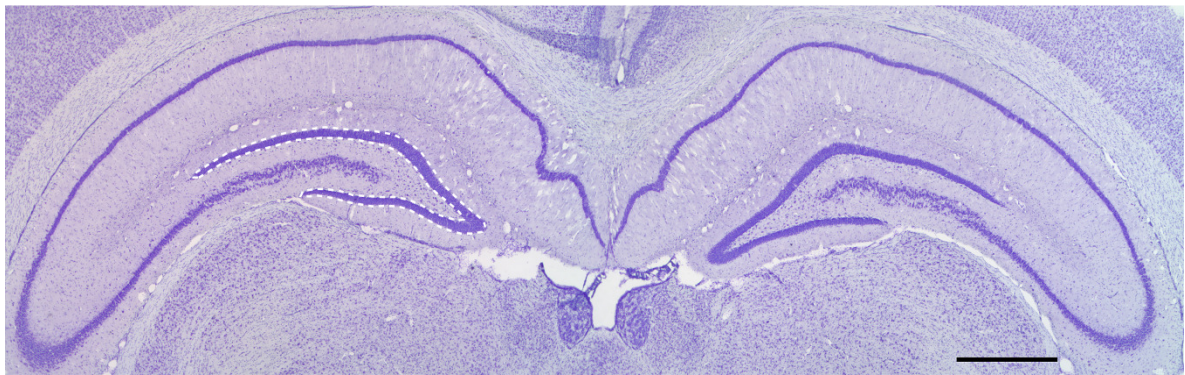
(B)



(C)



(D)



(E)

