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RELEVANCE OF KIN SELECTION ON THE EVOLUTION OF COOPERATION IN  
HYSTRICOGNATH RODENTS, *Octodon degus* (Molina, 1782) AS A STUDY CASE.

IMPORTANCIA DE LA SELECCIÓN DE PARENTESCO EN LA EVOLUCIÓN DE LA  
COOPERACIÓN EN ROEDORES HISTRICOGNATOS Y EN *Octodon degus* (Molina,  
1782) COMO CASO DE ESTUDIO.

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*A la memoria de mi padre.*

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## RESUMEN

La cooperación en animales ha sido uno de los temas centrales en ecología y evolución durante las últimas décadas. Para explicar su origen y mantenimiento, se han propuesto una serie de mecanismos evolutivos dentro de los que destaca la selección de parentesco. Una predicción central de este mecanismo es la ocurrencia de nepotismo, donde los individuos benefician preferentemente a sus parientes. En este marco conceptual existe la denominada “hipótesis de la monogamia” la cual plantea que el requisito para el origen de sociedades altamente cooperativas (e.g. con crianza cooperativa), es la existencia de monogamia social y sesgo reproductivo, lo cual genera grupos conformados por parientes cercanos. Existe sustento para esta hipótesis en himenópteros, aves y mamíferos, sin embargo, la monogamia social está ausente en la mayoría de los grupos de mamíferos, con excepción de algunos, como los roedores histicognatos. Estos roedores presentan, además, un alto número de especies sociales y de conductas cooperativas. Por lo tanto, el objetivo central de esta tesis fue evaluar la validez de la hipótesis de la monogamia como explicación principal para la existencia de cooperación en Hystricognathi y evaluar la importancia de la selección de parentesco en una especie en particular de este grupo, el degú (*Octodon degus*), la cual presenta cooperación en la crianza y un sistema social de características variables en relación a su estructura de parientes. Para la evaluación a nivel de los histicognatos se empleó el método comparativo filogenético con datos para 120 especies, mientras que para la evaluación en el degú, se ocuparon datos conductuales y genéticos de una población silvestre para un total de 8 temporadas. Los

resultados mostraron que la hipótesis de la monogamia tiene alto sustento como explicación para el origen de la crianza cooperativa, de la sociabilidad y de otras conductas cooperativas en conjunto en *Hystriognathi*; además, se determinó que los ancestros del grupo probablemente fueron sociales, con monogamia social y altamente cooperativos. Por lo tanto, es probable que la cooperación haya aparecido tempranamente en el origen del grupo, y donde la selección de parientes jugó un rol preponderante. Por otro lado, el análisis particular en el degú reveló que el nivel de parentesco entre las hembras de un grupo social no influye sobre la conducta de crianza comunal nocturna por parte de las hembras, por lo que la selección de parentesco probablemente no tiene relevancia en explicar esta conducta cooperativa en el degú. Sin embargo, también se registró un efecto del número de hembras del grupo sobre la conducta de crianza comunal diurna y nocturna, y un pequeño grado de coordinación entre las hembras en el cuidado diurno de las crías del grupo, por lo que es posible que existan beneficios directos asociados a la conducta de crianza comunal, y donde probablemente sean más relevantes otros mecanismos evolutivos de la cooperación, más allá de la selección de parientes. En resumen, estos resultados ponen de manifiesto la importancia histórica de la selección de parientes en el origen y en la generalidad de la cooperación en los *hystriognatos*, pero también muestran que en ciertas especies modernas más derivadas, como el degú, la cooperación puede interpretarse como un rasgo conservado, mientras que su sistema de apareamiento promiscuo se puede considerar como un rasgo derivado en la historia evolutiva del grupo.

## ABSTRACT

Cooperation in animals has been one of the central themes in ecology and evolution during the last decades. To explain its origin and maintenance, several evolutionary mechanisms have been proposed, among which kin selection stands out. Main prediction of this mechanism is the occurrence of nepotism, where individuals preferentially benefit their relatives. In this conceptual framework there is the “monogamy hypothesis” which states that the requirement for the origin of highly cooperative societies (e.g., cooperatively breeding species) is the preexistence of social monogamy system, which generates groups made up of closely relatives. There is support for this hypothesis in hymenopterans, birds, and mammals; however, social monogamy is absent in most mammalian groups, with exceptions, such as hystricognath rodents. These rodents also present a high number of social species and cooperative behaviors. Therefore, thesis main objective was to evaluate the validity of monogamy hypothesis as the main explanation for the observed cooperation in Hystricognathi and to evaluate the relevance of kin selection in a particular hystricognath species, the degu (*Octodon degus*), which exhibit cooperation in breeding context and a social system with variable kin structure. To evaluate at the hystricognath level, comparative phylogenetic method was used with data for 120 species; while to the degu analysis, behavioral and genetic data from a wild population were used for a total of 8 seasons. The results showed that the monogamy hypothesis has high support as main explanation to the origin of cooperative breeding, sociality and other cooperative behaviors in Hystricognathi. Furthermore, it was determined that ancestors were probably social, socially monogamous, and highly cooperative.

Therefore, it is probable that cooperation appeared early in the origin of the group, and where kin selection played a main role. On the other hand, the particular analysis in the degu revealed that kinship level between group females does not influence night communal rearing by the females, so that kin selection probably has no relevance in explaining this cooperative behavior in the degu. However, there was an effect of the number of group females on both daytime and night communal rearing, and a small coordination level between group females in the daytime communal rearing; so it is possible that there are direct benefits associated with communal rearing, and where other cooperation evolutionary mechanisms are probably more relevant, beyond the kin selection. Overall, these results reveal the historical relevance of kin selection in the origin and extent of cooperation in hystricognaths; but also show that in more derived current species, such as degu, cooperation can be interpreted as a conserved trait, while their promiscuity can be considered as a derived trait in the evolutionary history of these rodents.

## GENERAL INTRODUCTION

The origin, evolution and maintenance of cooperation have been central themes in ecology and evolution (Owens, 2006) mostly because cooperation remains paradoxical in a Darwinian world (Kay *et al.* 2020). Group-living provides the conditions for the emergence of cooperative behaviors, which are defined as social interactions where participants attain net fitness benefits (Bergmüller *et al.* 2007). The multiple mechanisms invoked to explain cooperation can be split into two broad categories: direct- and indirect-fitness benefits (Nowak, 2006; West *et al.* 2007). Individuals attain direct fitness benefits whenever cooperative behavior enhances copies of alleles by direct descend that are associated with cooperative behavior compared with non- or less cooperative individuals (Nowak, 2010; West *et al.* 2007). In contrast, individuals attain indirect benefits whenever cooperative behavior enhances copies of alleles associated with cooperative behavior indirectly through favoring the reproduction and survival of close kin compared with more distant kin or genetically unrelated individuals (Hamilton, 1964; West *et al.* 2007).

Kin selection (Hamilton, 1964) is the most frequently invoked mechanism to explain cooperation and is based in indirect benefits, where individuals behave in ways to favor genetic kin despite direct costs experienced (Nowak *et al.* 2017; Smith, 2014). A main prediction of this mechanism is the occurrence of nepotism, where individuals preferentially benefit their relatives (Nowak, 2006; West *et al.* 2007). In a context aimed to explain the evolution of social behavior, the ‘monogamy hypothesis’ (Boomsma, 2007, 2009; Cornwallis *et al.* 2010; Hughes *et al.* 2008), argues that a monogamous mating system is a fundamental

requirement for the evolution of highly cooperative societies. Whenever monogamy is the dominant mating system in the population, descendant offspring tends to be genetically more related compared with a population exhibiting a more promiscuous mating system (Boomsma, 2007; Hughes *et al.* 2008). Thus, monogamy may provide opportunities for kin selection to take place. Intriguingly, studies indicate that once cooperative breeding has evolved in previously monogamous forms, the mating system may drift towards increasing promiscuity (Cornwallis *et al.* 2010; Hughes *et al.* 2008), implying that kin selection might be important to the origin, but not necessarily for the maintenance of cooperation. Most critical however, the relevance of both monogamy and kin selection as main drivers of the evolution of cooperation has been questioned (Birch & Okasha, 2015; Nonacs, 2011; Nowak *et al.* 2010; 2017), and several other mechanisms based in direct benefits may provide alternative routes to the evolution of cooperation, including reciprocity (Trivers, 1971), mutualism (Clutton-Brock 2002) and group selection (Nowak 2006; Wilson, 1975). Furthermore, these mechanisms may act together with kin selection (Carter *et al.* 2019).

Cooperative behavior is widespread across social mammals with multiple explanations invoked (Clutton-Brock 2016). Among these, kin selection, through the monogamy hypothesis, has been given a predominant role (Lukas & Clutton-Brock, 2012). Within mammals, Hystricognath rodents remain conspicuous due to their relatively high diversity of social and mating system, and where social monogamy and group-living are both common traits (Herrera, 2016, Burger & Maher 2016). Moreover, cooperation is frequent in these rodents and phylogenetical approaches indicate that ancestors of these organisms were probably social (Burda *et al.* 2000; Ebensperger & Hayes, 2016; Sobrero *et al.* 2014; Vásquez 2016). Indeed, Burda *et al.* (2000) hypothesized that social monogamy was an ancestral state

that drove the emergence of cooperative behavior and the rising of sociality through all hystricognaths. Thus, in Chapter 1, I tested the relevance of the ability of this hypothesis in explaining the evolution of sociality and cooperative behavior across the hystricognath rodents, and whether social monogamy and cooperative behavior have been associated with an early origin in these rodents.

On the other hand, the extent of group-living and prevailing mating system seems variable within species of hystricognaths (Maher & Burger 2016). Among Neotropical hystricognaths, the degu (*Octodon degus*) stands as a highly social species, with groups of variable size and sex composition, and with a variable, yet generally promiscuous mating system (Ebensperger *et al.* 2019). As a result, genetic relatedness within groups varies, with some groups consisting of closely related or completely unrelated individuals (Ebensperger *et al.* 2004; Quirici *et al.* 2011; Davis *et al.* 2016), suggesting that the relevance of kin selection may be similarly variable across groups. Degus also exhibit different cooperative behaviors within which communal rearing stands out, and where an important proportion of females the population rear their offspring communally (Ebensperger *et al.* 2002; 2004). Both the role of kinship and the extent to which females coordinate their care during communal rearing to enhance fitness benefits remains both debated and unexamined. Thus, I use Chapter 2 to determine the effect of relatedness on communal rearing by means of examining the influence of kinship on strength of associations of lactating females during nest sharing at nighttime. Additionally, I assessed how communally rearing females coordinate their attendance to communal litters during daytime.

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**Early evolution of cooperative behavior is mediated by social and mating system across hystricognath rodents (Rodentia: Hystricognathi)**

**Abstract**

The monogamy hypothesis states kin selection is a relevant mechanism underlying the evolution of cooperative societies. In mammals, 4-5% of species exhibit social monogamy, but this proportion is higher among hystricognath rodents. These rodents also exhibit a high diversity of both social and mating system, and cooperative behaviors. I examined the relevance of monogamy to explain the evolution of this diversity of cooperative behaviors across Hystricognaths. I found correlated evolution between mating system and group-living (sociality), and with different forms of cooperation, including reproductive cooperation. Social monogamy preceded transitions to sociality and cooperation. Ancestors exhibited social monogamy, sociality, reproductive cooperation and other forms of cooperation. Together, results confirmed that Hystricognathi evolved from a social ancestor exhibiting social monogamy or low promiscuity. Furthermore, different forms of cooperative behavior also evolved early, implying that relatively high levels of cooperation and group-living were associated with the origin of these rodents. Overall, these findings support the monogamy hypothesis as an explanation for the evolution of sociality and cooperative behavior, with kin selection as main evolutionary force.

**Key Words:** cooperation, sociality, monogamy hypothesis, kin selection, social monogamy, correlated trait evolution, ancestral states, social behavior, Hystricognathi, Caviomorphs.

## 1. Introduction

The mating system is a key component of the social system of a species (Emlen & Oring, 1977), and variation in this component has consequences on the expression of the sociality (Kappeler *et al.* 2013; Lukas & Clutton-Brock, 2011, 2013). In this context the ‘monogamy hypothesis’ (Boomsma, 2007, 2009; Cornwallis *et al.* 2010; Hughes *et al.* 2008) argues that a mating system close to monogamy or with a low extent of promiscuity is a fundamental requirement for the evolution of highly cooperative societies (e.g. eusociality, cooperative breeding). Evidence from hymenopterans, birds and mammals supports this hypothesis (Cornwallis *et al.* 2010; Hughes *et al.* 2008; Lukas & Clutton-Brock, 2012). For instance, monogamy predate the evolutionary transition into cooperative breeding in mammals where reproduction is skewed within groups and non-breeding individuals provide care to the offspring of breeders (Lukas & Clutton-Brock 2011; 2012). Kin selection is the underlying mechanism argued to explain cooperation in the context of the monogamy hypothesis, since social groups with a monogamous mating system would be composed mostly by close kin (i.e. family groups), in which only a some individuals breed and the offspring subsequently remains in the group as non-breeding “helpers” (Emlen, 1995; Lukas & Clutton-Brock, 2012), attaining indirect fitness benefits (Boomsma, 2009; Bourke, 2011, 2014; Cornwallis *et al.* 2010; Foster *et al.* 2006; Nowak, 2006; West *et al.* 2002). Intriguingly however, other studies indicate that once cooperative breeding has evolved in previously monogamous forms, the mating system may drift towards increasing promiscuity (Cornwallis *et al.* 2010; Hughes *et al.* 2008). Thus, open are the questions of whether kin selection is the single most relevant mechanism driving cooperative breeding and other forms of cooperation. Since single species

may exhibit more than one cooperative trait (Duncan *et al.* 2019; Madden & Clutton-Brock, 2011; Smith *et al.* 2012; Ly-Prieto *et al.*, unpublished data), kin selection might be expected to influence multiple cooperative traits, beyond cooperative breeding (Arnold *et al.* 2005; Bourke, 2014; Foster *et al.* 2006; Hatchwell, 2010; Smith, 2014), implying that social monogamy might explain the evolution of other forms of cooperation. However, the relevance of both monogamy and kin selection as drivers of the evolution of cooperation has been questioned (see Birch & Okasha, 2015; Nonacs, 2011; Nowak *et al.* 2010). Monogamy seems to be a strong requirement in some cases, but its evolution in others may be associated with life history traits (Nonacs, 2011). Most critical, additional mechanisms (e.g., reciprocity, mutualism, etc.) may represent evolutionary relevant forces driving cooperation (Carter *et al.* 2017; Clutton-Brock 2006; 2009; 2016; Hatchwell 2010; Taborsky *et al.* 2016; van Schaik & Kappeler 2006; Vásquez 2016).

Only 4-5% of total extant mammalian species exhibit social monogamy as the predominant mating system (Lukas & Clutton-Brock, 2013; Ly Prieto *et al.*, unpublished data). Of these, only some species are characterized by a social system of families with natal philopatry; in others, the social unit includes only a reproductive pair, and for some of these species there is insufficient information about the social structure (Lukas & Clutton-Brock, 2012, 2013; Maher & Burger, 2016). Interestingly however, social monogamy seems more frequent in some clades like Callithricidae, Canidae, and Hystricognathi (Burda *et al.* 2000; Emlen, 1995; Kleiman, 1977; Lukas & Clutton-Brock, 2012). Of these, the hystricognath rodents are conspicuous because they exhibit a surprisingly high diversity of social and mating systems that range from solitary living species through the unique eusocial mole-rats, and from monogamous to highly promiscuous species (Herrera, 2016; Maher & Burger, 2016).

Hystricognaths exhibit cooperative breeding, where breeding females are assisted to rear their offspring by non-breeding helpers, communal rearing, where breeding females pool their young and share care (Silk, 2007; Lukas & Clutton-Brock, 2012), collective vigilance, including the presence of active sentinels and antipredator alarm calls, communal burrowing, the communal defense of a territory or of resources, among others (Vásquez 2016; this study).