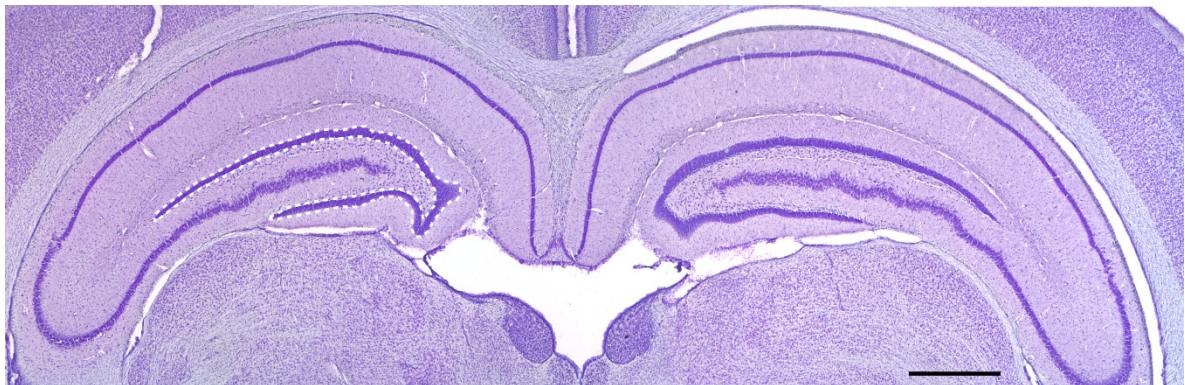


Figure 2

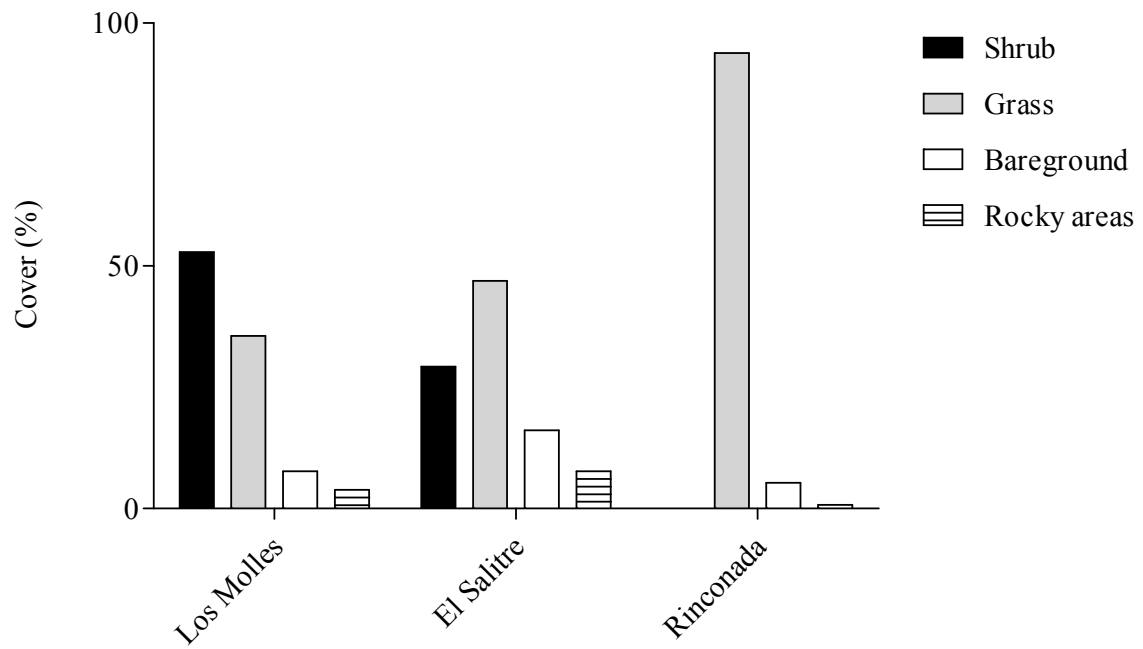


Figure 3

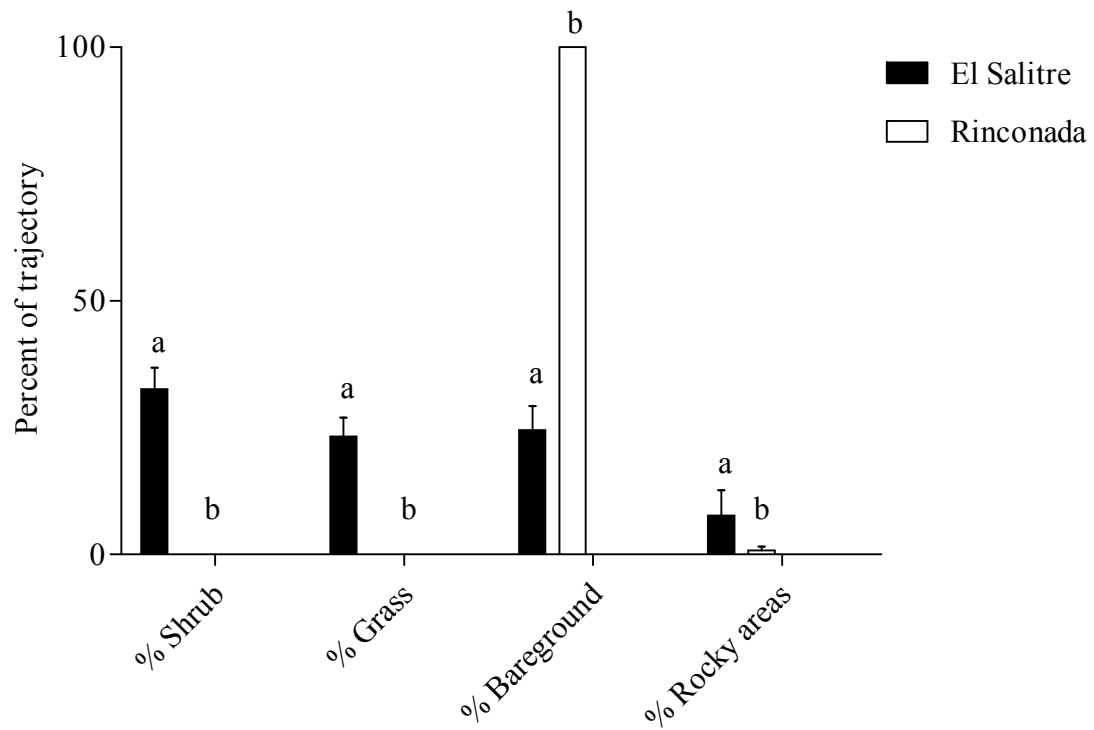


Figure 4

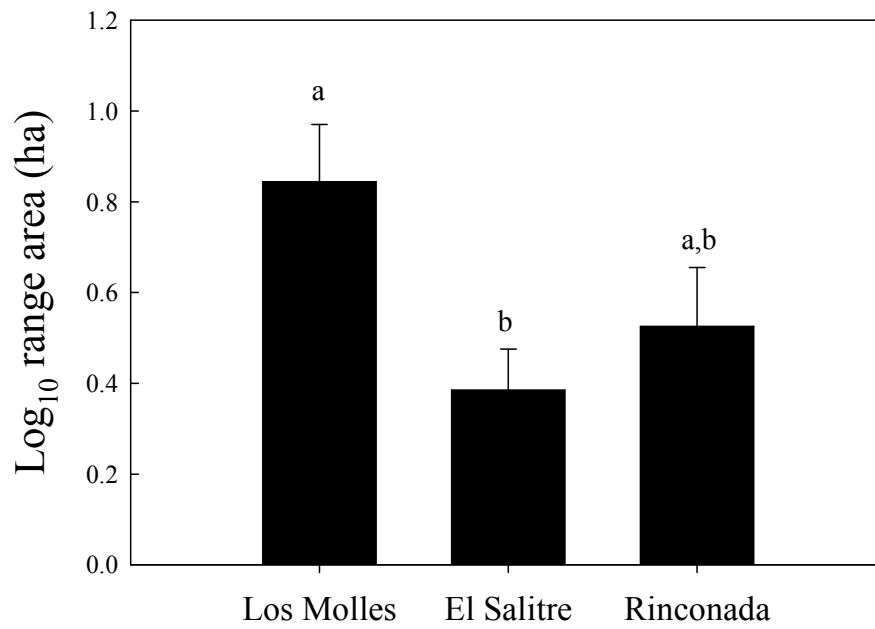


Figure 5

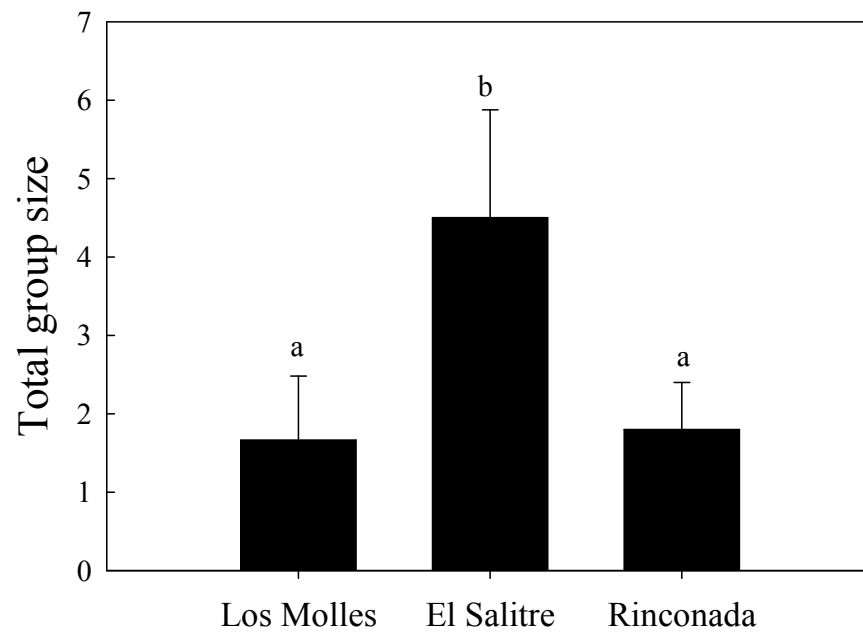


Figure 6

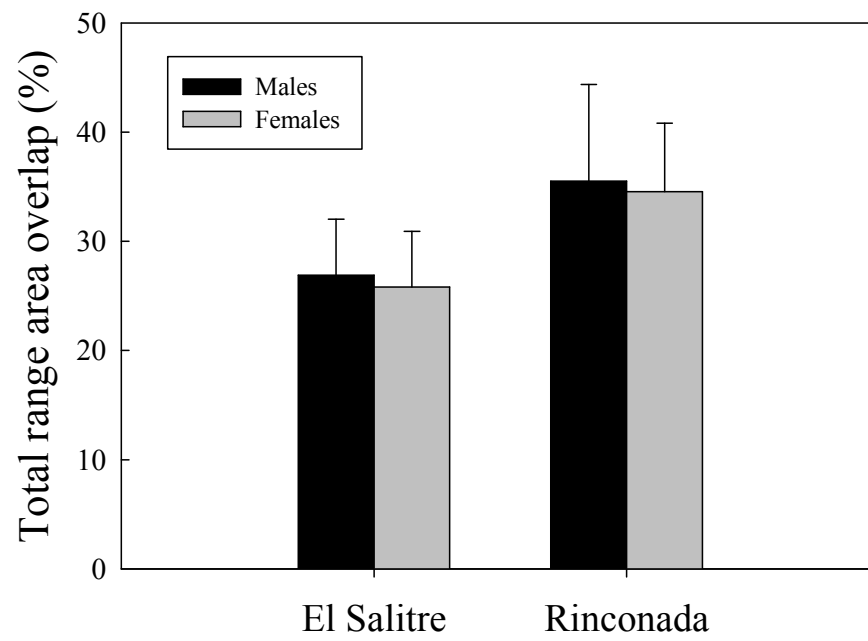


Figure 7

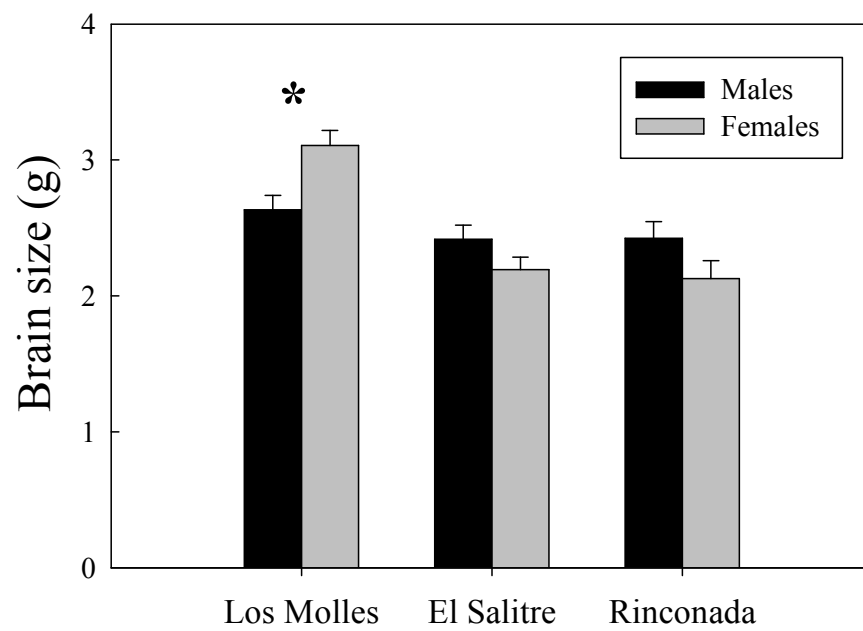


Figure 8

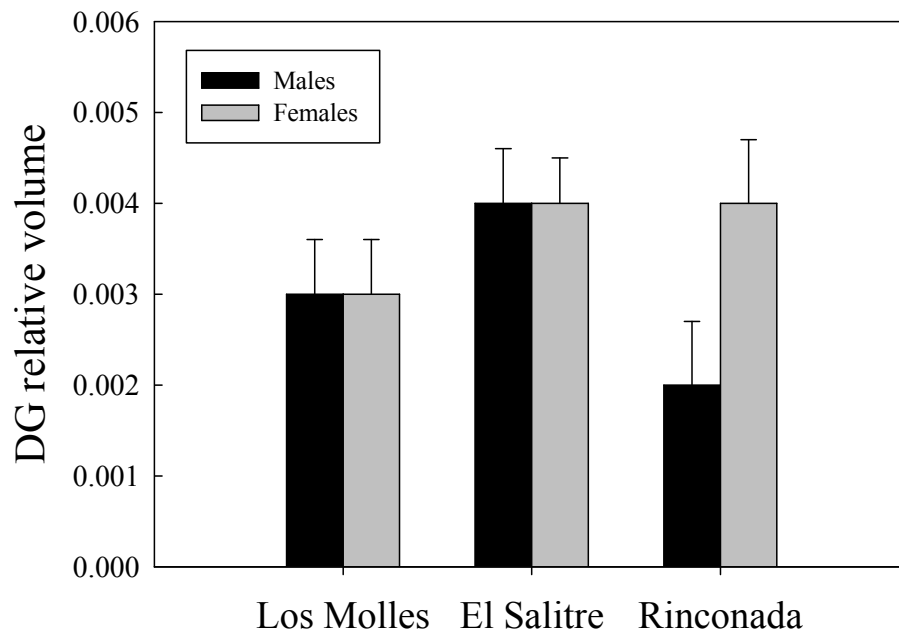
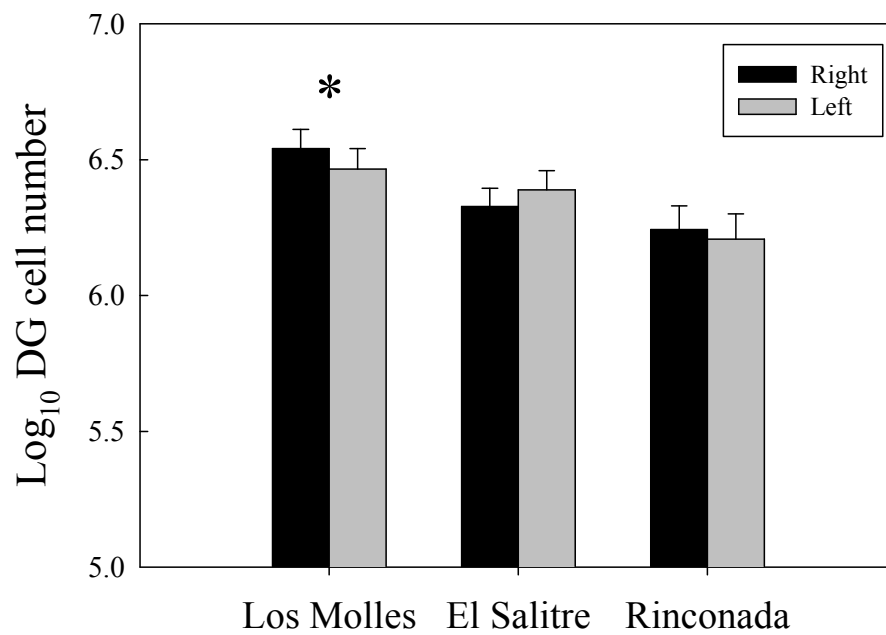


Figure 9



CAPÍTULO III

ACTIVITY, OVERLAP OF RANGE AREAS, AND SHARING OF RESTING LOCATIONS IN THE MOON-TOOTHED DEGU, *OCTODON LUNATUS*

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RH: BEHAVIOR AND ECOLOGY OF *OCTODON LUNATUS* (OCTODONTIDAE)

**ACTIVITY, OVERLAP OF RANGE AREAS, AND SHARING OF RESTING
LOCATIONS IN THE MOON-TOOTHED DEGU, *OCTODON LUNATUS***

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ABSTRACT

The evolution of sociality across octodontid rodents remains puzzling. While basal species are solitary living, the most derived octodontids studied so far are social, implying that sociality evolved recently from solitary living ancestors. However, the social behavior of some octodontids remains anecdotal. We aimed to provide the 1st systematic data on activity, space use, and social behavior of the moon-toothed degu (*Octodon lunatus*), a derived octodontid rodent. We used live trapping and radio-telemetry to monitor patterns of aboveground activity, aboveground range areas and overlap, and use of resting locations in a coastal population in central-north Chile. Activity of *O. lunatus*, was statistically similar during night and daytime, implying no clear diurnal or nocturnal activity. During daytime the animals used resting locations that were associated with high shrub cover and *Pouteria splendens*. Radio-collared males and females shared resting locations on multiple occasions. There was a non-significant trend on degus that used same resting locations to exhibit greater range overlap than degus using different resting locations. Associations based on resting locations revealed a total of 5 social groups. Taken together, these results indicate that adult *O. lunatus* exhibit some sociality, a finding consistent with a trend in which group-living is more frequent in the most derived compared with basal octodontids.

Key words: group-living, nesting site, *Octodon*, range area, range overlap, space use

INTRODUCTION

Most available data and theory developed to explain how sociality (or group living) evolved in rodents come from the study of a sample of taxonomic groups, typically from African mole-rats (Bathyergidae) and North American squirrels and marmots (Sciuridae) (Ebensperger 2001). Evolutionary trends in African bathyergids generally support sociality and cooperation during breeding are the consequence of ecological restrictions associated to foraging and dispersal (Faulkes and Bennett 2013). Sociality measures are associated with variation in mean abundance and variation of food resources across bathyergids (Faulkes et al. 1997). In contrast, life history may have played a greater role in ecological constraints among sciurids. In particular, sociality in sciurids seems associated with the time required by the offspring to reach sexual maturity and independence (Blumstein and Armitage 1998), implying that sociality in these rodents is driven by life history, species-specific level attributes. This potential difference in the importance of ecology and life history as social drivers of bathyergids and sciurids may, to some extent, reflect a focus on single hypothesis driven studies. Collectively however, these studies highlight how sociality may be driven by multiple factors (Ebensperger 2001). Clearly then, studies on the sociality of other rodent clades are needed before strong generalizations about these traits are made.