The relatively high percentage of social species across Hystricognathi (~33%, Ebensperger & Hayes, 2016; Maher & Burger, 2016; this study) contrasts with the lack of information about evolutionary mechanisms explaining this diversity (Ebensperger & Hayes 2016; Vásquez 2016). Thus, the relative importance of kin selection and that of other mechanisms such as reciprocity and mutualism in explaining cooperative behaviors remains unclear (Vásquez 2016). Interestingly however, previous comparative studies have reported that ancestors of these rodents were social and that sociality disappeared and reappeared several times through the evolutionary history (Sobrero *et al.* 2014), a finding that support the social ancestor hypothesis (SAH; Beauchamp, 1999; Cardinal & Danforth, 2011; Wcislo & Danforth, 1997). Additionally, both ecology (predation risk) and ancestor-descendant relationships (phylogeny) have been influential in driving this evolutionary history (Ebensperger & Blumstein 2006, Sobrero *et al.* 2014). These findings generally support Burda *et al.*'s (2000) hypothesis, who set out that ancestors of these rodents probably had social life, a monogamous mating system, and exhibit cooperative breeding. Burda *et al.*'s (2000) hypothesis predicts that social monogamy was an ancestral state that drove the emergence of cooperative behavior and the rising of sociality. In support of this possibility, social monogamy seems to have originated from solitary ancestors in most of current mammalian

orders (Lukas & Clutton-Brock 2013). Therefore, it is plausible that social life of Hystricognathi ancestors was initially linked to the formation of monogamous pairs.

Therefore, I first aim this chapter to examine the relevance of the monogamy hypothesis in explaining the evolution of sociality and cooperative behavior in the Hystricognath rodents, an ancient and socially diverse mammalian taxon. Secondly, I determined whether monogamy and cooperative behavior have been associated with an early origin in these rodents.

## **2. Methods**

### 2.1 Hystricognathi data base

I collected data on sociality, mating system, and cooperative behaviors reported across species of Hystricognaths (species-level taxonomy according to Woods & Kilpatrick, 2005). These data were obtained from scientific articles available on ISI Web of Science and Google Scholar. I searched these data bases with the terms "social behavior", "cooperative behavior", "mating system", "hystricognath", "caviomorph", and with the scientific name of each species of hystricognath. I also collected information from pre-existing mammalian databases and encyclopedias, specifically from PanTHERIA (Jones *et al.* 2009), Animal Diversity Web (Myers *et al.* 2017) and "Walker's Mammals of the World" (Nowak 1999). I also reviewed the articles of the journal "Mammalian Species" (published by the American Society of Mammalogists) that included hystricognath species. From these searches I collected the following data on the following variables:

(1) Sociality (social organization): I classified species as being social (1) whenever it includes social groups or long-term associations of two or more adult individuals; or solitary (0). I

considered female-male pairs as forming a group whenever evidence supported they associate beyond time of breeding and offspring rearing, exclusively.

(2) Mating system: since mating system is known to exhibit intraspecific variation in hystricognaths (Maher & Burger 2016), I chose the most categorized each species to a predominant mating system based on the number of studies reporting it. In species (n = 46) where this rule was not possible, I considered the two most common together. I followed Clutton-Brock (1989) and Barnard (2004, p. 484) to classify mating systems. Subsequently, I grouped the eight mating systems reported into two qualitative discrete binary categories according to the degree of promiscuity. A value of 0 represented highly promiscuous mating systems (i.e., variable and indeterminate number of mates), promiscuous multi-male polygyny, polygynandry, polygynandry-monogamy combination, and single male polygyny (harem type). A value of 1 was assigned to species exhibiting social monogamy or/and polyandry. Polyandry is rare in mammals, and in hystricognaths has only been recorded in the naked mole-rat (*Heterocephalus glaber*), reported in behavioral studies in captivity (Jarvis, 1991).

(3) Within-group kinship: since kinship structure is available for a reduced number of species, I also considered data on pedigree on father / mother-offspring relationships inferred from direct observation, and from descriptive accounts of kinship group composition. I classified within-group kinship as a qualitative variable with 2 ordinal categories: species without kinship structure, whenever estimates of genetic relatedness "R" reported were negative or smaller than 0.05 (value 0); and species with some extent of kinship structure whenever "R" values are equal to or greater than 0.05 (value 1). In cases where "R" was not reported, I

estimated this from kinship relationships reported (e.g., parents-offspring, half-siblings, uncles-nephews).

(4) Cooperative behavior: I collected the number of different cooperative behaviors reported for each species of hystricognath rodent. I then used this number to quantify a “Cooperation Score” (Smith *et al.* 2012) that ranged from 0 and 16. This score represents the sum of values of presence (value 1) or absence (value 0) for each potential behavior. Exceptionally, cooperative behavior in a reproductive context had 4 ordinal categories based on the classification proposed by Silk (2007). Specifically, I assigned a value 0 to species lacking behavior and to plural breeding species without communal care. I assigned a value 1 to species with plural breeding with communal care (communal rearing), species that breed in pairs (male/female with active parental care of both) and to species with cooperative breeding, (i.e. presence of non-breeders that provided care to the offspring of breeders). During assignment of presence/absence of each cooperative behavior to each species, I considered any direct (e.g., visual) or indirect (e.g., spatio-temporal association) records of the behavior. During analyzes of discrete binary measures, I considered whether the species exhibits cooperation or not for a certain cooperative behavior. Here the Cooperation Score was binarily-transformed (presence of cooperation: Cooperation Score with positive values; lack of cooperation: Cooperation Score = 0). Finally, I recorded whether the species exhibit communal nesting, which is similarly considered as a form of cooperative behavior. Although communal nesting may be related to limitations in breeding habitat, it may represent a component of cooperative breeding and communal rearing (Hayes 2000; Williams *et al.* 2013), leading to multiple social benefits, and potentially predisposing other prosocial behaviors (Ebensperger *et al.* 2004; Williams *et al.* 2013; Hayes 2000), especially in rodents (Hayes 2000).

## 2.2 Phylogeny of Hystricognath rodents

I used recent phylogenetic reconstructions of mammals that included Ctenohystrica, Hystricognathi and Caviomorpha rodents (Fabre *et al.* 2012; Upham & Patterson 2012; 2015; Voloch *et al.* 2013). However, several species in our database were not included in these phylogenies (see Results, 3.2 section). Therefore, I constructed a Hystricognathi phylogeny from DNA sequences of two genes: one mitochondrial (cytochrome b, CYTB) and one nuclear (growth hormone receptor, GHR) obtained from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>). We chose these two molecular markers because they were represented in the hystricognaths; GHR and CYTB sequences were available for 188 species (CYTB: 185 species; GHR: 95 species; Table S1 of Supplementary Material). Previous studies highlight the relevance of combining multiple molecular markers, both mitochondrial and nuclear, to improve node/topology resolution and recover ancestor-descendant relationships more reliably (Upham & Patterson 2012, 2015; Garamszegi & González-Voyer 2014; Fabre *et al.* 2013; Huchon *et al.* 2002). I occupied *Pedetes capensis*, *Ctenodactylus sp.* (chimera taxon; see Upham & Patterson 2015), *Felovia vae* and *Massoutiera mzabi* as outgroups, based on recent phylogenies of this Hystricognaths (Upham & Patterson 2012; 2015).

I used the Xia's test (Xia *et al.*, 2003; Xia, 2018), implemented in DAMBE v7.2.152, to determine the potential for mutational saturation of sequences examined, particularly CYTB (Upham & Patterson 2012; 2015). The Xia's test compares a standard index of substitution saturation (Iss) with an index of critical substitution saturation (Iss.c) calculated from the data using a random resampling process. I ran tests for two genes using all sites and specifying the proportion of invariant sites (Xia & Lemey, 2009). Additionally, I assessed neutrality of both

molecular markers using the Tajima's neutrality test (Tajima, 1989), implemented in MEGA 6.0.6 (Tamura *et al.* 2013). This test compared the difference between two measures of genetic diversity (mean number of pairwise differences and number of segregating sites) and nucleotide diversity. The magnitude of the difference between observed and expected estimates quantified neutral or non-random evolution (called D statistic; Nei & Kumar, 2000; Tajima, 1989). The Xia's test revealed that CYTB exhibited a level of saturation as previously reported in hystricognaths and other vertebrates (Upham & Patterson 2012; 2015). However, saturation was not statistically significant and this gene contributed highly to the resolution at the terminal nodes. The Xia's test also revealed that the GHR gene was not saturated as reported in other hystricognath studies (Upham & Patterson 2012; 2015). Tajima's neutrality test revealed that both CYTB and GHR genes deviated from neutrality (D statistic equal to zero), but not statistically significantly so (see Table S2 of Supplementary Material for Xia's and Tajima's test results).

I performed alignment of sequences in MEGA 6.0.6 (Tamura *et al.* 2013), and directly verified and corrected ambiguous sites of alignment by eye. The total number of base pairs was 1140 for CYTB and 888 for GHR (2028 bp for total sequence length). I obtained the best nucleotide substitution models for each gene with the Akaike's Information Criterion (AIC) using ML fit in the jModelTest v2.1.7 software (Darriba *et al.* 2012). I performed the phylogenetic analysis of the 2-gene matrix with Bayesian Inference (BI) in MrBayes v3.2.5 software (Ronquist & Huelsenbeck 2003). I used partitioned analyzes with one partition for each gene, and where each had a best model of nucleotide substitution (GTR+G+I for both). Therefore, each parameter in the model was estimated independently for each partition using the "partitioned analysis model" command implemented in MrBayes. I performed two independent runs of

four chains each (MCMC) and 30 million generations each, with sampling every 1000 generations. After discarding the first 25% of samples as burn-in, I used convergent MCMC searches to combine 62,000 total trees into a single consensus tree. The resulting maximum clade credibility tree represents the best a posteriori topology, with nodal support indicated by Bayesian posterior probabilities. I performed this procedure three times to compare the final consensus trees (i.e., all 3 trees with same topology and nodes). I compared my phylogenetic reconstruction with the most complete and methodologically similar pre-existing phylogenies (Fabre *et al.* 2012; Upham & Patterson 2012; 2015) to verify the consistency of nodes obtained, mostly at the deepest levels of the phylogeny. During this procedure I obtained only one node as being discordant with previous phylogenies. Within the Caviomorpha I recorded the association Erethizontoidea + (Cavioidea + (Chinchilloidea + Octodontoidea)), but most previous phylogenies report this association as (Erethizontoidea + Cavioidea) + (Chinchilloidea + Octodontoidea). However, these nodes represent the most discordant across the phylogeny of hystricognaths. This is probably the result of a rapid process of diversification among basal caviomorphs into current superfamilies and families (Upham & Patterson 2015; Upham *et al.* 2019). I pruned the phylogenetic tree in BayesTrees V1.3 software (Meade 2019) to match the number of species with behavioral data and molecular data.

### 2.3 Reconstruction of ancestral states

I used maximum likelihood (ML) approaches to reconstruct the ancestor of all hystricognaths for each cooperative behavior, social system (social/solitary), mating system (binary) and kinship (binary), in module Multistate of BayesTraits V3.0.2 software (Pagel & Meade 2019).

Each trait was estimated separately, and ML analyses were set to 10000 ML tries per tree, and branch length of trees was scaled to optimize rates estimation. I used multistate estimates of ancestral states only for the root node of the tree and added all other basal nodes by hand with AddNode and AddTag commands in the Multistate module. This procedure allowed me to obtain the probabilities of character state for each trait examined and a detailed reconstruction of the most probable social system and social attributes in each node of the phylogeny, including the first ancestor of the entire clade.

#### 2.4 Correlated evolution of social traits

I examined for evolutionary correlations between mating system, cooperative behaviors, and sociality by contrasting combined evolution models of traits. I used Discrete: Independent and Discrete: Dependent modules in the BayesTraits software to implement these two-trait models and reconstruct correlated evolution. I used this procedure to search possible evolutionary dependent transitions of character states with maximum likelihood approaches. I compared the fit of models based on that two traits evolve independently with that of models assuming traits evolve dependently. For independent evolution models each trait had two transition rates that were independent of rates of other traits (four parameters). In models of dependent evolution transition rates between states of one trait are contingent on states of the other trait (eight parameters). This approach allowed me to reconstruct the most likely scenario of evolution between two linked traits according to phylogenetic relationships of the species. Discrete module analyzes were ML-based, set to 10,000 ML tries per tree, and scaled to branch length to optimize rates estimation. I used the likelihood ratio (LR) test to compare the two maximum likelihoods derived from nested models (two traits evolved independently vs. same two traits

evolved dependently). The likelihood ratio statistic was calculated as:  $LR = 2[\log\text{-likelihood (better fitting model)} - \log\text{-likelihood (worse fitting model)}]$ . The likelihood ratio statistic is asymptotically distributed as a chi-squared with degrees of freedom equal to the difference in the number of parameters between the two models (four parameters in this case) (Pagel & Meade 2019). Additionally, I used BayesTraits to estimate the state of characters for the basal node. I conducted this analysis for the following pairs of traits (binary): mating-social system, mating system-cooperation, mating system-communal nesting, mating system-within-group kinship, and mating system vs. each cooperative behavior.

### 3. Results

#### 3.1 Social traits of Hystricognathi

I obtained complete information on all cooperative traits examined for 120 species. Out of this number of species with complete information, 67 were social (56%) and 53 solitary (44%). Regarding the mating system, 25% of species were categorized as socially monogamous or exhibiting low promiscuity, while 75% were promiscuous (e.g., polygyny, polygynandry). Ten out of 14 cooperative behaviors documented across mammals were also present among the hystricognaths. These were reproductive cooperation (including cooperative breeding and communal rearing), mutual allogrooming, communal territory or resource defense, communal burrowing, alarm calling, the presence of active sentinels, antipredator cooperative defense, food sharing, information transfer, and the formation of male coalitions. Cooperative scores ranged from 0 to 10, and only *Heterocephalus glaber* (naked mole-rats) exhibited a value of 10. Mean ( $\pm$  SD) of cooperative score was 2.13 ( $\pm$  2.67). I also found that 53% of the species

have at least one cooperative behavior (binary cooperation, value 1). For a detailed summary of hystricognath database see Table S3 of Supplementary Material.

### 3.2 Phylogeny of Hystricognath rodents

Of 188 species with molecular data, 120 were included in the social/cooperative database. A total of 19 species categorized as social were excluded from analyses because they did not have molecular data available. Ten other species had sequences but were excluded because only binary social/solitary data were available. Therefore, species examined represented 81% of species with behavioral data.

### 3.3 Ancestral state estimation for social and cooperative traits

Estimation of ancestral character states of basal nodes revealed that the common ancestors of Hystricognathi, Caviomorpha + Phiomorpha, Phiomorpha, and Caviomorpha most likely were socially monogamous or exhibiting low levels of promiscuity (Figure 1 and Table 1). These 4 ancestors most likely exhibited social lifestyle (Figure 2 and Table 1), reproductive cooperation (cooperative breeding or communal rearing; Figure 3 and Table 1), communal nesting, communal territory or resource defense, mutual allogrooming, alarm calling, food sharing, and within-group kinship (Table 1). Both cooperation (binary) and information transfer were likely present in two of four mentioned basal nodes (Figure 4 and Table 1). Communal burrowing was most likely the ancestral state only in Phiomorpha. Finally, cooperative antipredator defense, the presence of active sentinels, and formation of male coalitions were not found as the ancestral state in any of basal nodes (Table 1). A summary for ancestral estimates, model likelihood, and estimated rates of state change is provided in Table S4 of Supplementary Material.

### 3.4 Correlated Evolution

The analysis of correlated evolution of traits revealed that the dependent model of evolution between mating system and reproductive cooperation (i.e., including cooperative breeding or communal rearing) is significantly more likely than the independent evolution model (log-likelihood of models: dependent model, -115.07 vs. independent model, -125.25; Table 3). This dependent model indicated that transition to reproductive cooperation is an order of magnitude more likely from a state with social monogamy or low promiscuity than from a state with promiscuity (Figure 5). Likewise, the dependent evolution model between mating system and group-living (sociality) was significantly more likely than the independent evolution model (log-likelihood of models: dependent model, -73.62 vs. independent model, -83.83; Table 3), implying that by an order of magnitude social monogamy was a precondition to the transition from solitary-living to group-living (Figure 6). The dependent evolution model between mating system and cooperation (binary) was significantly more likely than the independent evolution model (log-likelihood of models: dependent model, -68.32 vs independent model, -79.80; Table 3), and showed that social monogamy was an order of magnitude the most likely precondition for the transition from non-cooperative to cooperative behavior (Figure 7). Finally, the dependent evolution model exhibited a significant greater probability for associations between mating system and alarm calling, cooperative antipredator defense, communal burrowing, communal territory or resource defense, and within-group kinship. On the other hand, the dependent and independent evolution models were not significantly different in explaining an association between mating system and active sentinels, or between mating system and formation of male coalitions. The independent evolution model exhibited a statistically significant greater probability compared with

dependent evolution models for associations between mating system and mutual allogrooming, food sharing, information transfer, and communal nesting, implying a lack of association between predominant mating system and the evolution of these traits (Table 3).