One potentially informative group of rodents to determine the relative roles of ecological conditions and intrinsic, species-specific attributes as drivers of social evolution are the caviomorph (New World Hystricognaths) rodents (e.g., guinea pigs, degus, viscacha rats—Ebensperger 1998; Tang-Martínez 2003). Intriguingly, both ecological conditions and species-specific traits seem implied in caviomorph social evolution (Lacher 1981; Rowe

and Honeycutt 2002; Trillmich et al. 2004). On the one hand, data available on 6 caviomorph species shows that group size covaries with differences in the abundance of food resources, flooded areas, and predation risk within species (Maher and Burger 2011), implying a role for ecological conditions. Across species, however, variation in group size seems associated with differences in body size, activity time, and the habit of digging burrows when phylogeny is taken into account. These associations support a role for predation risk (Ebensperger and Blumstein 2006), but also for species-specific attributes. This last alternative is further supported by comparative analyses showing a non significant association between habitat conditions and sociality (Rowe and Honeycutt 2002).

Within caviomorphs, the octodontids (Octodontidae) consist of 13 currently recognized species that are ecologically and taxonomically diverse (Woods and Kilpatrick 2005). While 3 species basal to the clade are solitary living, the most derived octodontids studied so far are social (Lacey and Ebensperger 2007), implying that sociality evolved relatively recently from solitary living ancestors. However, data for some octodontids, including derived species, remain anecdotal (Gallardo et al. 2007; Ojeda et al. 2013; Woods and Kilpatrick 2005). Four species comprise the *Octodon* derived clade, including *O. degus*, a social and communally rearing species (Ebensperger et al. 2004; Hayes et al. 2009). In contrast, the social behavior of the other 3 species, *O. lunatus*, *O. bridgesi*, and *O. pacificus*, remain virtually unknown (Woods and Kilpatrick 2005). The social behavior of *O. lunatus* remains critical to determine whether ecological conditions and species-specific attributes drove the evolution of group living in the octodontids. The scarce available evidence suggests that *O. lunatus* is restricted to rocky and highly dense coastal shrub lands (Contreras et al. 1987; Glanz and Meserve 1982), do not build underground burrows, and is

suspected to be nocturnally active (Ocampo-Garcés et al. 2003). These ecological features of *O. lunatus* contrast with those of *O. degus*, a species that forages in more open, unprotected areas during daytime, and builds underground burrows actively.

Habitat openness has been shown to predict sociality in relatively large terrestrial and marine mammals (Brashares et al. 2000; Caro et al. 2004; Gygax 2002). However, the use of unprotected habitat in terms of overhead cover is not strongly associated with social living across species of caviomorph rodents (Ebensperger and Blumstein 2006). Instead, social behavior in these rodents seems associated with diurnality, as well as the habit of actively digging burrows, with the exception of capybaras (Herrera et al. 2011). Thus, the extent to which *O. lunatus* exhibit sociality and remain active during daytime may shed light on the roles of habitat cover, aboveground activity, and burrow digging in shaping the evolution of group living across the octodontids. In particular, the apparently nocturnal activity, the absence of active burrow digging, and the use of highly dense (with considerable overhead cover) habitat predict a relatively low extent of sociality in *O. lunatus*. Based on these considerations, we predict that *O. lunatus* exhibits minimal range overlap and minimal sharing of their nest sites, 2 measures of sociality in rodents.

MATERIALS AND METHODS

Study population.—Observations were made near the coastal town of Los Molles, Chile (32°, 13'S, 71°, 31'W; Fig. 1) in 2010 and 2011. Los Molles is a semi-arid, Mediterranean location where annual rainfall does not exceed 300 mm and the ambient temperature averages 14.4°C (Luebert and Plischoff 2006; Muñoz et al. 1996). The habitat used by *O.*

lunatus is described as complex, with patches of shrubs, grasses, and rocks (Luebert and Plischoff 2006). During 2010 and 2011 we used 5 randomly placed 50 m transects and determined that shrub cover averaged $54 \pm 1.50\%$ and grass cover averaged $41 \pm 1.36\%$. The extent of bare ground was low and averaged $3 \pm 0.49\%$ and slab rock areas averaged $2 \pm 0.24\%$. The dominant plant species were *Pouteria splendens* (lúcumo), *Bahia ambrosioides* (manzanilla cimarrona), and *Lithraea caustica* (litre). The total area examined at Los Molles was nearly 15 ha and did not vary during the years of our study.

Initial trapping and radio-tagging.— Animal trapping and handling followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011). We first used 13 days in 2010 and 14 days in 2011 to trap and radio-collar adult sized (assessed from body mass) male and female *O. lunatus*. During the study period, the total number of traps used in 2010 and 2011 was 232 and 194, respectively. Animals were captured using 14 x 14 x 40 cm Tomahawk traps (model 201, Tomahawk Live Trap Company, Hazelhurst, Wisconsin). Based on previous information, we placed traps inside patches with high shrub cover and baited them with rolled oats, fruity cereals, and sunflower seeds. We shifted traps to adjacent areas (with similarly high cover of shrubs) if no animals were trapped during 3 consecutive days. Traps were opened near sunset (2000 h) and closed during early morning (0600 h). During each capture, we recorded sex, body mass, reproductive condition (e.g., whether females were perforate, pregnant, or lactating) and each animal was assigned a unique identification number. Upon 1st capture, each animal was marked with an ear tags (Monel 1005-1, National Band and Tag Co., Newport, Kentucky). We used 2 ear tags (with identical ID codes) because this minimized the probability that an animal would lose both

tags during the study period. In addition, all adult-sized individuals were fitted with a radio-collar weighing 7–9 g (RI-2D, Holohil Systems Limited, Carp, Ontario, Canada; SOM-2190A, and BR radio-collars, AVM Instrument Co., Colfax, California) with unique pulse frequencies. At the end of our study all radio-collared animals were recaptured and radio-collars removed.

Temporal pattern of activity.—Moon-toothed degus are reportedly nocturnal; however, this statement is based on laboratory observations of a single individual (Ocampo-Garcés et al. 2003). Thus, we recorded locations of all radio-collared animals for a total of 3 days and 4 nights in 2010 and 3 days and 4 nights in 2011. We recorded locations of collared degus each hour between 2100 to 0700 h (night time) and between 0700 to 2100 h (daytime). Sunrise occurred at approximately 0630 h whereas sunset occurred around 2030 h. Daily patterns of activity were monitored using triangulation (Kenward 2001). 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. Distance between antenna stations was about 120 m. To ensure independence of data points (Kenward 1987; Swihart and Slade 1985), intervals between fixes were approximately 1 h. Every hour, two 2 observer teams simultaneously recorded bearings of every radio-collared subject ($\pm 5^\circ$) using the same previously defined subject sequence. 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 (MCP) algorithm of the software Ranges VI (Kenward et al. 2003).

Determination of social groups.—The main criterion used to assign moon-toothed degus to social groups was the sharing of resting locations (i.e., putative nest places). Given that activity seemed lower during afternoon hours (see “Results,” Fig. 2), the sharing of resting locations was inferred from (1) trapping and (2) telemetry at this time. We defined resting location as areas of (4-9 m²) covered by shrub vegetation, with signs of *O. lunatus* (i.e., feces, dustbathing spots) and where radio-collared individuals were repeatedly found during daytime telemetry and daytime trapping. The total number of resting locations trapped per year at Los Molles was 8 in 2010 and 11 in 2011. These areas were trapped for 13 consecutive days during late November-early December 2010 and 14 consecutive days during November 2011. Ten traps (Tomahawk model 201, Tomahawk Live Trap Company, Hazelhurst, Wisconsin) were used per day at each resting location. Typically, traps were placed at locations with putative evidence of *O. lunatus*, including runways and dustbathing spots. Traps were baited with rolled oats, fruity cereals, and sunflower seeds, opened at sunset (2000 h), and closed in the early morning (0600 h).

During 1700-1800 h, all radio-collared animals were radio-tracked to their putative resting locations. 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, California) and a hand-held, 3-element Yagi antenna (AVM instrument Co., Colfax, California). On average, 2 observers required 40 min to track all radio-collared animals. Once located, the position of each animal was marked with flagging material coded for individual animals. Each radio-fix location was then referenced twice with a Garmin

portable GPS (Garmin International Inc., Olathe, Kansas). The precision of GPS readings was always within 5 m.

The determination of group composition required the compilation of a symmetric similarity matrix of pairwise association of the resting locations of all adult moon-toothed degu during trapping and telemetry (Whitehead 2008). We determined the association (overlap) between any 2 individuals by dividing the number of evenings that these individuals were captured at or tracked with telemetry to the same nesting area by the number of evenings that both individuals were trapped or tracked with telemetry on the same day (Ebensperger et al. 2004). 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 the same resting location were also socially cohesive when active, we monitored patterns of space use by radio-collared animals. In particular, we examined the prediction that spatial overlap of range areas between individuals assigned to the same resting location would be larger than overlap between individuals assigned to different resting locations. The range area of each radio-collared degu was determined from locations recorded through triangulation during night time. Data points from each individual were mapped using the 95% minimum convex polygon algorithm in Ranges VI (Kenward et al. 2003). Pairwise estimates of the percent overlap between polygons for different females were also calculated using Ranges VI.

Habitat and resting locations.—Resting locations (i.e., putative nest sites) were located always near the base of shrubs and under the cover of dominant shrubs. Thus, for every

resting location (recorded to have been used by at least 1 radio-collared degu), we established 2 transects in a crossed design and where each resting site corresponded to the intersection point; these transects had north-south and east-west orientations. We estimated the amount of overhead shrub cover and recorded the maximum vegetation height (in m), covering 1 m² of ground area. Soil penetrability as an index of soil hardness (Ebensperger et al. 2012) was recorded at 1, 3, and 5 m from the intersection point in the north-south and east-west cardinal directions. These measures were taken with the use of a hand-held soil compaction meter (Lang Penetrometer Inc., Gulf Shores, Alabama), and units transformed to kPa. These measures were averaged per resting location before further analysis.

Data analyses.—We calculated distance between successive scans as a measure of the moon-toothed degu above ground activity. For each animal we calculated distance traveled (in m) between each pair of successive scans. Same individuals were monitored throughout consecutive days and nights within each study year. As a result, locations recorded at 24 h intervals were not independent of one another. Consequently, and for statistical analyses, we divided the entire data collection period into 3 day and 4 night cycles, defined on the basis of sunrise and sunset at each study site. For the daytime portion of each activity cycle, we calculated the mean distance travelled for each radio-collared individual within each study year. We used a similar approach for the night time portion of the activity cycle. As a result, each radio-collared individual contributed 2 dependent data points to our analysis of activity. We used repeated-measures ANOVA to examine the effect of activity time (day versus night) on individual activity of females. Since activity of individuals from same resting locations may not be statistically independent, the effect of group ID was included in a preliminary analysis. Given that this analysis revealed a statistically significant effect

of group ID (not reported), we conducted a subsequent analysis in which activity of animals from the same resting locations was averaged. Only females were included in this analysis because only a single male was radio-collared during 2010. For comparative purposes, we also examined how male activity differed between day and night times during 2011.

We compared the mean size (in m²) of range areas and percent range overlap by male and female moon-toothed degus with Mann–Whitney *U* tests. We used the relationship between home range size and the number of observation days to determine sampling saturation (Quirici et al. 2010). Then we used Wilcoxon-matched pair tests to compare percent overlap in range areas of individuals assigned to same resting location associations and percent overlap that these individuals had with individuals assigned to different associations in 2011.

We used Spearman rank correlation analysis to examine potential associations between the number of degus that used each resting location and plant cover, maximum vegetation height, and soil hardness. We used the Dunn-Sidak correction to prevent inflation of type I statistical error during these explorative analyses.

All statistical analyses were calculated using Statistica 7.0 (StatSoft Inc. 1984-2004), Prism 5.0 (GraphPad Software Inc. 1992-2007), and Minitab 14.2 (Minitab Inc. 2005). Data are reported as mean \pm *SE*. All tests were 2-tailed, and unless stated differently, we considered a significant difference at $P < 0.05$.

RESULTS

Characteristics of radio-collared animals and trapping effort.—A total of 44 adults (27 females, 17 males) and 13 juveniles (7 females, 6 males) were captured or recaptured during this study. Overall, the number of captures/recaptures per degu averaged 3.23 ± 0.70 during 2010 and 5.48 ± 0.61 during 2011. Eleven of the females trapped were lactating, confirming breeding activity. A total of 20 adult-sized individuals (2010: 7 females 169 ± 18 g, and 1 male 128 g; 2011: 8 females 169 ± 8 g, and 4 males 187 ± 9) were fitted with radio-collars.

Temporal pattern of activity.—Above-ground activity recorded as distance moved between radio-scans was variable through time of day or night (Fig. 2). Although female activity recorded during night time ($\bar{X} \pm SE = 216 \pm 90$ m, range: 4–1,571 m, $n = 12$) was 1.6 times greater than activity recorded during daytime ($\bar{X} \pm SE = 136 \pm 67$ m, range: 4–1,786 m, $n = 12$), this difference was not statistically significant ($F_{1,1} = 1.69$, $P = 0.223$). Likewise, the difference in male activity between night time ($\bar{X} \pm SE = 374 \pm 200$ m, range: 20 – 1,521 m, $n = 4$) and daytime ($\bar{X} \pm SE = 209 \pm 122$ m, range: 12–888 m, $n = 4$) recorded in 2011 was not statistically significant ($F_{3,3} = 3.01$, $P = 0.410$).

Resting locations and social groups.—We monitored 7 females and 1 male, and 8 females and 4 males during 2010 and 2011, respectively. A total of 24 radio-telemetry scan sessions (2010: 10 sessions; 2011: 14 sessions) were completed during daylight hours and used to assign radio-tagged subjects to resting locations. Daytime trapping of resting locations and daytime telemetry revealed that animals used from 1 to 3 different resting locations ($\bar{X} \pm$

$SE = 1.8 \pm 0.2$; number of the used nests = 13), namely locations where an animal was found repeatedly during 2 or more scans.

During 2010 we recorded 2 females using the same resting place during the day on only 2 occasions. In contrast, during 2011 we recorded 45 occasions in which animals shared resting locations. Of these, 27 observations involved male-female pairs, 12 were female-female pairs, 1 involved 2 male-2 female associations, 4 involved 1 male-2 female associations, and 1 involved 1 male-3 female associations. Provided that resting location associations represent truly social groups, we identified 1 social group in 2010 and 4 groups in 2011. Social groups ranged from 2 to 4 adults throughout the study. Groups contained 1–3 females and 1–2 males.