## 4. Discussion

### 4.1 Social monogamy and reproductive cooperation

Social monogamy preceded the appearance of reproductive cooperation (i.e., either cooperative breeding or communal rearing) in hystricognath rodents, a finding supporting Lukas & Clutton-Brock (2012)'s similar finding across all mammals. However, and departing from Lukas & Clutton-Brock (2012), I found a small yet statistically significant probability that cooperative breeding evolved from ancestors exhibiting a promiscuous mating system. Likely, this difference resulted from differences in trait categorization used by these authors. Lukas & Clutton-Brock (2012) split cooperative breeding species (i.e., species characterized by the presence of non-reproductive helpers) from communally breeding species (i.e., all females reproduce and communally rear their offspring). By definition, cooperative breeding is observed mostly if not exclusively in species with social monogamy. Instead, we followed Silk's (2007) "broad sense" classification of breeding systems, allowing us to examine potential associations between all cooperative breeding systems (encompassing cooperative breeding and communal rearing) and mating systems. For instance, communal breeding is usually seen in species having relatively more polygynous or promiscuous mating system (Clutton-Brock 2016; Lukas & Clutton-Brock, 2012; Silk, 2007).

## 4.2 The monogamy hypothesis and other cooperative behaviors

I found that the evolution of some cooperative behaviors reported in hystricognath rodents has been associated to social monogamy on the ancestral states (Table S4 in Supplementary Material). These cooperative behaviors included alarm calling, cooperative antipredator defense and communal territory or resource defense, all of which have been linked to different evolutionary mechanisms across mammals. For example, alarm calling has been associated to kin selection (Dugatkin, 1997; Sherman, 1977) or direct benefits (Caro 1986; Shelley & Blumstein, 2005), and communal territory/resource defense to mutualism (Grinnell *et al.* 1995), reciprocity, or kin selection (Clutton-Brock 2002; 2009), and cooperative antipredator defense has been similarly linked to kin selection (Dugatkin, 1997). Thus, findings from this study support the seemingly important role of kin selection suggested previously (Dugatkin, 1997; Sherman, 1997; Clutton-Brock 2002). On the other hand, cooperative behaviors that remained unassociated to social monogamy or low promiscuity during this study have been previously linked to multiple evolutionary mechanisms. For example, communal nesting has been associated with kin selection (König, 1994; Koprowski, 1996; Rusu & Krackow, 2004), communal burrowing linked to reciprocity or kin selection (Vásquez 2016) and mutualism (Clutton-Brock, 2009); mutual allogrooming to reciprocity (Clutton-Brock, 2009; Hart & Hart, 1992; Schino & Aureli, 2008, 2010), , and food sharing associated with reciprocity (Carter & Wilkinson, 2013; Dugatkin, 1997; Jaeggi & Gurven, 2013). Thus, each particular cooperative trait may be associated with multiple mechanisms. However, both the presence of cooperation (measured as a binary trait) and of reproductive cooperation were similarly associated with social monogamy of the ancestral states. These findings strongly support that the evolution of these some individual cooperative traits and of cooperation overall have been linked to low

rates of promiscuity. Therefore, cooperation in this rodent clade represents a single evolutionary origin from the oldest ancestors, mainly by kin selection, which satisfies the scenario previously suggested for this group (Burda, 1999; Burda *et al.* 2000). Under this evolutionary scenario, the main mechanism favoring the origin of group-living and cooperation across hystricognaths is the formation of close-kin social units through social monogamy. Notably, findings from this study support this explanation by showing that social monogamy precedes the emergence of within-group kinship. Presumably, this provided appropriate conditions for kin selection to favor generalized cooperation in different contexts (Boomsma, 2009; Bourke, 2011, 2014; Cornwallis *et al.* 2010; Foster *et al.* 2006; Nowak, 2006; West *et al.* 2002), a possibility that has been barely assessed (Madden & Clutton-Brock, 2011). With some exceptions (e.g., food sharing in vampire bats, Carter & Wilkinson 2013; Carter *et al.* 2017), each behavior is examined independently and linked to a particular mechanism such as kin selection as an explanation (e.g. kin groups versus non-kin groups: Clutton-Brock 2006; Hatchwell, 2010; Taborsky *et al.* 2016; van Schaik & Kappeler 2006).

Some cooperative behaviors documented for Hystricognathi such as communal burrowing, the presence of active sentinels, and formation of male coalitions were not associated with low promiscuity, probably because its evolution has responded to a more diverse array of selective pressures across certain taxa. For instance, eusociality seems associated to subterranean life in bathyergids (*Heterocephalus* and *Cryptomys-Fukomys*): (Burda *et al.* 2000; Faulkes & Bennett, 2001; Lacey & Sherman 2007), and group-living seems associated with habitat-resource conditions in caviids (*Dolichotis* and *Hydrochoerus*) (Ebensperger & Hayes, 2016; Herrera, 2016; Taber & Macdonald, 1992).

### 4.3 Monogamy and sociality

Findings from this study also highlighted that social monogamy has been associated with the transition from solitary to group-living; suggesting that social monogamy also supersedes the formation of social groups in hystricognaths. However, this evolutionary association may be biased (Kappeler *et al.* 2013; Lukas & Clutton-Brock, 2012; Shultz *et al.* 2011; Silk, 2007). Solitary-living species typically are promiscuous or “sequentially monogamous”, and monogamous species generally live in pairs or family groups, which in turn are classified as social (Clutton-Brock, 1989; Shuster & Wade 2003; Barnard, 2004; Lukas & Clutton-Brock, 2012). Overall however, I recorded that within-group kinship has been important to both group-living and different cooperative behaviors (Boomsma, 2009; Bourke, 2011, 2014; Burda *et al.* 2000; Hughes *et al.* 2008; Queller, 2000). Additionally, the current distribution of mating systems across hystricognath rodents is significantly influenced by ancestor-descendant relationships (Figure 1). Then, social monogamy or low promiscuity, as ancestral trait, was probably an important driver of sociality and cooperation in Hystricognathi, which besides is reflected in its predominance as a social/mating system in the most basal clades of the group, as porcupines (Hystricidae), the rock rat (Petromuridae) and the eusocial bathyergids (Rathbun & Rathbun, 2006; Waterman 2007; Solomon & Getz 1997; Kleiman, 1977). This scenario agrees with evidence found in mammals, suggesting that monogamy was originated from solitary ancestors and cooperative social systems emerged after the evolution of social monogamy, including species with non-reproductive adult helpers (e.g., naked mole-rat) (Lukas & Clutton-Brock, 2013).

#### 4.4 Early origin of sociality and cooperation

Ancestors of hystricognaths were social, confirming a previous examination (Sobrero *et al.* 2014). Additionally, most cooperative behaviors reported in current-day species evolved early, supporting that relatively high levels of cooperation and group-living were associated with the origin of Hystricognathi. These findings support Burda *et al.*'s (2000) hypothesis stating that cooperative breeding was associated with the origins of Bathyergidae, and of an early origin of sociality through all Hystricognathi. Likely, the transition into sociality may have been one main evolutionary event that took place early in the origins of the clade about 50-45 Ma during Middle Eocene (Upham & Patterson, 2015). Intriguingly, the sister group of Hystricognathi, the Ctenodactylidae, includes social and colonial species with cases of cooperative behavior well documented (Nutt, 2005; 2007). Therefore, it seems likely that the whole suborder Ctenohystrica (Fabre *et al.* 2012; Huchon *et al.* 2000) may have had social ancestors.

Previously, Sobrero *et al.* (2014) reported that transitions from social to solitary-living were associated with closed, high vegetation cover habitats, and that the ancestral habitat of hystricognaths was likely open, with scarce vegetation cover. These findings suggest that sociality was advantageous mostly in habitats with high risk of predation (i.e. open habitats; Ebensperger & Blumstein 2006, Sobrero *et al.* 2014). However, most phylogenetic, evolutionary and paleontological studies have placed estimation of divergence time for the early hystricognath ancestors spanning from the Early Eocene Climatic Optimum until the Middle Eocene Climate Optimum (between 53 – 41 Ma; Ctenohystrica, Hystricognathi and Caviomorpha/Phiomorpha splits; Antoine *et al.*, 2012; Barbrière & Marivaux, 2015; Lazo

2018; Marivaux & Boivin, 2019; Upham & Patterson, 2012; 2015; Upham *et al.*, 2019). Thus, hystricognath ancestors faced hot and wet conditions that lacked polar icecaps and had mean global temperatures  $>10$  °C warmer than current temperatures, and where dominant tropical and sub-tropical forest ecosystems reached high latitudes (Zachos *et al.*, 2008). This scenario poses the absolute opposite of reconstructed environmental scenario for hystricognath ancestors. Nevertheless, the presence of semi-open habitats cannot be ruled out in the context of such “greenhouse tropical forest” conditions. Paleobotanical studies support that ecosystems during these times were diverse, characterized by the onset of grasses, and included regions with seasonally dry climate conditions (Strömberg, 2011; Utescher & Mosbrugger, 2007). Alternatively, incongruence between ancestral habitat reconstruction and Eocene environmental-climatic conditions during the origin of hystricognaths may imply a secondary role for predation risk. The formation of monogamy pairs, and subsequently family groups, preceded the origin of sociality in these rodents. Lukas & Clutton-Brock (2013) reported that social monogamy in mammals evolved from solitary and territorial female ancestors, and that cooperative social systems emerged after the evolution of social monogamy (within close-kin social groups). Therefore, habitat characteristics associated with relatively high predation risk may have played only a secondary role on the evolution of Hystricognathi sociality. Remarkably, communal burrowing (characteristic of some fossorial and semifossorial species) is not the ancestral state in Hystricognathi, suggesting that ancestors had an above-ground lifestyle. Therefore, fossoriality, which leads to cooperatively burrowing and nesting, would be a derived trait in this lineage. This possibility is consistent with the suggestion that underground life represents a derived trait that originated from social ancestors across all rodents (Smorkatcheva & Lukhtanov 2014).

Lastly, Hystricognathi represents a clear example of how ancestor-descendant relationships influence the current expression of phenotypic traits, namely social traits in the current context. Thus, both phylogeny and ecological conditions represent relevant drivers of social behavior in hystricognaths (Rowe & Honeycutt, 2002; Sobrero *et al.* 2014). These findings add to the importance of phylogenetic relationships on the evolution of behavioral, life history and ecological traits reported previously in different taxa (Briga *et al.* 2012; Cornwallis *et al.* 2010; Dugatkin, 2002; Kappeler *et al.* 2013; Linklater, 2000; Lukas & Clutton-Brock, 2012; Thierry, 2013).

## **5. Concluding remarks**

Together, results from this study confirmed that Hystricognathi evolved from a social ancestor exhibiting a mating system characterized by low promiscuity or social monogamy. Additionally, different forms of cooperative behavior evolved early, implying that relatively high levels of cooperation and group-living were associated with the origin of these rodents. These findings support the monogamy hypothesis as an explanation for the evolution of sociality and cooperative behavior, with kin selection as an underlying evolutionary mechanism (Burda *et al.* 2000, Boomsma, 2009).

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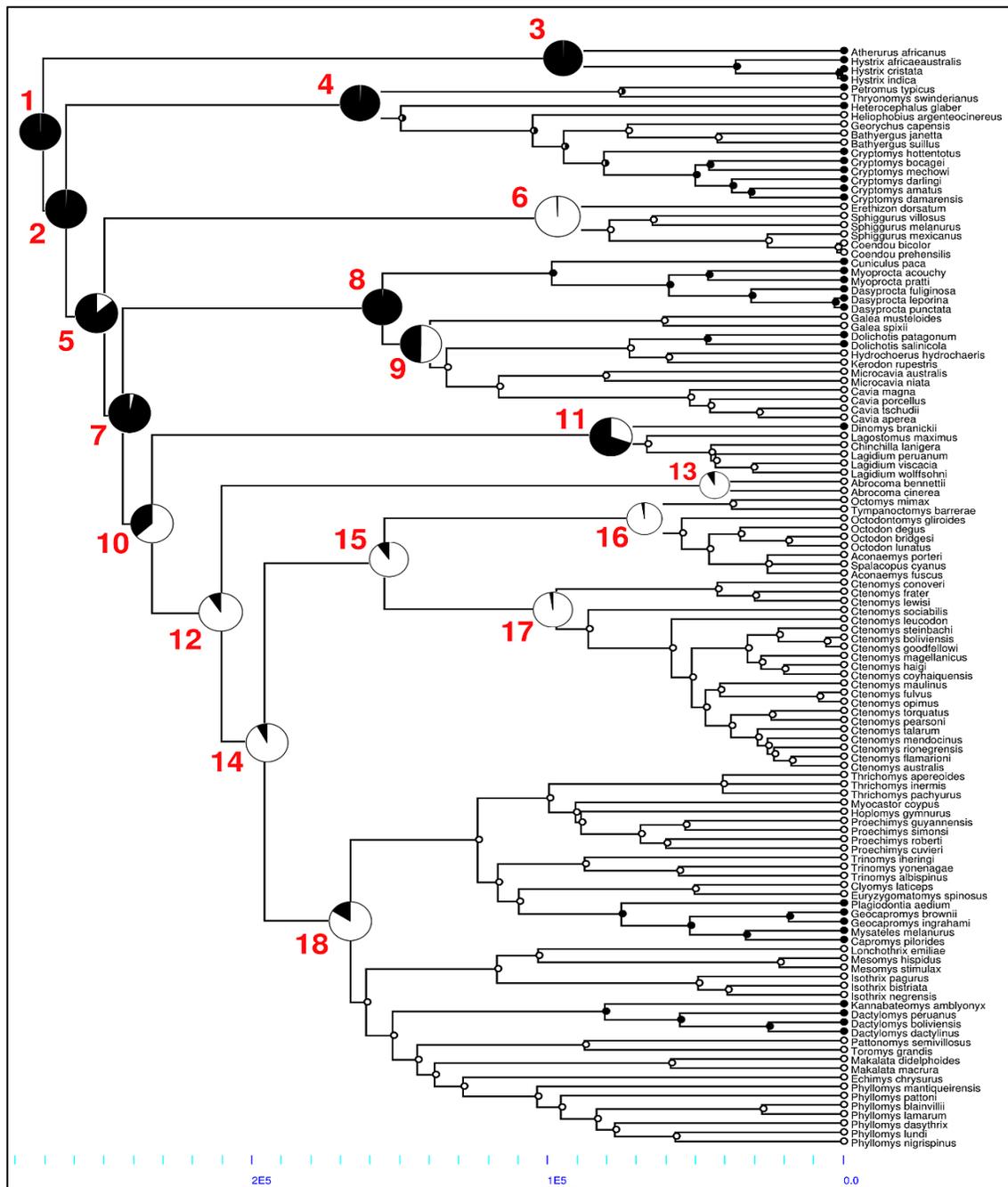
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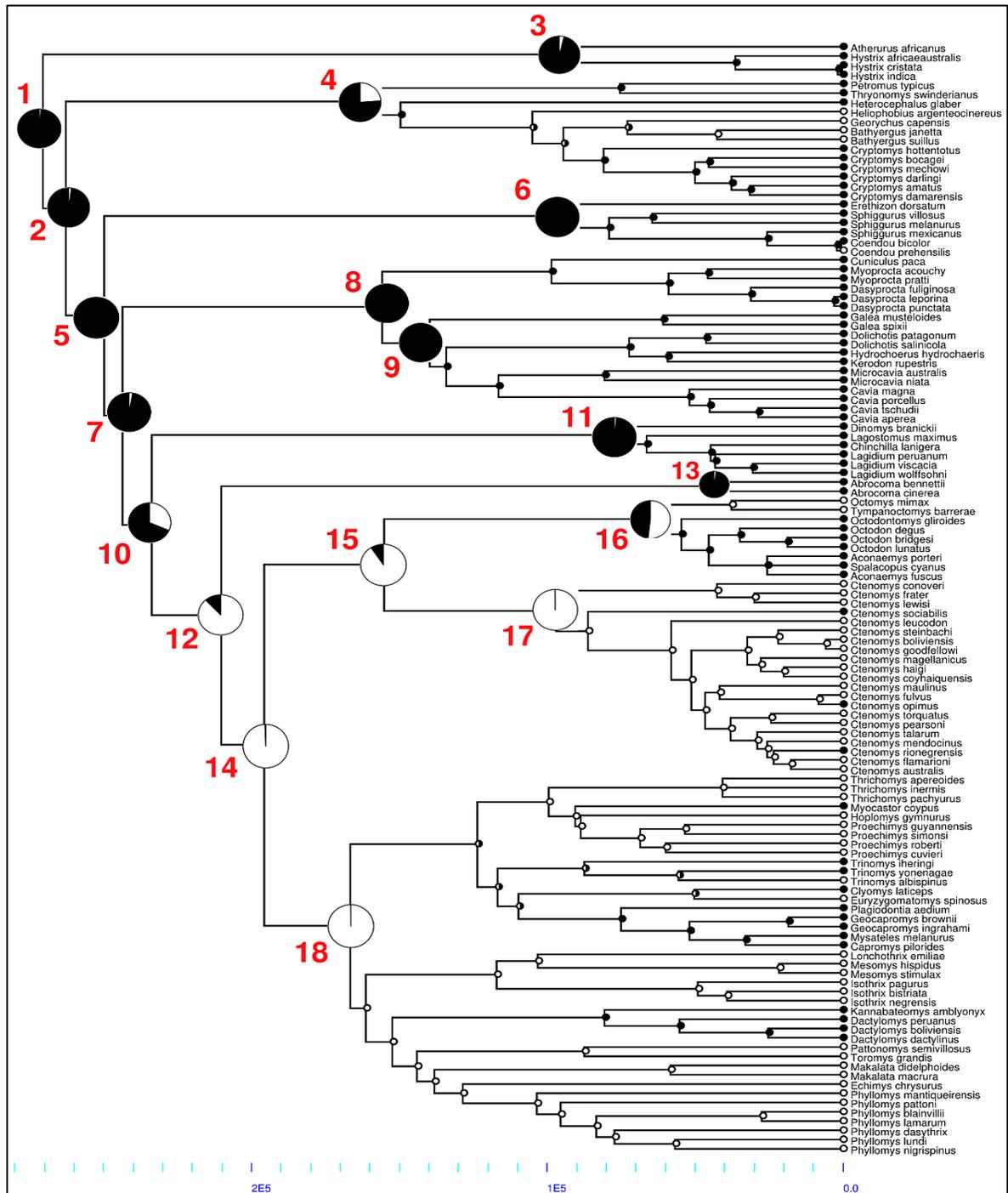
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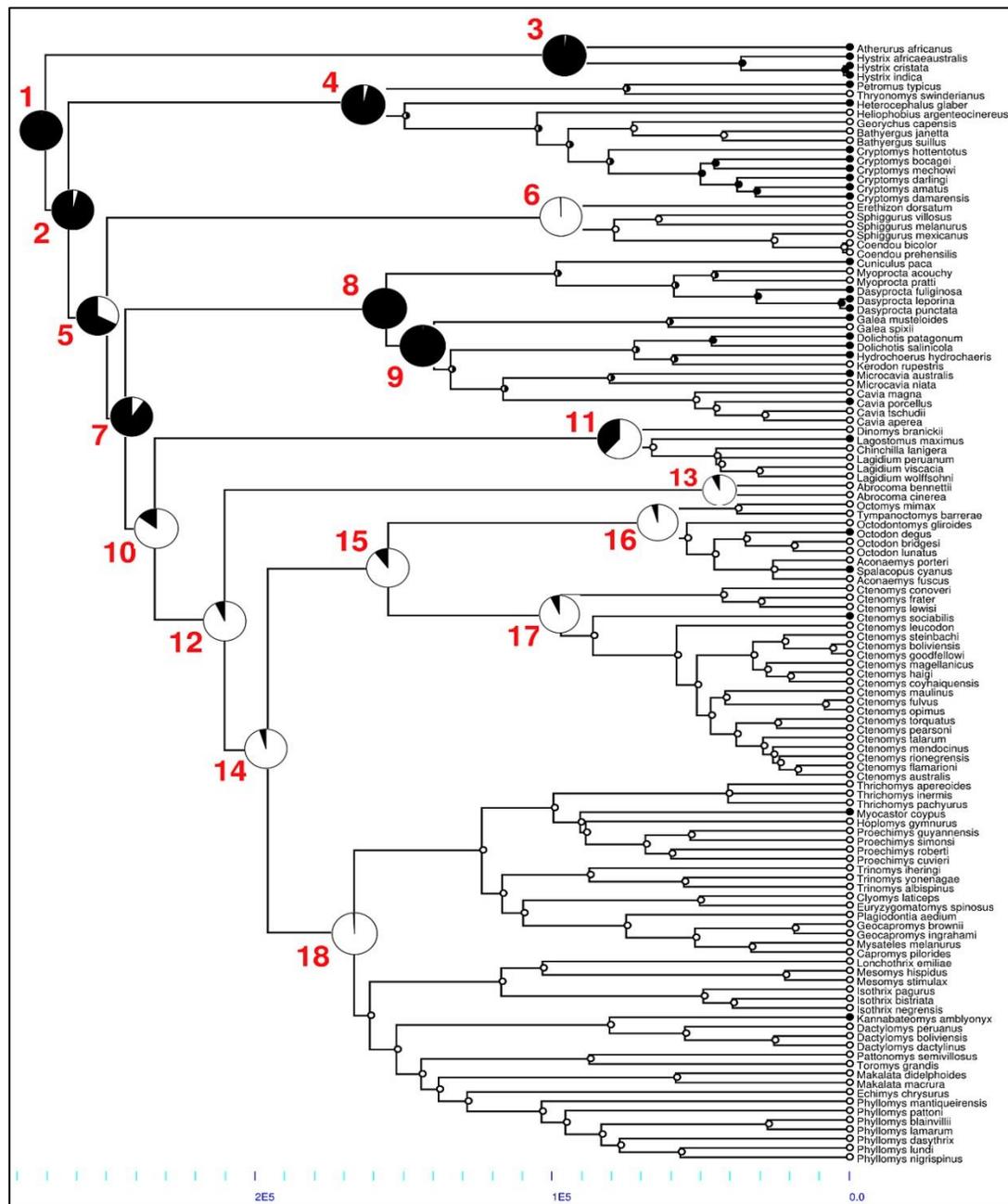
## FIGURES