Range areas and overlap.—During 2010 and 2011, male range areas ($237,360 \pm 158,780 \text{ m}^2$, $n = 5$) were 2.4 times larger than female range areas ($100,833 \pm 47,203 \text{ m}^2$, $n = 15$), though this difference was not statistically significant (Mann–Whitney U test, $U = 23.00$, $P = 0.223$, Fig. 3). When only radio-collared females were considered, the size of 95% MCPs did not differ between years (2010: $85,743 \pm 36,909 \text{ m}^2$, $n = 7$; 2011: $114,038 \pm 90,546 \text{ m}^2$, $n = 8$; Mann–Whitney U test, $U = 22.00$, $P = 0.536$). Sampling saturation was recorded upon 3 days of observation in 2010 and 2011. These findings suggested that range areas recorded during the 2 years of study were appropriate estimates of the true *O. lunatus* range areas.

Range overlap among males with any other radio-collared subject ($20.68 \pm 14.02\%$) was similar to that recorded in the females ($14.69 \pm 6.84\%$; Mann–Whitney U test, $U =$

5382, $P = 0.085$). During 2011, a marginally significant difference (Wilcoxon-matched pairs test, $Z = 1.82$, $P = 0.068$, Fig. 4) indicated that overlap between range areas of degus assigned to the same resting locations ($61.9 \pm 7.3\%$) tended to be greater than overlap between range areas of degus assigned to different resting locations (22.5 ± 1.2 , $n = 4$ social groups).

Characterization of resting locations.—A total of 13 resting locations (putative nests) were identified during 2010 and 2011. Plant cover across all resting locations averaged $98.5 \pm 1.0\%$, $n = 13$). Maximum shrub height averaged 3.5 ± 0.2 m ($n = 13$), and soil hardness averaged $2,679.4 \pm 56.4$ kPa ($n = 13$). There was not a statistically significant association between the number of degus that used each resting location and plant cover ($r_s = 0.000$, $P = 1.000$), maximum vegetation height ($r_s = 0.140$, $P = 0.647$), or soil hardness ($r_s = 0.383$, $P = 0.196$)

Lúcumo (*Pouteria splendens*) was present in 9 out of 13 (60%) resting locations, with a height that averaged 3.6 ± 0.2 m ($n = 9$). Resting locations included other plant species, such as *Puya chilensis* and *Escallonia pulverulenta*. Rock outcroppings were present in 2 out of 13 resting locations.

DISCUSSION

Our results do not support previous claims describing activity of *O. lunatus* as exclusively nocturnal (Begall 2005; Díaz 1999; Ocampo-Garcés et al. 2003; Muñoz-Pedreros et al. 2010). In contrast, these results support other studies that suggest *O. lunatus* are active during day and night time (Jaksic et al. 1997; Muñoz-Pedreros 2000; Torres-Contreras et al.

1994). A more continuous pattern of activity throughout the day and night in these rodents may be the consequence of relatively stable microclimatic conditions. Stable conditions may result from relatively high shrub cover (e.g., Jensen et al. 2003), and from the relatively low thermal amplitude due to ocean influence.

Relative to the range areas of similar- sized *O. degus* (Hayes et al. 2007), *O. lunatus* exhibited extensive range areas, where polygons generally matched the spatial distribution of shrub patches (Fig. 3). Although several factors may contribute to determining range areas in rodents (e.g., Getz et al. 2005), overhead plant cover is likely to be the ultimate, major factor in moon-toothed degus. Relatively high and continuous shrub cover conditions likely provide *O. lunatus* with cover from visual predators, stable microclimate, preferred food, and appropriate nesting sites. Spatial and temporal variation in these resources (e.g., food) or conditions should be examined to determine how these predict the size of range areas in these rodents.

Both the sharing of resting locations and overlap of range areas indicated these animals are social to some extent. Pending studies aimed to confirm that sharing of resting locations and range areas translate into communal nesting and other affiliative aspects of group-living, social behavior of *O. lunatus* seems intermediate between solitary (Ebensperger et al. 2008; Mares et al. 1997) and highly social octodontids (Ebensperger et al. 2004; Lacey and Ebensperger 2007) studied so far. These findings represent an important piece of information to the evolution of sociality in Octodontids, as they confirm the generally social nature of the most derived octodontids compared with basal species studied so far. Thus, differences in sociality across Octodontids are consistent with the

pattern of social living in these animals evolving relatively recently from a solitary-living ancestors.

The amount of plant overhead cover has been linked to sociality, with relatively large terrestrial mammals generally being social in open habitats (Brashares et al. 2000; Caro et al. 2004). Group-living would confer survival benefits in open, more risky environments through several mechanisms, including dilution or improved predator detection (Ebensperger 2001; Krause and Ruxton 2002). In contrast, social living across species of caviomorph rodents seems more associated with diurnal activity and the habit of actively digging burrows (Ebensperger and Blumstein 2006). The observation that social *O. lunatus* use habitats with relatively high plant overhead cover remains inconsistent with the hypothesis that predation risk drives social behavior in this species. Subsequent comparative analyses are needed to determine the extent to which this mismatch between the social phenotype and ecological conditions in terms of predation risk represents phylogenetic inertia.

Caviomorph rodents are known to exhibit intraspecific differences in social systems that generally correlate with variation in ecology (Maher and Burger 2011). Subsequent studies are then needed to determine the extent to which social behavior in *O. lunatus* may vary with density or other ecological conditions, as shown in other rodents (Randall et al. 2005; Wolff 1994). In particular, the social behavior of *O. lunatus* at Los Molles may be compared with that of *O. lunatus* from Lago Peñuelas National Reserve, and where abundance of this species seems lower based on the number of captures reported there (Muñoz-Pedreros et al. 2010).

In summary, our study yields insights into previously unknown aspects of behavior, including general activity, spatial ecology, and social behavior of *O. lunatus*. These rodents exhibit locomotor activity during day and night time and use 1 or more resting locations associated with high shrub cover. The sharing of resting locations and overlap of range areas support the idea that these rodents are to some extent social compared with solitary and highly social octodontids.

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RESUMEN

Nuestro conocimiento sobre la evolución del comportamiento social en roedores octodóntidos es aún fragmentario. La información disponible indica que las especies filogenéticamente basales son solitarias, mientras que las más derivadas tienden a ser sociales. Sin embargo, la información sobre la estructura social disponible para varias especies es anecdótica, lo cual dificulta el establecimiento de conclusiones robustas sobre la evolución del comportamiento social en este clado. Este es el primer estudio que cuantifica la actividad, uso del espacio, y comportamiento social del degú costino (*Octodon lunatus*), una especie derivada de octodóntido. Durante noviembre y diciembre de 2010 y 2011 se utilizaron métodos de captura-recaptura y telemetría para cuantificar el patrón diario de actividad superficial, ámbitos de hogar, solapamientos entre ámbitos de hogar, y uso compartido de parches de descanso y nidificación en una población costera localizada en el centro-norte de Chile. La actividad de *O. lunatus*, medida como desplazamientos individuales entre localizaciones consecutivas, mostró una tendencia estadísticamente no significativa a ser mayor en horas de la noche. Durante el día los animales usaron 1 a 3 sitios de descanso y anidamiento asociados con una alta cobertura arbustiva, donde *Pouteria splendens* (lúcumo) fue la especie dominante. Machos y hembras compartieron estos sitios de descanso en múltiples ocasiones. El solapamiento entre los ámbitos de hogar tendió a ser mayor en animales que además compartieron sitios de descanso comparado con animales que no compartieron estos sitios. En base al uso compartido de refugios se identificó 1 grupo social en 2010 y 4 grupos en 2011. La composición de estos grupos fue de 1 a 3 hembras adultas y de 1 a 2 machos adultos (2 a 4 adultos en total). Globalmente, los resultados indicaron que *O. lunatus* muestra algún grado de sociabilidad, observación que apoya una tendencia en la cual el comportamiento social es más frecuente en especies filogenéticamente derivadas de octodóntidos.