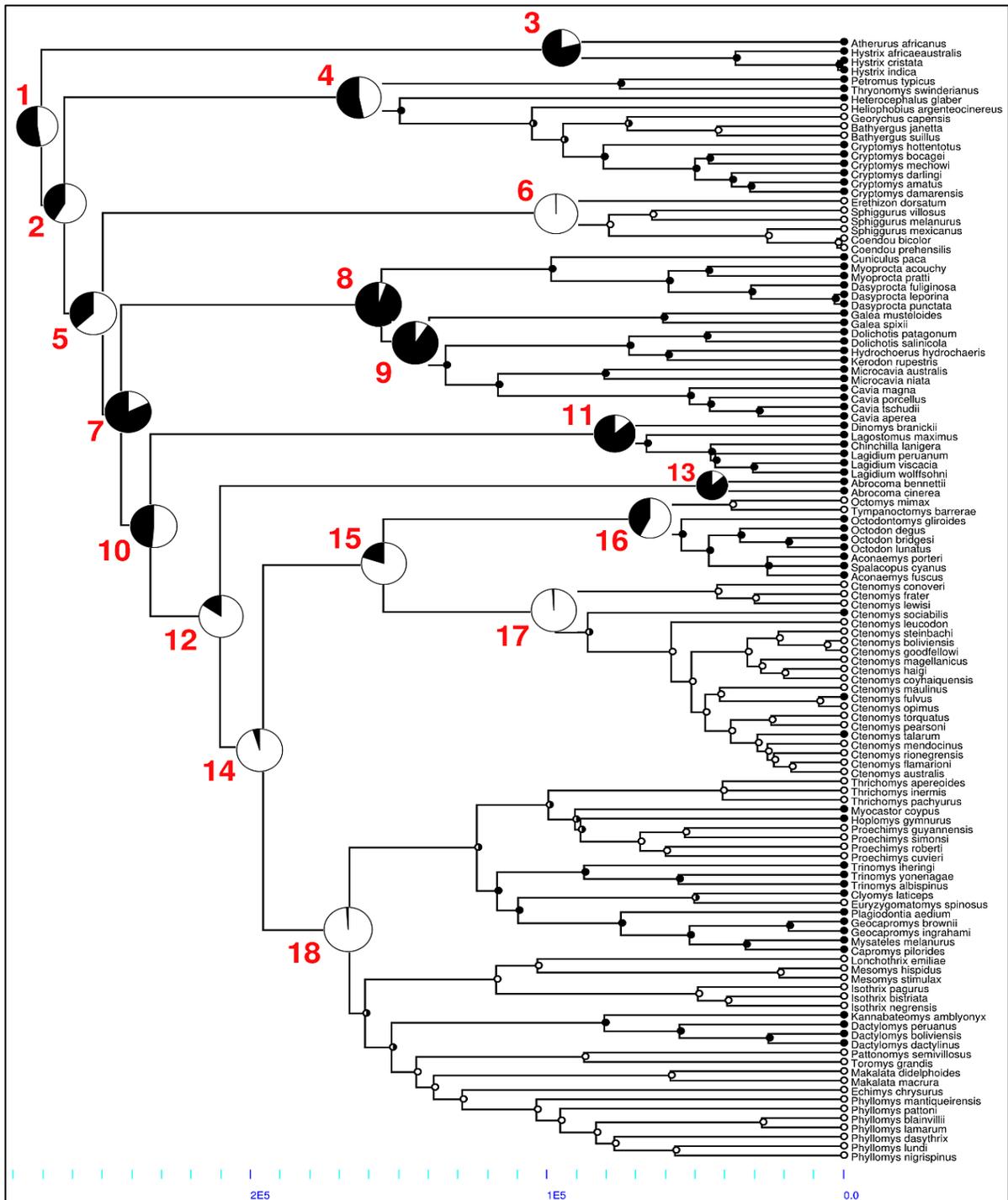
**Figure 1.** Ancestral states reconstruction of mating system in hystricognath rodents. Circles in the tips of the phylogenetic tree represent presence of social monogamy or low promiscuity (black), or predominance of a promiscuous mating system (white). Large sized pie charts in the phylogeny nodes quantifies the proportional likelihood of each state estimated. Red node ID numbers in each large sized pie chart are those same listed in Table 2. The phylogenetic tree was ultrametrized and branch lengths scaled for visual purposes only.



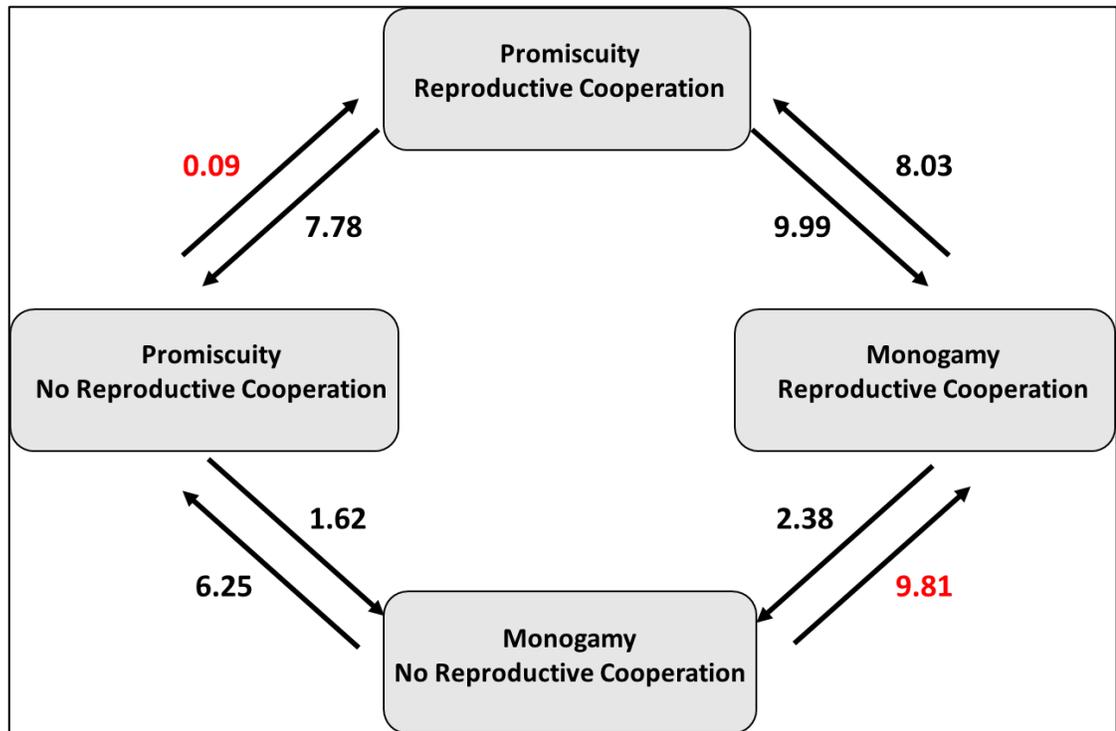
**Figure 2.** Ancestral states reconstruction of social system in hystricognath rodents. Circles in the tips of the phylogenetic tree represent presence (black) or absence (white) of group-living (sociality). Large-sized pie charts in the phylogeny nodes represent the proportional likelihood of each state estimated. Red node ID numbers in each large-sized pie chart are those same listed in Table 2. Phylogenetic tree was ultrametrized and branch lengths scaled for visual purposes only.



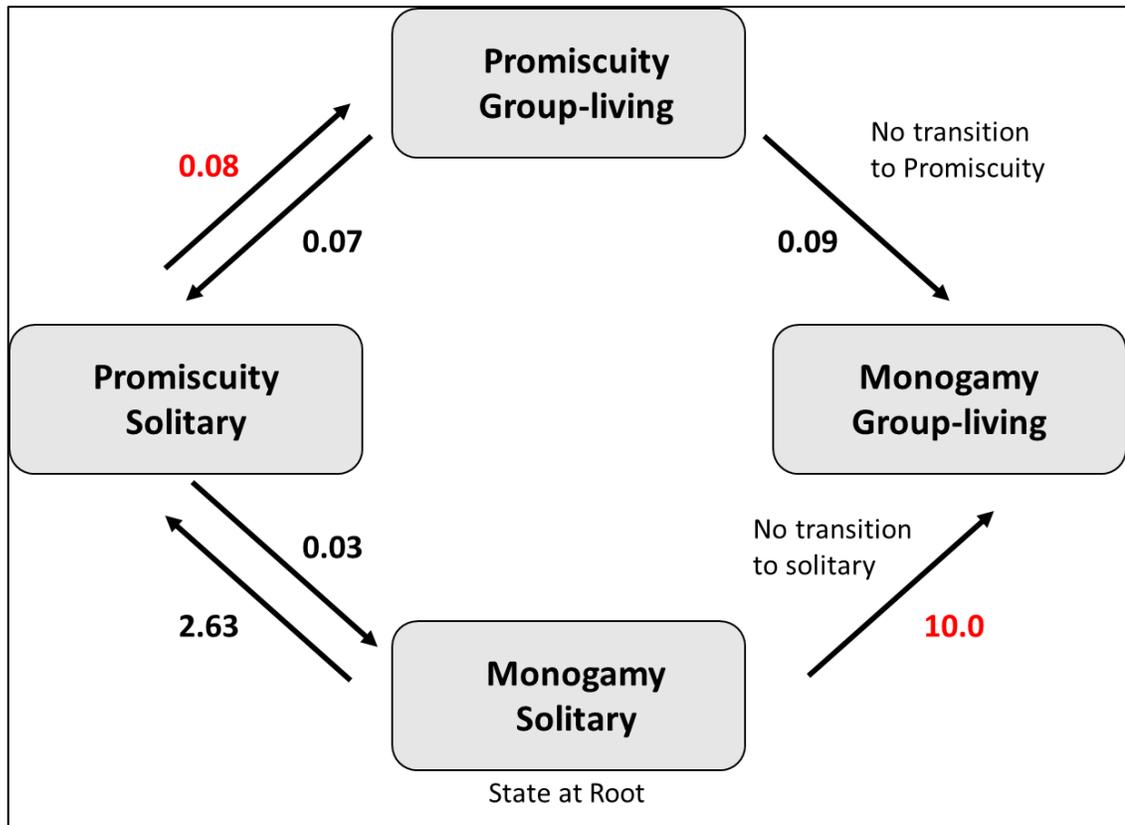
**Figure 3.** Ancestral states reconstruction of reproductive cooperation in hystricognath rodents. Circles in the tips of the phylogenetic tree represent presence of cooperative breeding, paternal care, or communal rearing (black), or absence of reproductive cooperation (white). Large-sized pie charts in the phylogeny nodes represent the proportional likelihood of each state estimated. Red node ID numbers in each large-sized pie chart are those same listed in Table 2. Phylogenetic tree was ultrametric and branch lengths scaled for visual purposes only.