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FIGURE LEGENDS

FIG. 1.—Known distribution of moon-toothed degu (*Octodon lunatus*; gray shading) according to Contreras et al. (1987), Mares and Ojeda (1982), Gallardo et al. (2007), Ojeda et al. (2013); the cross symbol indicates the location of the study site Los Molles (32°14' S, 71°33'W, elevation = 33.58 m).

FIG. 2.—Mean ($\pm 1 SE$) distance moved (m) since previous scan of moon-toothed degus (*Octodon lunatus*) monitored every 1 h for 6 days and 8 nights at Los Molles, Chile. A total of 8 adult degus were recorded in 2010 and 12 more degus were studied in 2011. Black bars at the top of graphs indicate night hours.

FIG. 3.—Range areas (95% minimum convex polygons) of the moon-toothed degu (*Octodon lunatus*) recorded during a) 2010 ($n = 8$) and b) 2011 ($n = 12$). Dashed lines represent adult males. Identical colors are used to label individuals assigned to the same social groups based on daytime telemetry and resting location trapping. The arrow indicates geographic north.

FIG. 4.—Mean ($\pm SE$) overlap in range areas between degus (*Octodon lunatus*) assigned to the same or different social groups.

Figure 1

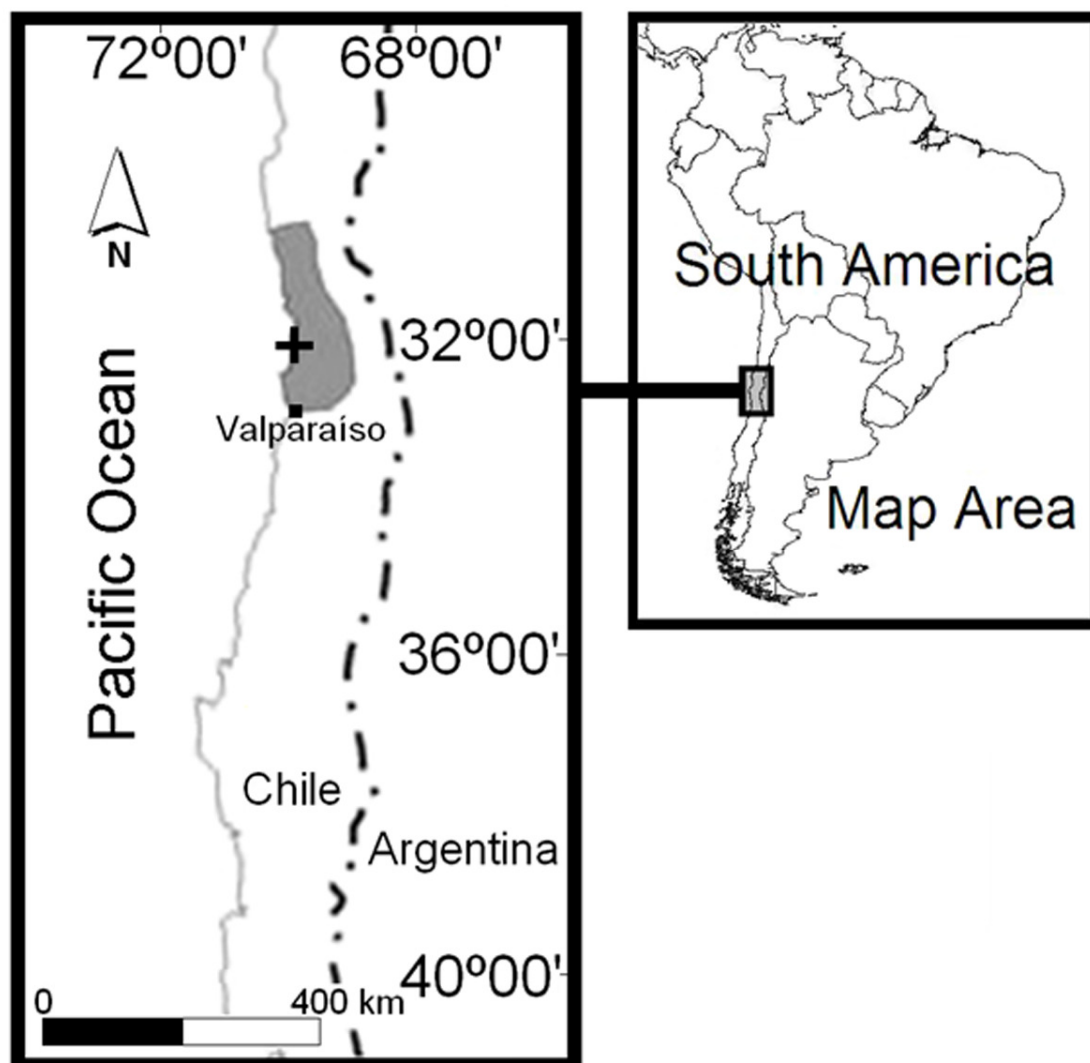


Figure 2

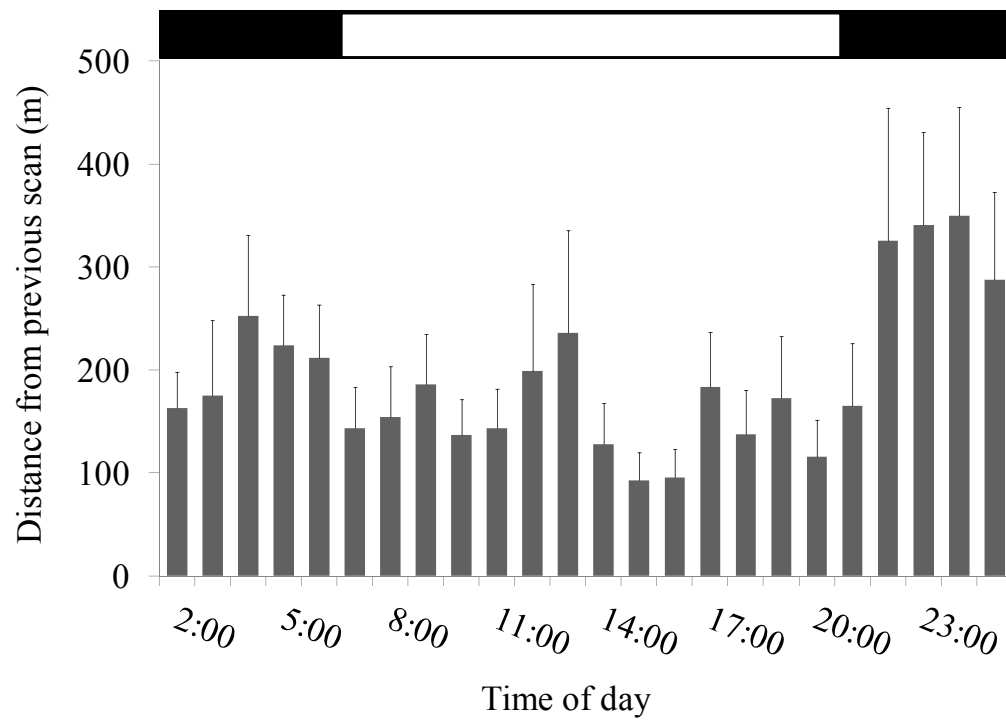


Figure 3

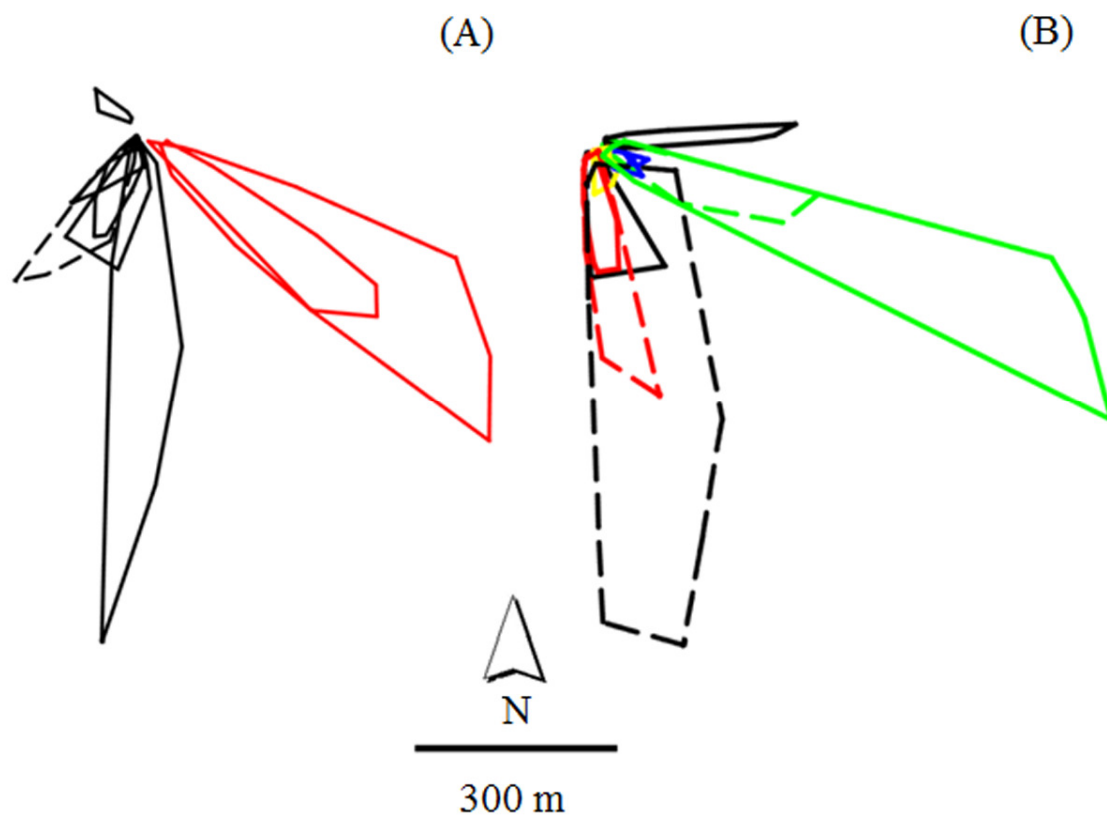
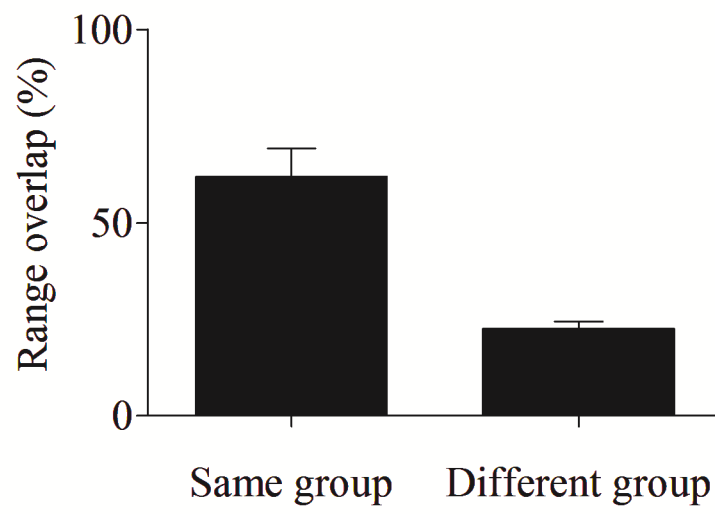


Figure 4



ASSOCIATIONS BETWEEN HABITAT CONDITIONS, SOCIALITY, AND BRAIN ORGANIZATION IN OCTODONTID RODENTS

GENERAL CONCLUSIONS

Several studies conducted so far support vegetation cover through its effects on predation risk contributes to maintain group living in current day social mammals. However, the influence of habitat conditions through its effects of vegetation cover on the early evolution and subsequent diversification of sociality remained unclear. Thus, in Chapter 1, I showed that indeed group living in caviomorph rodents has been associated to diversification in the use of habitats with different vegetation cover. However, this study also revealed how ancestor-descendent relationships mediate the effect of changes in habitat use on the evolution of sociality across these rodents. In particular, this study supported the hypothesis that sociality in Old World Phiomorpha and New World Caviomorpha had an early origin. Subsequently, this aspect of social behavior has been generally being lost, giving rise to species that are secondarily asocial. I