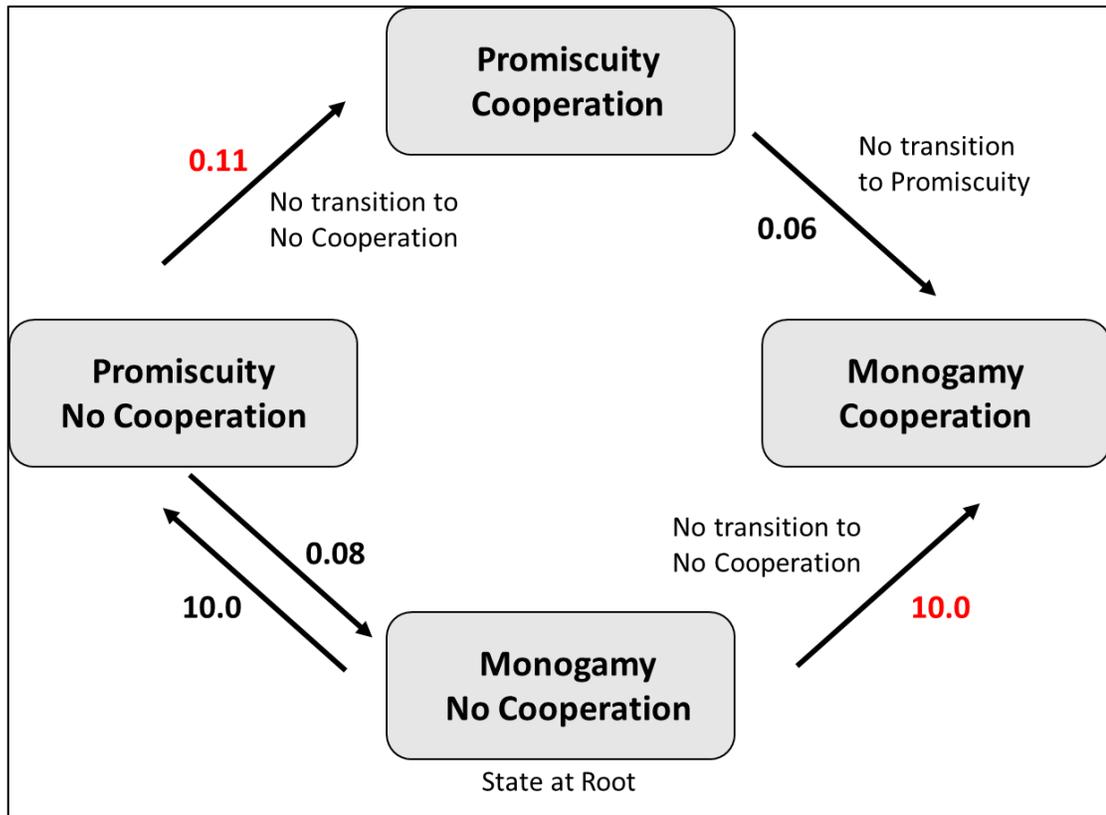
**Figure 4.** Ancestral states reconstruction of cooperation in hystricognath rodents. Circles in the tips of the phylogenetic tree represent presence (black) or absence (white) of at least one cooperative behavior. Large-sized pie charts in the phylogeny nodes represent the proportional likelihood of each state estimated. Red node ID numbers in each large-sized pie chart are those same listed in Table 2. Phylogenetic tree was ultrametricized and branch lengths scaled for visual purposes only.



**Figure 5.** Correlated evolution between mating system and reproductive cooperation. Rates in bolded red indicate transitions to reproductive cooperation from promiscuity and monogamy states. State of characters at the root of Hystricognathi not defined (all probabilities was roughly equal).



**Figure 6.** Correlated evolution between mating system and group-living (sociality). Rates in bolded red indicate transitions to group-living from promiscuity and monogamy states. State of characters at the root of Hystricognathi has 0.58 of probability.



**Figure 7.** Correlated evolution between mating system and cooperation. Rates in bolded red indicate transitions to cooperation from promiscuity and monogamy states. State of characters at the root of Hystricognathi has 0.76 of probability.

## TABLES

**Table 1.** Ancestral trait states for most basal nodes of Hystricognathi phylogenetic reconstruction. Column State (1) denotes the “presence” character state (1) for each binary trait enlisted. Values in the ancestral node columns are probabilities (0-1) for state “presence” (1) or absence (0) for binary traits. Node ID is marked with the same number ID in phylogenetic trees illustrate in Figures 1-4 and correspond with nodes number ID denoted in Table 2. Horizontal solid line divides between “social organization” characters (above the line) and cooperative behaviors (below the line).

Trait	State (1)	P(1) Ancestral Hystricognathi (node 1 or root)	P(1) Ancestral Caviomorpha + Phiomorpha (node 2)	P(1) Ancestral Phiomorpha (node 4)	P(1) Ancestral Caviomorpha (node 5)
Social system	Social	0.988	0.979	0.762	0.993
Mating system	Monogamy (low promiscuity)	0.998	0.996	0.995	0.862
Communal nesting	Presence	0.992	0.986	0.799	0.995
Within-group kinship	Some level of kin-presence	0.99	0.963	0.814	0.913
Cooperation	Presence at least 1 cooperative behavior	0.527	0.414	0.533	0.369
Reproductive cooperation	Allomothering care	0.992	0.958	0.961	0.676
Alarm calls	Presence	0.951	0.811	0.795	0.581
Allogrooming	Presence	0.751	0.909	0.77	0.833
Communal territory/resource defense	Presence	0.999	0.997	0.996	0.916
Food sharing	Presence	0.936	0.962	0.946	0.731
Information transfer	Presence	0.958	0.407	0.915	0.007
Cooperative antipredator defense	Presence	0.5	0.5	0.5	0.498
Communal burrowing	Presence	0.308	0.05	0.537	0.003
Active sentinels	Presence	0	0	0	0
Male coalitions	Presence	0	0	0	0

**Table 2.** Node number ID of Hystricognathi phylogenetic tree. These ID identified a particular taxon show in column “Node grouped taxa”. These node ID is the same used in Figures 1-4 and Table 1.

<b>ID Node</b>	<b>Node grouped taxa</b>	<b>Node level</b>
1 (Root)	Hystricognathi	Infraorder
2	Caviomorpha + Phiomorpha	Infraorder-Parvorder
3	Hystricidae	Family
4	Phiomorpha	Parvorder
5	Caviomorpha	Parvorder
6	Erethizontoidea	Superfamily
7	Cavioidea + (Chinchilloidea + Octodontoidea)	Superfamilies
8	Cavioidea	Superfamily
9	Caviidae	Family
10	Chinchilloidea + Octodontoidea	Superfamilies
11	Chinchilloidea	Superfamily
12	Octodontoidea	Superfamily
13	Abrocomidae	Family
14	(Octodontidae + Ctenomyidae) + Echimyidae	Families
15	Octodontidae + Ctenomyidae	Families
16	Octodontidae	Family
17	Ctenomyidae	Family
18	Echimyidae	Family

**Table 3.** Models of dependent (correlated) or independent evolution between two discrete binary traits tested with Likelihood Ratio (LR) and chi-square ( $X^2$ ) tests. P values < 0.05 and numbers in bolded red indicate statistical significance. The column “Monogamy Hypothesis support” denotes with “yes” when the dependent model revealed a relatively high probability that social monogamy preceded the transition from absence to presence of the other trait.

Trait	Log-lh dependent model	Log-lh independent model	LR	$X^2$ test (p value)	Significant model	Monogamy Hypothesis support
Mating system -- Reproductive cooperation	-115.066	-125.25	20.367	<b>0.0004</b>	dependent	yes
Mating system – Social system	-73.617	-83.834	20.435	<b>0.0004</b>	dependent	yes
Mating system – Cooperation	-68.318	-79.804	22.972	<b>0.0001</b>	dependent	yes
Mating system – Alarm calls	-79.387	-84.369	9.964	<b>0.041</b>	dependent	yes
Mating system – Cooperative antipredator defense	-42.221	-46.994	9.546	<b>0.049</b>	dependent	yes
Mating system – Communal burrowing	-72.923	-79.398	12.949	<b>0.012</b>	dependent	no
Mating system – Communal territory or resource defense	-62.082	-74.761	25.357	<b>&lt; 0.0001</b>	dependent	yes
Mating system – Within-group kinship	-83.139	-88.965	11.652	<b>0.02</b>	dependent	yes
Mating system – Active sentinels	-52.631	-50.765	3.731	0.444	---	---
Mating system – Male coalitions	-34.475	-38.747	8.543	0.074	---	---
Mating system -- Allogrooming	-133.544	-113.449	40.191	<b>&lt; 0.0001</b>	independent	---
Mating system – Food sharing	-105.535	-96.834	17.403	<b>0.002</b>	Independent	---
Mating system – Information transfer	-95.4	-88.593	13.613	<b>0.009</b>	independent	---
Mating system – Communal nesting	-144.334	-139.167	10.334	<b>0.035</b>	independent	---

**SUPPLEMENTARY MATERIAL**

**Table S1.** Characteristics of the sequence data partitions occupied in phylogenetic reconstruction. CYTB: cytochrome b mitochondrial gene; GHR: growth hormone receptor nuclear gene.

	<b>mtDNA</b>	<b>Exon</b>	<b>Combined two-gene</b>
	<b>CYTB</b>	<b>GHR</b>	
N° of species aligned	185	95	188
Aligned sites	1140	888	2028
N° variable sites	744	586	1330
N° conserved sites	396	302	698
N° parsimony informative sites	642	463	1105
Best-fit model of DNA substitution	GTR+G+I	GTR+G+I	----

**Table S2.** Results of the Xia's test of substitution for each gene. Saturation is indicated whenever  $I_{ss} > I_{ss.c}$ , and a non-significant difference (NS) indicates some degree of saturation. Tajima's test of neutrality compares the number of segregating sites per site with the nucleotide diversity. A  $D$  statistics = 0 indicates neutrality,  $D < 0$  indicates recent selective sweep, and  $D > 0$  indicates balancing selection, but only if estimates are statistically significant (NS: non-significant). A  $p$ -value  $< 0.05$  indicates statistical significance; CYTB: cytochrome b mitochondrial gene; GHR: growth hormone receptor nuclear gene.

	mtDNA	Nuclear Exon
	CYTB	GHR
Xia's test	NS	Unsaturated
$I_{ss}$	0.677	0.410
$I_{ss.c}$	0.728	0.712
$p$ -value	0.0676	$< 0.0001$
Tajima's neutrality test	NS	NS
$D$ statistic	1.199078	-0,844060
$p$ value	0,1195	0,0984

**Table S3.** Hystricognathi Database: list of species used in this study.

Species	Family	CYTBank accession number	GHR GenBank accession number	Mating system	Mating system (binary)	Social system (binary)	Kinship category (binary)	Communal nesting	Breeding system (reproductive cooperation)	Reproductive cooperation (binary)	Cooperation score	Cooperation score (binary)	Communal Territory or resource defense	Mutual Allogrooming	Antipredator cooperative defense	Food sharing	Communal burrowing	Active sentinels	Information Transfer	Alarm callings	Male Coalitions	References
<i>Abrocoma bennettii</i>	Abrocomidae	AF244387	JN414754	2	0	1	1	1	0	0	3	1	1	1	0	0	1	0	0	0	0	13
<i>Abrocoma cinerea</i>	Abrocomidae	AF244388	AF520643	2	0	1	1	1	0	0	3	1	1	1	0	0	1	0	0	0	0	35; 43
<i>Aconaemys fuscus</i>	Octodontidae	KC731571	AF520657	0	0	1	0	1	0	0	3	1	0	0	0	1	1	0	0	1	0	33
<i>Aconaemys porteri</i>	Octodontidae	-	AF520644	0	0	1	0	1	0	0	3	1	0	0	0	1	1	0	0	1	0	33
<i>Atherurus africanus</i>	Hystricidae	KJ193304	-	3	1	1	1	1	3	1	7	1	1	0	0	0	1	0	1	1	0	5; 23; 25; 43; 48
<i>Bathyergus janetta</i>	Bathyergidae	AF012241	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Bathyergus suillus</i>	Bathyergidae	AY425913	FM162080	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23
<i>Capromys pilorides</i>	Capromyidae	KM014004	AF433949	3	1	1	0	1	0	0	2	1	0	1	0	0	0	0	0	1	0	43
<i>Cavia aperea</i>	Caviidae	GU136754	AF433930	2	0	1	1	1	1	0	3	1	0	1	0	0	0	0	0	1	0	2; 13; 21; 23; 43; 49; 57
<i>Cavia magna</i>	Caviidae	GU136735	-	1	0	1	0	1	0	0	2	1	0	1	0	0	0	0	0	1	0	2; 13; 57
<i>Cavia porcellus</i>	Caviidae	AY247008	AF433931	2	0	1	1	1	2	1	5	1	0	1	0	1	0	0	0	1	0	30; 43; 48
<i>Cavia tschudii</i>	Caviidae	GU136731	FJ855206	2	0	1	1	1	1	0	3	1	0	1	0	0	0	0	0	1	0	15
<i>Chinchilla lanigera</i>	Chinchillidae	AF464762	AF332036	2	0	1	1	1	1	0	4	1	1	1	0	0	0	0	0	1	0	13; 23; 26; 34; 43; 50
<i>Clyomys laticeps</i>	Echimyidae	AF422918	KJ742628	1	0	1	0	1	0	0	2	1	0	1	0	0	1	0	0	0	0	9
<i>Coendou bicolor</i>	Erethizontidae	KC463859	-	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Coendou prehensilis</i>	Erethizontidae	KC463873	AF520663	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24; 26; 43
<i>Cryptomys amatus</i>	Bathyergidae	EF043468	-	3	1	1	1	1	2	1	7	1	1	1	0	1	1	0	1	0	0	45
<i>Cryptomys bocagei</i>	Bathyergidae	AF012229	-	3	1	1	1	1	2	1	7	1	1	1	0	1	1	0	1	0	0	4
<i>Cryptomys damarensis</i>	Bathyergidae	AY425857	FN984748	3	1	1	1	1	3	1	9	1	1	1	1	1	1	0	1	0	0	8; 19; 21; 47
<i>Cryptomys darlingi</i>	Bathyergidae	AF012232	-	3	1	1	1	1	3	1	8	1	1	1	0	1	1	0	1	0	0	19; 47
<i>Cryptomys hottentotus</i>	Bathyergidae	AF012232	FJ855202	3	1	1	1	1	3	1	8	1	1	1	0	1	1	0	1	0	0	10; 19; 47

Species	Family	CYTB GenBank accession number	GHR GenBank accession number	Mating system	Mating system (binary)	Social system (binary)	Kinship category (binary)	Communal nesting	Breeding system (reproductive cooperation)	Reproductive cooperation (binary)	Cooperation score	Cooperation score (binary)	Communal Territory or resource defense	Mutual Allogrooming	Antipredator cooperative defense	Food sharing	Communal burrowing	Active sentinels	Information Transfer	Alarm callings	Male Coalitions	References
<i>Cryptomys mehowi</i>	Bathyergidae	EF043451	-	3	1	1	1	1	3	1	8	1	1	1	0	1	1	0	1	0	0	19; 21; 47
<i>Ctenomys australis</i>	Ctenomyidae	AF370697	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28; 45
<i>Ctenomys boliviensis</i>	Ctenomyidae	AF007037	JN414757	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Ctenomys conoveri</i>	Ctenomyidae	AF007054	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Ctenomys coyhaiquensis</i>	Ctenomyidae	AF119112	KF590678	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Ctenomys flamarioni</i>	Ctenomyidae	AF119107	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28; 45
<i>Ctenomys frater</i>	Ctenomyidae	AF007046	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Ctenomys fulvus</i>	Ctenomyidae	AF370686	-	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	28; 45
<i>Ctenomys goodfellowi</i>	Ctenomyidae	AF007050	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Ctenomys haigi</i>	Ctenomyidae	HM777476	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28; 45
<i>Ctenomys leucodon</i>	Ctenomyidae	AF007056	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Ctenomys lewisi</i>	Ctenomyidae	AF007049	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Ctenomys magellanicus</i>	Ctenomyidae	DQ333326	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15; 45
<i>Ctenomys maulinus</i>	Ctenomyidae	AF370703	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28; 45
<i>Ctenomys mendocinus</i>	Ctenomyidae	AF370696	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28; 45
<i>Ctenomys opimus</i>	Ctenomyidae	AF370701	-	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28; 43
<i>Ctenomys pearsoni</i>	Ctenomyidae	HM777486	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28; 43; 45
<i>Ctenomys rionegrensis</i>	Ctenomyidae	AF538375	-	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	28; 54
<i>Ctenomys sociabilis</i>	Ctenomyidae	HM777495	-	1	0	1	1	1	2	1	5	1	0	0	0	1	1	0	0	1	0	18; 21; 27; 28; 31; 47
<i>Ctenomys steinbachi</i>	Ctenomyidae	AF007043	AF520656	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Ctenomys talarum</i>	Ctenomyidae	AF370698	-	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	11; 24; 28; 43; 49; 57; 59
<i>Ctenomys torquatus</i>	Ctenomyidae	AF119110	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28; 45
<i>Cuniculus paca</i>	Cuniculidae	AY206565	AF433927	3	1	1	1	1	2	1	6	1	1	1	0	1	0	0	0	1	0	11; 13; 23; 26; 43

Species	Family	CYTB GenBank accession number	GHR GenBank accession number	Mating system	Mating system (binary)	Social system (binary)	Kinship category (binary)	Communal nesting	Breeding system (reproductive cooperation)	Reproductive cooperation (binary)	Cooperation score	Cooperation score (binary)	Communal Territory or resource defense	Mutual Allogrooming	Antipredator cooperative defense	Food sharing	Communal burrowing	Active sentinels	Information Transfer	Alarm callings	Male Coalitions	References
<i>Dactylomys boliviensis</i>	Echimyidae	L23339	KF590679	3	1	1	0	0	0	0	2	1	1	0	0	0	0	0	0	1	0	45
<i>Dactylomys dactylinus</i>	Echimyidae	L23335	KF590681	3	1	1	0	0	0	0	2	1	1	0	0	0	0	0	0	1	0	43; 45
<i>Dactylomys peruanus</i>	Echimyidae	EU313206	-	3	1	1	0	0	0	0	2	1	1	0	0	0	0	0	0	1	0	45
<i>Dasyprocta fuliginosa</i>	Dasyproctidae	AF437784	-	3	1	1	0	0	2	1	5	1	1	1	0	0	0	0	0	1	0	13; 43
<i>Dasyprocta leporina</i>	Dasyproctidae	AF437783	FJ855207	3	1	1	1	0	2	1	5	1	1	1	0	0	0	0	0	1	0	13
<i>Dasyprocta punctata</i>	Dasyproctidae	-	AF433942	3	1	1	0	0	2	1	5	1	1	1	0	0	0	0	0	1	0	13; 23; 43
<i>Dinomys branickii</i>	Dinomyidae	AY254884	AF520659	3	1	1	1	0	0	0	2	1	0	1	0	0	0	0	0	1	0	13; 43
<i>Dolichotis patagonum</i>	Caviidae	AY382787	AF433939	3	1	1	0	1	2	1	7	1	1	1	0	0	1	1	0	1	0	13; 23; 43; 48; 52; 53; 57
<i>Dolichotis salinicola</i>	Caviidae	GU136723	AF433940	3	1	1	1	1	2	1	7	1	1	1	0	0	1	1	0	1	0	13; 43
<i>Echimys chrysurus</i>	Echimyidae	L23341	FM162082	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	43; 45
<i>Erethizon dorsatum</i>	Erethizontidae	KC463889	AF520658	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	23; 38; 43; 45; 51; 57
<i>Euryzgomatomys spinosus</i>	Echimyidae	EU544667	KJ742629	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Galea musteloides</i>	Caviidae	GU082485	AF433932	1	0	1	0	1	2	1	4	1	0	1	0	0	0	0	0	1	0	2; 13; 21; 23; 43; 57
<i>Galea spixii</i>	Caviidae	GU067492	AF433934	1	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	2; 13; 43
<i>Geocapromys brownii</i>	Capromyidae	KJ742653	KJ742644	3	1	1	1	1	0	0	2	1	0	1	0	0	0	0	0	1	0	13; 43
<i>Geocapromys ingrahami</i>	Capromyidae	KM014006	KM013985	3	1	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	13
<i>Georychus capensis</i>	Bathyergidae	AF012243	FJ855203	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Heliophobius argenteocinereus</i>	Bathyergidae	U87527	FJ855204	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23; 37
<i>Heterocephalus glaber</i>	Bathyergidae	AF155870	AF332034	3	1	1	1	1	3	1	10	1	1	1	1	1	1	0	1	1	0	9; 12; 19; 40; 43; 47; 57
<i>Hoplomys gymnurus</i>	Echimyidae	AF422922	JN414758	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	43
<i>Hydrochoerus hydrochaeris</i>	Caviidae	GU136721	FJ855208	1	0	1	1	0	2	1	7	1	1	1	1	0	0	0	0	1	1	13; 21; 22; 23; 36; 43
<i>Hystrix africaeaustralis</i>	Hystriidae	X70674	AF332033	3	1	1	1	1	2	1	6	1	1	0	0	0	1	0	1	1	0	5; 24; 43; 57
<i>Hystrix cristata</i>	Hystriidae	FJ472579	-	3	1	1	1	1	2	1	6	1	1	0	0	0	1	0	1	1	0	5; 23; 25; 29; 43

Species	Family	CYTB GenBank accession number	GHR GenBank accession number	Mating system	Mating system (binary)	Social system (binary)	Kinship category (binary)	Communal nesting	Breeding system (reproductive cooperation)	Reproductive cooperation (binary)	Cooperation score	Cooperation score (binary)	Communal Territory or resource defense	Mutual Allogrooming	Antipredator cooperative defense	Food sharing	Communal burrowing	Active sentinels	Information Transfer	Alarm callings	Male Coalitions	References
<i>Hystrix indica</i>	Hystriidae	AY692229	-	3	1	1	1	1	2	1	6	1	1	0	0	0	1	0	1	1	0	5; 26; 43
<i>Isothrix bistrata</i>	Echimyidae	EU313218	FJ855216	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Isothrix negrensis</i>	Echimyidae	L23355	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Isothrix pagurus</i>	Echimyidae	EU313227	KF590684	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Kannabateomys amblyonyx</i>	Echimyidae	EU544665	-	3	1	1	0	1	2	1	4	1	0	1	0	0	0	0	0	1	0	1; 43
<i>Kerodon rupestris</i>	Caviidae	GU136722	AF433938	2	0	1	0	1	1	0	3	1	0	1	0	0	0	0	0	1	0	2; 13; 34; 43
<i>Lagidium peruanum</i>	Chinchillidae	AY254885	-	2	0	1	1	1	0	0	2	1	0	1	0	0	0	0	0	1	0	13; 34; 43
<i>Lagidium viscacia</i>	Chinchillidae	AY254889	FJ855209	2	0	1	1	1	0	0	2	1	0	1	0	0	0	0	0	1	0	13; 43
<i>Lagidium wolffsohni</i>	Chinchillidae	AY227023	-	2	0	1	1	1	0	0	2	1	0	1	0	0	0	0	0	1	0	15
<i>Lagostomus maximus</i>	Chinchillidae	AF245485	FJ855210	1	0	1	1	1	2	1	6	1	1	1	0	0	1	0	0	1	0	6; 7; 13; 14; 23; 24; 43
<i>Lonchothrix emiliae</i>	Echimyidae	AF422921	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Makalata didelphoides</i>	Echimyidae	L23363	KJ742639	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	43; 45
<i>Makalata macrura</i>	Echimyidae	EU302693	KF590687	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Mesomys hispidus</i>	Echimyidae	L23395	KF590688	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Mesomys stimulax</i>	Echimyidae	L23392	KJ742630	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Microcavia australis</i>	Caviidae	AF491750	AF433936	1	0	1	1	1	2	1	5	1	0	1	0	0	1	0	0	1	0	2; 13; 21; 43; 56; 57
<i>Microcavia niata</i>	Caviidae	GU136725	-	1	0	1	0	1	1	0	4	1	0	1	0	0	1	0	0	1	0	2; 13; 43
<i>Myocastor coypus</i>	Myocastoridae	EU544663	AF520662	2	0	1	1	1	2	1	6	1	0	1	0	0	1	0	1	1	0	1; 8; 20; 24; 43; 55; 57
<i>Myoprocta acouchy</i>	Dasyproctidae	KJ742649	AF433944	3	1	1	1	0	0	0	3	1	1	1	0	0	0	0	0	1	0	13; 24; 43
<i>Myoprocta pratti</i>	Dasyproctidae	U34850	AF433946	3	1	1	1	0	0	0	3	1	1	1	0	0	0	0	0	1	0	13; 43
<i>Mysateles melanurus</i>	Capromyidae	KJ742669	-	3	1	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	25
<i>Octodon bridgesi</i>	Octodontidae	KJ742651	AF520646	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	28
<i>Octodon degus</i>	Octodontidae	AF422914	AM407928	1	0	1	1	1	2	1	7	1	1	1	0	1	1	0	0	1	0	8; 13; 17; 18; 23; 26; 43; 58



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<i>Thrichomys pachyurus</i>	Echimyidae	JX459899	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Thryonomys swinderianus</i>	Thryomyidae	KJ742647	AF332035	0	0	1	1	0	0	0	3	1	1	0	0	0	1	0	0	1	0	24; 43
<i>Toromys grandis</i>	Echimyidae	KF590699	KF590694	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45
<i>Trinomys albispinus</i>	Echimyidae	U34856	KM013987	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	43
<i>Trinomys iheringi</i>	Echimyidae	EU544664	KF590695	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1; 13; 43
<i>Trinomys yonenagae</i>	Echimyidae	AF194295	JX515328	0	0	1	0	1	0	0	3	1	0	1	0	0	1	0	0	1	0	1; 13; 42
<i>Tympanoctomys barrerae</i>	Octodontidae	AF007060	AF520655	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13; 32; 43

Notes = Mating system column codes: (0) highly promiscuous; (1) promiscuous or highly variable mating system (social groups ranging from promiscuous to monogamous); (2) polygynous; (3) monogamous (including only case of monogamous/polyandrous mating system in *Heterocephalus glaber*). Breeding system (reproductive cooperation) column codes: (0) solitary; (1) plural breeding without communal rearing; (2) communal rearing or singular breeding; (3) cooperative breeding. Cooperative score column: number of cooperative behaviors. All other columns: (0) absence; (1) presence. In References column the numbers are associated with number list in the database references.

**Table S4.** Models evaluated for ancestral states estimation of binary traits. Equal rates model of transitions between two states of traits and model of two rates of transitions (loss and gain with different rates) were tested searching for the best model with Likelihood Ratio (LR) and chi-square test ( $X^2$ ). Significant p value < 0.05 and numbers in bolded red indicate significance. Best model was used for ancestral states estimation. Column “higher rate” indicate if loss or gain of trait have higher rate and are more probably across phylogenetic tree.

Trait	Log-lh equal rates	Log-lh two rates	LR	X <sup>2</sup> test (p value)	Significant model	Higher rate
Social system	-51.07	-50.119	1.903	0.168	---	---
Mating system	-34.592	-35.318	1.453	0.228	---	---
Communal nesting	-57.199	-56.971	0.457	0.499	---	---
Within-group kinship	-57.468	-55.249	4.438	<b>0.035</b>	two rates	loss kinship
Cooperation	-82.485	-55.565	53.84	<b>&lt; 0.0001</b>	two rates	gain cooperation
Reproductive cooperation	-51.908	-47.202	9.411	<b>0.002</b>	two rates	loss reproductive cooperation
Alarm calls	-50.728	-50.654	0.148	0.701	---	---
Allogrooming	-47.08	-49.993	5.825	<b>0.016</b>	equal rates	---
Communal territory/resource defense	-43.602	-41.045	5.114	<b>0.024</b>	two rates	loss communal defense
Food sharing	-31.62	-30.034	3.172	0.075	---	---
Information transfer	-21.618	-21.192	0.851	0.356	---	---
Cooperative antipredator defense	-17.029	-13.279	7.5	<b>0.006</b>	two rates	loss antipredator defense
Communal burrowing	-45.687	-45.682	0.01	0.923	---	---
Active sentinels	-6.597	-6.585	0.024	0.877	---	---
Male coalitions	-5.791	-5.031	1.521	0.218	---	---

### Database references

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**Communal rearing by females enhances offspring attendance, but do not result in indirect benefits in the rodent *Octodon degus***

**Abstract**

Kin selection is commonly an invoked mechanism to explain cooperative behavior in social species, including communal rearing, where females provide indiscriminate care to own offspring and offspring of other females. Uncertain is yet how kin selection influences communally breeding in species exhibiting low kin structure and how females coordinate their attendance to communal litters. I assessed the role of kinship in explaining communal nesting, and the possibility that communally rearing females coordinate their attendance to offspring in the degu. I found that strength of spatial association among lactating females based on burrow sharing during nighttime was not predicted by kinship, implying kin selection is not a driving force explaining this aspect of communal rearing. Additionally, I found that daily time females spent underground (presumably attending their communal litter) did not fit expectations based on complete coordination but that lactating females exhibited some coordination during the short-term. However, female attendance to communal litters increased with the number of females within groups. Thus, kin selection is unlikely to explain communal rearing through enhancing indirect benefits to female degus. Instead, group-size effects on offspring attendance suggest direct benefits contribute to benefits derived from communal rearing.

**Key words:** communal breeding, cooperation, kin selection, relatedness, coordination, direct benefits, *Octodon degus*.

## 1. Introduction

Kin selection (Hamilton, 1964) is the most frequently invoked mechanism to explain cooperation in animals, and where individuals behave in ways to favor genetic kin despite direct costs experienced (Clutton-Brock, 2016; Nowak *et al.* 2017; Smith, 2014). A main prediction here is that frequency of cooperation should be higher among close kin compared with genetically unrelated participants (Hamilton, 1964; Nowak, 2006; West *et al.* 2007a).

Many studies support kin selection as the explanatory mechanism of cooperative behavior in multiple contexts and species (Bourke 2011, 2014; Abbot *et al.* 2011), including mammals (Smith, 2014). In these vertebrates, cooperation during reproduction varies with breeding structure (Clutton-Brock, 2016; Silk, 2007). Most females rear their own young, including solitary species and an important proportion of social species (Clutton-Brock, 2016; Lukas & Clutton-Brock, 2012). However, breeding females in a relatively small number of species either pool their young and share offspring care (i.e., they exhibit communal breeding or plural breeding with communal care strategy; Silk, 2007), or are assisted to rear their offspring by non-breeding helpers (i.e., they exhibit cooperative breeding or singular breeding with cooperative care strategy; Silk, 2007; Lukas & Clutton-Brock, 2012). Thus, individuals in communal breeding species provide indiscriminate care to own offspring and offspring of other females (Emlen 1991, 1995; Lewis & Pusey, 1997; Silk, 2007, Cockburn, 1998). A conspicuous behavior in these species is allonursing, meaning the sharing of milk with young of other females (König 1997; Hayes 2000).

Most female members of communally breeding and communal care species of mammals live in matrilineal groups (e.g., lions, killer whales and elephants; Clutton-Brock,

2016). The distribution of communal breeding is positively correlated with levels of kinship between group members, and cases in which breeding females assist non relatives within-groups remain rare (Briga *et al.* 2012). This pattern supports kin selection as a relevant force driving communal breeding. However, females may also perceive direct and short-term benefits derived from mutualistic or reciprocity-based mechanisms. For instance, female reindeer and sperm whales exhibit reciprocal and mutualistic based allonursing (Engelhardt *et al.* 2015; Gero *et al.* 2009), and alloparental care in sperm whales has been explained by reciprocity and by-product benefits, implying that multiple, non-mutually exclusive mechanisms may contribute to the maintenance of communal breeding. Females exhibiting this form cooperation may reduce energetic costs of parental care through sharing these duties with other mothers, including behaviors such as babysitting and allonursing (Hayes, 2000; König, 1997; Lewis & Pusey, 1997). More specifically, offspring rearing females may benefit directly through allocating more time to foraging, or through enhancing predator detection (Clutton-Brock, 2016; Silk, 2007). Additionally, mothers may improve their offspring growth and survival through reducing nest attendance without increasing the time that their offspring remain unattended. Thus, the amount of parental care received by the offspring either remain the same or increases as more females provide care (Auclair *et al.* 2014; König, 1997). Breeding females may achieve these benefits by alternating nest attendance, meaning they exhibit coordination. This hypothesis has been rarely examined. Some indirect support comes from the observation that lactating females of wild house mice (*Mus musculus*) spend less time at the nest in communally breeding groups compared with solitary nesting mothers, and that communally raised litters face less time unattended (Auclair *et al.* 2014).

Females in several species of rodents exhibit communal breeding and nesting (Hayes 2000), including degus (Ebensperger *et al.* 2002; 2004). Degus (*Octodon degus*) are highly social rodents that live in groups of variable composition and size (1-9 females and 0-3 males; Ebensperger *et al.* 2004; 2012; Hayes *et al.* 2009). Group members share one or more underground burrows and aboveground patches during foraging (Ebensperger *et al.* 2004; Ebensperger *et al.* 2016). Group-living degus are also colonial, meaning that social groups may be spatially clumped (Fulk 1976; Ebensperger *et al.* 2019). Several characteristics of degus suggest kin-related mechanisms may not play a sole role in explaining communal care of offspring. Immigration and emigration of adults into and out of groups are important components of dynamics of social groups (Ebensperger *et al.* 2009; 2016), implying that social group members may not be close relatives. Additionally, male and female degus produce offspring with multiple opposite-sex individuals within groups and with individuals of neighboring groups, a breeding strategy that may prevent inbreeding within groups (Ebensperger *et al.* 2019). As a result, genetic relatedness within groups varies, with some groups consisting of closely related or completely unrelated individuals (Ebensperger *et al.* 2004; Quirici *et al.* 2011a; Davis *et al.* 2016), suggesting that the relevance of kin selection may be similarly variable across groups. Communal rearing in degus has been well demonstrated, and where females often care for and nurse one-another's offspring (Ebensperger *et al.* 2002; 2004). However, the effect of kinship on communal rearing in degus remains debated. While one previous study suggested kin discrimination among captive co-nesting females when nursing their offspring (Jesseau *et al.* 2009), another reported no such kin preference (Ebensperger *et al.* 2006a).