found a significant correlation between vegetation cover and absence or presence of group-living. Nodes with social ancestors showed major associations with the use of open habitat. The loss of sociality across the phylogeny was associated with the use of closed habitat conditions. In contrast, no association was detected between changes in sociality and subterranean versus non subterranean modes of life.

Habitat conditions through vegetation cover and social living in turn may both affect the neurological phenotype of organisms. Controversy exists with regard to the relative roles of these two environmental factors. Thus, in Chapter 2, I simultaneously examined

how variation in the extent of group living and habitat conditions explain differences in brain size and dentate gyrus (DG) morphology in *Octodon degus* and *O. lunatus*. I compared these neuroanatomical structures in three natural populations that differ in sociality and habitat used in terms of vegetation cover. I concluded that population differences (or similarities) in brain size and DG cell number track differences in habitat conditions linked to spatial navigation closely. Instead, social environment seemed less important. Within populations, associations are consistent with a joint influence of habitat and social complexity on brain size in *O. lunatus*, and on DG cell number in both *O. degus* and *O. lunatus*. These results indicate that brain size and DG cell number in these octodontid rodents are sensitive to within and between population differences in habitat conditions. Instead, the effect of sociality in terms of group size and range area overlap was evident within but not between populations.

Given that social behavior of moon-toothed degus (*O. lunatus*) was virtually unknown, I dedicated Chapter 3 to quantify this phenotypic aspect in these rodents. This study represents the first systematic data on activity, space use, and social behavior of *O. lunatus*, a derived species of octodontid rodent. These rodents exhibit locomotor activity during day and night time and use one or more resting locations associated with high shrub cover. The sharing of resting locations and overlap of range areas support the tenet that these rodents are social compared with other solitary living octodontids. This finding confirms the macroevolutionary trend according to which group-living is more frequent in the most derived compared with basal octodontids.