Coordination may enhance hunting success rate, access to large-sized prey, and per capita rate of food intake as reported in cooperative hunting in mammalian carnivores (Bailey *et al.* 2013), and enhance collective vigilance as found in social herpestids group-members take turns as sentinels (Rasa, 1986; Santema & Clutton-Brock, 2013). However, coordination in communally breeding mammals remains relatively unexplored. In degus, coordinated behavior seems similarly variable. Foraging groups do not coordinate their vigilance (Ebensperger *et al.* 2006b; Quirici *et al.* 2008, 2013), but degus coordinate their behavior when digging burrows communally, potentially reducing the cost of burrow construction (Ebensperger & Bozinovic 2000). Coordination by degu breeding females has not been examined, yet Ebensperger *et al.* (2002) reported that young of communal litters spent less unattended and more time cared for by a lactating female than young of single rearing mothers in captivity. Therefore, it is possible that free-ranging females coordinate their attendance to offspring when communally rearing their litters, especially during daytime when females need to forage aboveground and their vulnerable offspring remain in their underground burrows. Thus, offspring may experience enhanced total care received and mothers may allocate more time to other energy enhancing activities such as foraging (Auclair *et al.* 2014).

I aim this study to test (i) the hypothesis that communal rearing of offspring is influenced by kinship among the females in degus. If so, I predicted that strength of association during communal nesting among the females during nighttime increases with genetic relatedness. Secondly, I tested (ii) the hypothesis that communal rearing is coordinated by females within social groups. If so, I predicted that females alternate their attendance to offspring during daytime, reducing both the time that offspring remain unattended

underground, and the time spent at nest by each female. Additionally, I predicted these benefits to increase with the number of females per group.

## **2. Methods**

### 2.1 Study population

I used data from a long-term study conducted between 2009 and 2017 on a natural degu population located at Estación Experimental Germán Greve Silva in Rinconada de Maipú (33°28'32.5"S 70°50'00.6"W, altitude 495 m), a field station of the Universidad de Chile. This study area is characterized by a Mediterranean climate with cold, wet winters and warm, dry summers. The site consisted of open areas with scattered shrubs that on average covered 14.5% of ground (Ebensperger & Hurtado 2005). The total area examined at Rinconada was 2 ha and did not vary through years.

### 2.2 Live trapping and telemetry

Yearly live trapping and telemetry were conducted from September through October, a time span that encompassed parturition, lactation, and offspring weaning. Degus are diurnally active and remain in underground burrows overnight (Ebensperger *et al.* 2004). Thus, a burrow system was defined as a group of burrow openings surrounding a central location spanning 1–3 m in diameter where individuals were repeatedly found during night-time telemetry (Hayes *et al.* 2007). Ten traps (Tomahawk model 201, Tomahawk Live Trap Company, Tomahawk, WI) were used at each burrow system daily. Traps were set prior to the emergence of adults during morning hours (06:00 h). After 1.5 h, traps were closed until the next trapping day.

I determined identity, location, sex, body mass (to 0.1 g) of all degus, and reproductive condition of all females (perforated, pregnant, or lactating). I marked every degu at the time of first capture with tags on each ear (Monel 1005-1, National Band and Tag Co., Newport, KY). Adults weighing more than 170 g were fitted with 5–6 g radiocollars (Holohil Systems, LTD, Carp, Ontario, Canada) with unique pulse frequencies. From 2009 through 2017, 421 degus (including adult males and females) were radio-tracked during the spring season (Table S1 of Supplementary Material). During night-time telemetry, degus were tracked to their home burrows via radio telemetry. Previous studies at Rinconada have confirmed that night-time locations represent underground nest sites (Ebensperger *et al.* 2004). Locations were determined once per night approximately 1 h before dawn using a TRX2000S receiver (Wildlife Materials, Inc., Murphysboro, IL), R2000 receiver (Advanced Telemetry Systems, Isanti, MN) or an LA 12-Q receiver (AVM Instrument Co., Auburn, CA) tuned to 150.000–151.999 MHz, and a handheld, 3-element Yagi antenna (AF Antronics, Inc., Urbana, IL).

### 2.3 Social group determination

The main criterion used to assign individuals to social groups was the sharing of burrow systems at night. The sharing of burrow systems was determined by (i) burrow trapping during early morning activity and (ii) night-time telemetry. To determine group composition, I first compiled a symmetric similarity matrix of pairwise association of burrow locations of all adult degus during trapping and telemetry (Whitehead 2008). The association (overlap) between any two individuals was determined by dividing the number of early mornings that these individuals were captured at or tracked with radiotelemetry to the same burrow system, by the number of early mornings that both individuals were trapped or tracked with radiotelemetry on

the same day (Ebensperger *et al.* 2004, Hayes *et al.* 2009). To determine social group composition, a hierarchical cluster analysis of the association matrix was conducted using SOCPROG software (Whitehead 2009) generate distinct social groups. Finally, components of social organization (total group size, number of females, number of males, and male-to-female ratio) were quantified for each social group. Social group membership was analyzed as an individual trait. The number of radiocollared degus and social groups monitored in spring season are given in Table S1 of Supplementary Material.

#### 2.4 Genetic methods

To determine within-group kinship and each female's litter I genotyped a total of 1982 adult and offspring degus from 2009 through 2015 (Table S4 of Supplementary Material). I estimated that this effort sampled >90% of breeding adults and offspring each year in the population. Tissue samples (a 1 × 5 mm ear snip) were taken from each individual when first captured and stored in ethanol 99% at 5–6 °C until analysis. I extracted DNA using the Reliaprep DNA animal tissue miniprep system kit (Promega) mouse tail protocol. DNA was eluted in 200 µl of nuclease-free water and stored at –20 °C. I worked with 10 microsatellite loci, 9 from *O. degus* (Quan *et al.* 2009) and one from *S. cyanus* (Schroeder *et al.* 2000). These loci were amplified via polymerase chain reaction (PCR), with the following protocol: 15 min at 94 °C for DNA denaturation, 30 cycles of a 1 min denaturation step at 94 °C, followed by 1 min of locus-specific annealing temperature (Table 4 of Supplementary Material), 1 min at 72 °C for elongation, and a final elongation step of 10 min at 72 °C. For fragment analysis, the PCR products were mixed in 3 combinations (2 with 3 loci each and one with 4 loci). Each of these mixes was contrasted with an internal size standard and

analyzed using an ABI Prism 3130Xl genetic analyzer and allele sizes were determined using the Genemapper software v4.1 (Applied Biosystems). All loci amplified successfully and were polymorphic (Table S5 of Supplementary Material). Genotypes for all individuals across years were complete with no missing data. I tested the Hardy-Weinberg observed and expected heterozygosity for each study year with ML-Relate (Kalinowski *et al.* 2006) and CERVUS 3.0 (Marshall *et al.* 1998) softwares. Deviations from Hardy-Weinberg expectations were detected in 6 out of 7 years (Table S6 of Supplementary Material) and verified that these were not the consequence of null allele presence (all markers were checked for null alleles with MicroChecker software, van Oosterhout *et al.* 2004). This finding was expected because our study population was open, non-panmictic, and characterized by a relatively high level of genetic relatedness (Quirici *et al.* 2011a).

I estimated genetic relatedness between group members based on the pairwise coefficient of relatedness ( $r$ ) using the ML-Relate software (Kalinowski *et al.* 2006). The ML-Relate provides a robust approach based on maximum likelihood estimates of genetic relatedness. Estimates of this coefficient were obtained after adjusting relatedness to accommodate for the possible presence of null alleles and simulate population sample parameters (e.g., allele frequency, heterozygosity, sample size). The ML-Relate generated an output list of pairwise coefficient of relatedness for all possible pairs that can be formed with total sampled animals in a year.

I determined maternity of females examined to verify these were rising own offspring during the time of behavioral observations (section on Communal breeding determination) and to estimate individual female litter size. This attribute was used as a predictor (fixed factor) during preliminary statistical analyses (see Statistical Analysis section). Specifically, I used

CERVUS 3.0.7 software (Marshall *et al.* 1998) to estimate maternity and paternity of each offspring during each study year. CERVUS settings and criteria used during offspring assignment methods and details are present in Supplementary Material. Based on estimates of genetic maternity and paternity we tallied the number of offspring weaned (litter size) by each female in the population during each year of study. I used litter size of each female group members to quantify communal litter size within groups, female litter size ratio (individual female litter size / communal litter size), and coefficient of variation (CV) in litter size between pairs of females within-groups. I used female litter size ratio to estimate relative contribution of each female litter to communal litter size, and (CV) in litter size between pairs of females within-groups to quantify litter size skew among female pairs within groups.

## 2.5 Determination of communal rearing

I quantified communal rearing of females based on (a) the communal use of underground burrows during nighttime (i.e., nocturnal associations), and (b) from time spent underground by group females during daytime. Most lactation of degu offspring occurs in underground burrows and emergence of young aboveground matches the end of lactation and weaning (~30 days). Thus, I used night time telemetry of females as a proxy of communal care. Typically, females from a same social group nest communally during lactation. However, variation exists and females may nest for one or more nights apart in nearby burrows (Ebensperger *et al.* 2019). Since field observations suggest females may move their offspring to a different burrow system, I cannot rule out the possibility that females nesting apart from other group members during nighttime do so with their own litter. I estimated the strength of nocturnal associations between group females using nighttime telemetry matrices based on burrow use

during lactation time. Specifically, I calculated the half-weight association index (hereafter HWI):

$$\frac{x}{x+y_{AB}+\frac{1}{2}(y_A+y_B)},$$

where  $x$  is the number of nights in which female A and female B were associated;  $y_A$  is the number of nights with just female A identified,  $y_B$  is the number of nights with just female B identified, and  $y_{AB}$  represents the number of nights with female A and B monitored but not associated (Whitehead 2008). This association index ranges from 0 to 1, and was calculated for all possible female pairs within social groups. I used these data to estimate mean per individual female HWI values and mean female HWI per group. I calculated values of HWI for a total of 84 females from years 2009 to 2015 that were members of 38 social groups (see Table S3 of Supplementary Material).

I recorded the time spent by lactating females at underground burrows during daytime to estimate communal rearing during daytime. To distinguish time spent underground from that spent aboveground I equipped 10 lactating females in 2015, 31 females in 2016 and 29 females in 2017 (see Table S3 of Supplementary Material) with 0.7 g IntigeoW65A9 light loggers (Migrate Technology Ltd., Cambridge, United Kingdom). These loggers were programmed to record light intensity every minute and to save the highest value at 5-min intervals. I attached loggers to radiocollars with odontologic acrylic and insulate tape, and fitted females with these collars at first capture after parturition. I used trapping to monitor parturition and early lactation of females. I removed radiocollars with loggers after first emergence of offspring aboveground.

Before using readings from light loggers to estimate below and aboveground use of space by lactating females, I conducted field measurements in the study area to determine

sensitivity of light loggers to individuals switching from underground to aboveground activity during daytime. Specifically, I placed rodent models attached with light loggers at different locations within burrows (at entrance holes, at 5, 10, 20 and 30 cm within first section of galleries), and in burrows exhibiting openings with different cardinal orientations at dawn-sunrise hours. As a result, I determined that light loggers always recorded values greater than 1.0 lux about 20 min after sunrise on average. Therefore, I considered 5-min intervals with minimum low light levels ( $< 1.0$  lux) 20 min after sunrise and 20 min before sunset to represent the collared female was using the communal underground burrow system. All lux data recorded outside this daily schedule were discarded. I also discarded lux data recorded during the time the females were caught in traps. I conducted direct observations of radio-collared females ( $n=4$ ) to verify that lactating females spent time underground in same burrows used previously during nighttime. Specifically, I verified that females inspected underground burrows other than those used during nighttime only during short periods of time (mean = 1.16 min; range = 0-4 min). Therefore, I used records of light values to calculate the total amount of time lactating females spent underground (i.e., presumably at the nest with the offspring) or aboveground each day, the number of aboveground and underground bouts during the day, the total amount of time per day that communal litters spent without any of the lactating females of the group. All time measures were calculated as proportion of total diurnal time of light data sampling period per female.

To quantify coordination of lactating females to attend communal litters during daytime, I first quantified the number of 5-min intervals that one female switched between aboveground to underground activity (or vice versa) while one other female group member changed her activity in the opposite direction. In social groups with three or more adult

females, these coordination events involved switching of activity by 2 or more females. Additionally, I quantified the total daily amount of time that communal litters were presumably attended by one or more female group members during daytime. Then, I contrasted these observed patterns with random expectations implying no coordination, and with sequential expectations, implying complete (100%) coordination (Ebensperger *et al.* 2006b). To achieve this, and for each group of size  $n$ , I took values for daily time spent underground by females ( $TU_{Fem}$ ) from a normal distribution with parameters (mean and standard deviation) equal to observed values at each group size (after arcsine of squared-root data transformation to fit normality). I restricted this examination analysis to social groups in which all female members were radio-collared and had data on time spent aboveground and underground during daytime. As a result, I included social groups of 2, 3, and 5 females, and solitary nesting females. (Table S3 of Supplementary Material).

I calculated random expectations for daily time that communal litters were attended by one or more females ( $TA_{Offs}^r$ ) by:

$$TA_{Offs}^r = 1 - \prod_{i=1}^n (1 - TU_{Fem}),$$

and calculated sequential expectations ( $TA_{Offs}^s$ ) from:

$$TA_{Offs}^s = \sum_{i=1}^n TU_{Fem}$$

where  $n$  is the number of females per group. I constrained values of  $TA_{Offs}^s$  to a maximum of 1. I ran 5000 simulations for each group size to calculate mean values of expected daily time

that communal litters were with one or more females. I contrasted observed and expected values of daily time that group offspring were attended by one or more females under random and sequential model scenarios with the use of one-sample Student's tests.

## 2.6 Statistical analyses

I first used a generalized linear modelling (GLM) approach to test the effects of female relatedness on communal rearing during nighttime based on the examination of variation in female HWI (half-weight association index). I examined HWI at three levels. At an individual female level (i) I quantified the effect of mean relatedness between each focal female and all other group females on its individual mean HWI. At the level of paired females within groups (ii) I assessed how paired genetic relatedness influenced paired HWI values of same paired females. Finally, at the group level (iii) I examined the effect of mean within-group relatedness among all females on mean group HWI.

Initial full models built included mean focal female relatedness with other group females, mean focal female relatedness with all other group members (i.e., including male members), total group size, female group size, number of group males, communal litter size and litter size ratio as fixed factors (level i). For level (ii), model included paired female relatedness, total group size, female group size, number of group males, total group litter size, female pair litter size and coefficient of variation of litter size between paired females as fixed factors. For level (iii), fixed factors included mean group relatedness, female group relatedness, total group size, female group size, number of group males, total group litter size, and litter size per female. However, preliminary analysis revealed high collinearity (variance inflation factor,  $VIF > 3$ ) in several predictors. As a result, I retained female group size, litter

size ratio (individual female litter size / communal litter size) and mean relatedness between a focal female and all other group females (level i), female group size, female pair litter size and paired genetic relatedness (level ii), and female group mean relatedness, female group size, and communal litter size (level iii).or Always I favored female-based factors because females were the main target of interest. I verified that all VIFs were  $<3$  after these model reductions (see Table S7 of Supplementary Material for Spearman rank correlation between model predictors). I added year of study and social group ID as random effects to all models, and female ID to the paired-female model. Distribution of errors was fit to a normal distribution with an identity link function in all models.

I selected the best model for retained predictors from each level of analysis by using the Akaike Information Criterion (AIC). Selection was done using the best subset model selection approach. Under this approach I built a set of alternative models using combinations of predictors, fit them all, and ranked them according to AIC values. I used an  $\Delta AIC > 2$  to discard models of low quality. Table S8 of Supplementary Material includes the best model ranking for each level of analysis. All GLM procedures with relatedness and female group size as predictors (one for each level of analysis) were conducted in R 3.4.3 (R Development Core Team, 2017).

I also used a generalized linear modelling (GLM) approach to test the effects of female group size on communal rearing during daytime. Specifically, I examined the effect of female group size on variation of daily time that offspring were potentially attended by one or more females, the number of daily bouts and total daily time that each female spent underground (i.e., potentially attending the communal litter),and the number of coordination events between same group females. These responses were squared-root transformed, and I added year of

study, female ID, and social group ID as random factors. All initial full GLM models during these analyses contained female group size, total group size, and number of group males as fixed factors. To reduce collinearity (variance inflation factor,  $VIF > 3$ ) among these predictors, I retained female group size exclusively (Spearman rank correlation between female group size and total group size:  $r_s = 0.880$ ,  $p < 0.001$ ; and between female group size and number of group males:  $r_s = 0.645$ ,  $p < 0.001$ ), therefore, I could not perform model selection. Distribution of errors in the response variable in all these models was fit to a normal distribution with an identity link function.

All statistical analyses were performed using R 3.4.3 (R Development Core Team, 2017). All statistical tests were two-tailed and reporting statistically significant differences at  $p < 0.05$ . Data are reported as means  $\pm$  SE. Schematic GLM model steps for nighttime and daytime approach was illustrated in Table S9 and S10 of Supplementary Material, respectively.

## 2.7 Ethical note

All animal handling techniques and protocols used in this study were approved and supervised by the Ethics Committee of the Pontificia Universidad Católica of Chile (CBB-155, 2012 resolution, supervised and approved 03/03/2015), and adhered to the Chilean Legislation for use of native species during research (Permits 1–31/2009 [1956], 3881/2012, and 2826/2013 by the Servicio Agrícola y Ganadero).

### 3. Results

#### 3.1 Communal rearing during nighttime

Associations among within-group females during nighttime revealed variable HWI and relatedness (Table 1). Selection of best model for associations across all three levels of analysis revealed that the best predictor was female group size: (ii) group-level analysis (AIC = -7.11;  $\Delta$ AIC = 0), (i) pairwise-level analysis (AIC = 18.4;  $\Delta$ AIC = 0), and (iii) individual-level analysis (AIC = -16.76;  $\Delta$ AIC = 0; see Table 8 of Supplementary Material for best model ranking for three level of analysis). Genetic relatedness among the females always appeared in second or third place in best model ranking in all three levels of analyses, always in the presence of female group size, and always within models with  $\Delta$ AIC < 2 (Table 8 of Supplementary Material). Thus, HWI did not covary with genetic relatedness among the females (Table 2, Figure 1a, 1b, 1c), but decreased in groups with increasing number of females in all three levels of analyses (Table 2, Figure 1d, 1e, 1f) (group-level model,  $\beta = -0.530 \pm 0.15$ ; pair-level model,  $\beta = -0.606 \pm 0.12$ ; individual-level model,  $\beta = -0.597 \pm 0.09$ ).

#### 3.2 Communal rearing during daytime

When coordination within-group females was examined, the daily time that communal litters potentially spent with one or more females increased with the number of females within groups ( $\beta = 0.531 \pm 0.04$ ), a statistically significant effect ( $F_{1, 518} = 202.95$ ;  $p < 0.001$ ; Figure 2). Additionally, the proportion of daily time that communal litters were potentially attended by one or more females did not differ from random and sequential expectations in solitary nesting females ( $p > 0.1$  in both; Figure 2). In contrast, this proportion of time was lower than

expected by both random and sequential expectations in groups of two, three, and five females ( $p < 0.0001$ ; Figure 2).

The number of females per group influenced the female's mean time per bout spent underground ( $F_{1, 2190} = 17.55$ ;  $p < 0.001$ , Figure 3a), the proportion of daily time that females spent underground ( $F_{1, 2216} = 9.57$ ;  $p = 0.002$ , Figure 3b), but not the female's daily number of bouts spent underground ( $F_{1, 2216} = 0.04$ ;  $p = 0.845$ , Figure 3c). Finally, the number of female group members influenced significantly and positively both the daily number of coordination events of individual females ( $F_{1, 1642} = 371.37$ ;  $p < 0.001$ ;  $\beta = 0.45 \pm 0.02$ , Figure 4a), and the daily number of coordination events recorded among all group females ( $F_{1, 1642} = 902.36$ ;  $p < 0.001$ ;  $\beta = 0.618 \pm 0.04$ , Figure 4b).

#### 4. Discussion

I first examined the hypothesis that communal rearing of offspring is influenced by kinship among the females of the caviomorph rodent *Octodon degus*. Contrary to expectations, genetic relatedness among the females did not influence strength of female nesting associations during nighttime. Thus, sharing of burrows with other lactating females did not increase with kinship within-groups. Secondly, I tested the hypothesis that attendance to offspring during communal rearing is coordinated among the females within social groups. On the one hand, I recorded that observed daily time spent underground (i.e., potentially attending communal litters) by the females during daytime was always lower than expectations based on perfect (100%) sequential coordination. However, the number of group females influenced time that each female spent underground (i.e., potentially attending communal litters), time that communal

litters were potentially attended by one or more offspring, and the number of coordination events between same group within-group females during daytime. Highly intriguing, the daily number of coordination events recorded among of all group females increased with number of female members, implying a greater propensity of females to coordinate time spent underground during daytime, and therefore, attendance to communal litters.

#### 4.1 Kin selection and communal rearing

The observation that relatedness among lactating females did not influence the strength of communal nesting during nighttime (Figure 1a, b, c) was consistent with most previous studies in degus. Neither quantity nor quality of offspring were influenced by kinship among communally rearing females in captivity (Ebensperger *et al.* 2007), and lactating females do not discriminate when retrieving own or alien offspring to the nest (Ebensperger *et al.* 2006a). The seemingly unimportance of kinship on communal rearing female degus departs from findings on other group-living rodents such as edible dormice (*Glis glis*), where communally rearing females are always close kin (Marin & Pilastro, 1994), or as in laboratory house mice (*Mus musculus*) where communally rearing females tend to be kin (Manning *et al.* 1995), and on other mammals such as lions (*Panthera leo*), where allonursing is positively related with proportion of first-order relatedness within group females (Pusey & Packer, 1994). However, findings in degus parallel those reported in other group-living rodents such as wild house mice (*Mus musculus*), where relatedness between communally breeding females do not influence time that communal litters are left unattended (Auclair *et al.* 2014), and those reported in other communal rearing mammals like sperm whales (*Physeter macrocephalus*) and African elephants (*Loxodonta africana*) where unrelated females frequently care non-offspring (Gero

*et al.* 2009; Lee, 1987). Moreover, some bird studies indicate that genetically unrelated females may form strong associations to communally rearing nestlings in greater anis (*Crotophaga major*; Riehl & Strong, 2018). The unimportance of genetic relatedness seems similarly unimportant in other potential contexts of cooperation in degus. Specifically, scanning during foraging is not influenced by genetic relatedness (Quirici *et al.* 2008; 2013).

In contrast to the seemingly unimportant effect of kinship among the females, the strength of social associations during nighttime decreased in groups with a larger number of female members (Figure 1d, 1e, 1f). Thus, females seem less consistent in nesting with other group females when in groups with more females. This finding may reflect a strategy of females to reduce costs of offspring care. Provided that communal litters are less likely to be left alone in groups with more females, individual females may decrease attendance during nighttime without compromising quality and survival of their own offspring. Previous studies support that the probability that breeding females produce a second litter during the same breeding season increases in females exhibiting relatively low cortisol levels, a proxy of energetic costs (Ebensperger *et al.* 2013). Thus, females of groups with more females may benefit from communal rearing though enhancing the probability of producing a second litter as a result of postpartum estrus. Such additional increase in reproductive success may be functionally relevant to degus. Only 7% of adult females breeding for the first time during a particular year survive to subsequent year to reproduce again (Ebensperger *et al.* 2013).

Alternatively, decreased consistency to nest communally by the females in groups with more females may reflect increased variability in strength of social associations, which is consistent with previous findings that female degu coefficient of variation in association strength increased with group size (Wey *et al.* 2013). Moreover, group size is known to

influence social ties in some colonial rodents and primates, and where social interactions decrease with increased group size in yellow-bellied marmots (*Marmota flaviventris*; Maldonado-Chaparro *et al.* 2015), and also influenced negatively strength and positively variability in social ties in primates (Lehmann *et al.* 2007; Sueur *et al.* 2011).

#### 4.2 Coordination during communal rearing

During daytime, the proportion of time that communal litters were potentially attended by one or more females was always lower than expectations assuming random or complete coordination by the females (Figure 2). Thus, lactating females in degus attend their offspring independently of the behavior of other female group-members and exhibit temporal overlap among them. The absence of complete sequential coordination in distribution of daily bouts of attendance to offspring recorded in this study adds to some previous findings of coordination in other cooperation contexts. Degus do not coordinate their vigilance when foraging socially (Ebensperger *et al.* 2006b; Quirici *et al.* 2008). Overlap in nursing bouts by the females at nest has been reported in other communally nesting rodents such as meadow voles (*Microtus pennsylvanicus*) and wild house mice (*Mus musculus*; Auclair *et al.* 2014; McShea & Madison, 1984). Overlap by the females during offspring attendance enhance continuity of nursing bouts, or enhance other communal rearing benefits such as enhancing social thermoregulation (Hayes, 2000). Overlap during attendance to communal litters may provide information on the other group female's contribution to collective care of the offspring which may enhance reciprocity among the females. The presence of an "audience effect" is known to enhance cooperation (Nowak & Sigmund, 2005; Pinto *et al.* 2011). Cooperation and competition are closely linked, and cheaters are very common in a wide range of cooperative

behaviors (West *et al.* 2002; West *et al.* 2007b); thus, degu females may monitor the amount of care provided by other group females.

Departing from my previous finding, I detected short-term coordination of females during potential attendance to offspring during daytime. Specifically, both the daily number of coordination events recorded to individual females (Figure 4a), and the daily number of coordination events recorded among all group females (Figure 4b) were more prevalent in social groups with more females. Discrepancy between these two examinations of coordinated attendance to communal litters may reflect the different in the time scales associated with each measure. Sequential model expectations are based on records from all daytime data. In contrast, point events of coordination typically lasted a few 5-min intervals, and represented no more than 1 hour of total time record of participant females. Therefore, short-term coordination events do not imply lack of temporal overlap during most of daytime bouts of visits to underground burrows.

Furthermore, these relatively short-term coordination events probably contribute to the observed positive relationship between female group size and time in which communal litters remain attended, similarly as suggested to occur during coordinated digging (Ebensperger & Bozinovic, 2000). Likely, this positive association reflects an increase in the number of possible relationships (connections) among all group female networks (Whitehead, 2008). Moreover, this positive association is consistent with a previous degu study that reported communally reared litters experience less time unattended compared with litters reared by solitary nesting females (Ebensperger *et al.* 2002). My results expanded these findings, through revealing that time offspring remain attended increases with the number of lactating females within the group. Notoriously, female group size influenced communally rearing

female associations in both nocturnal and diurnal approximations, strongly suggesting group-size effects (Ebensperger & Hayes, 2016). Group-size effects may involve benefits for social groups but do not necessarily imply the existence of cooperative behaviors (Vásquez, 2016). However, communal rearing in degu females is well demonstrating, including nurse and lactating one-another's offspring (Ebensperger *et al.* 2002; 2004). Therefore, an increase in number of females of the group could imply greater opportunities for active cooperation between mothers. On the other hand, I took both reduction of the proportion of daily time that females spent underground and reduction in female's mean time per bout spent underground cautiously due to both, very small amount of diminution across increment of female group size and the pattern was founded only until female group size of four (Figure 3a, 3b).

Offspring experiencing more time attended by one of more females benefit by means of enhancing thermoregulation and enhancing milk intake through experiencing shortened lactation intervals (Auclair *et al.* 2014; Hayes, 2000; König, 1997; Lewis & Pusey, 1997). Findings from this study suggest that offspring experiencing a 5-12% increase in per female attendance will be attended 62% of time in a five-female social group. However, from the mother's perspective, current findings support that females may benefit by means of lightening maternal care costs through reducing time spent underground with the communal litter, potentially allocating more time to other essential activities such as foraging (Auclair *et al.* 2014; Clutton-Brock 2016; Hourlay *et al.* 2020).

## 5. Concluding remarks on degu sociality

Previous studies indicate that reproductive benefits to communally rearing female degus in terms of direct fitness materialize mostly under harsh conditions with low precipitation and low food availability (Ebensperger *et al.* 2014). Results from this study imply kin selection is unlikely to explain communal rearing and contribute with indirect benefits to female degus. Subsequent studies are needed to examine the role of other mechanisms, including reciprocity and mutualism (Clutton-Brock, 2002; Engelhardt *et al.* 2015; Gero *et al.* 2009). Some forms of reciprocity seem to explain food sharing in laboratory rats (Rutte & Taborsky, 2008), and future studies might wish to examine how reciprocity plays any role among lactating females during attendance to the communal litters in degus.

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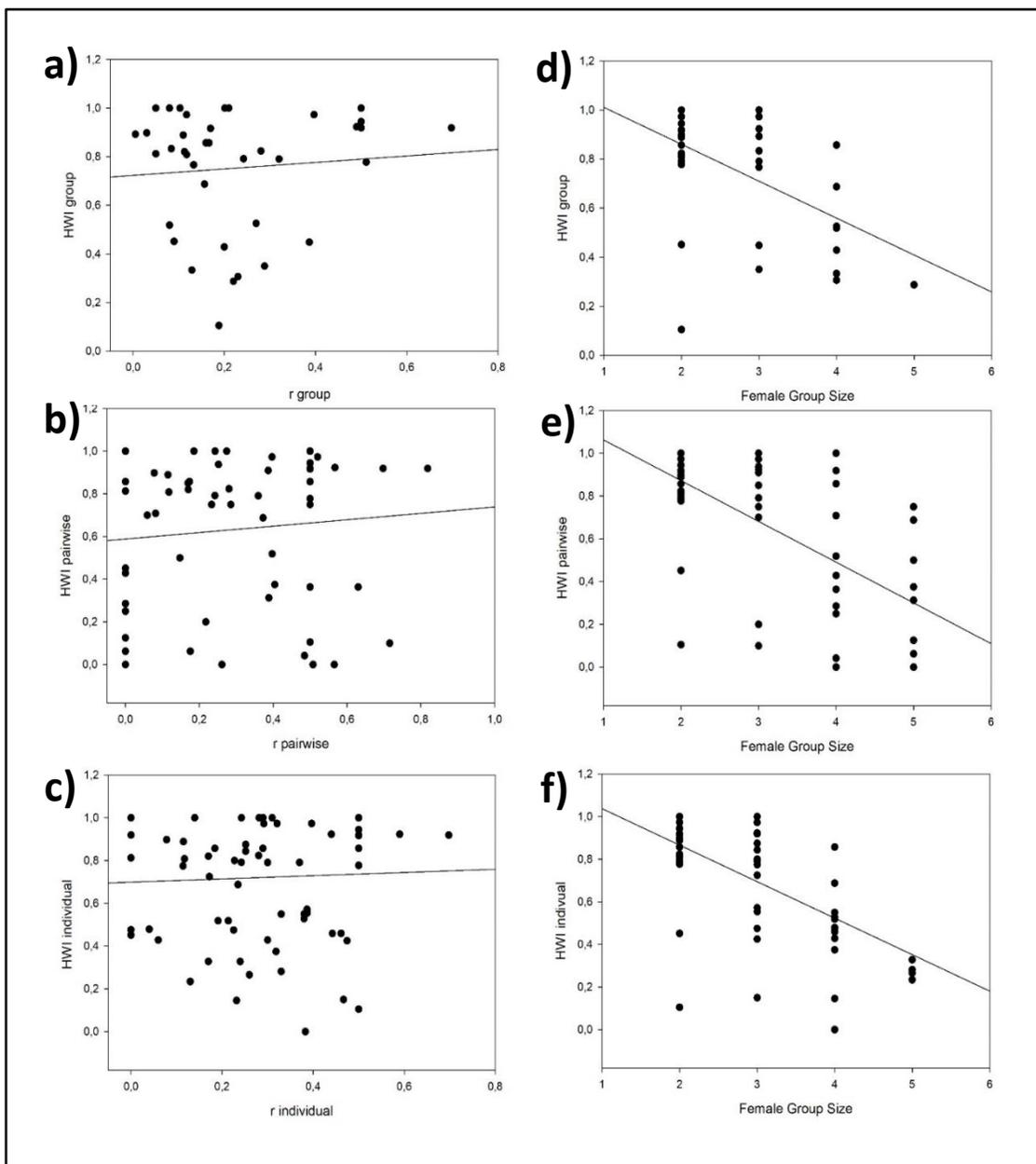
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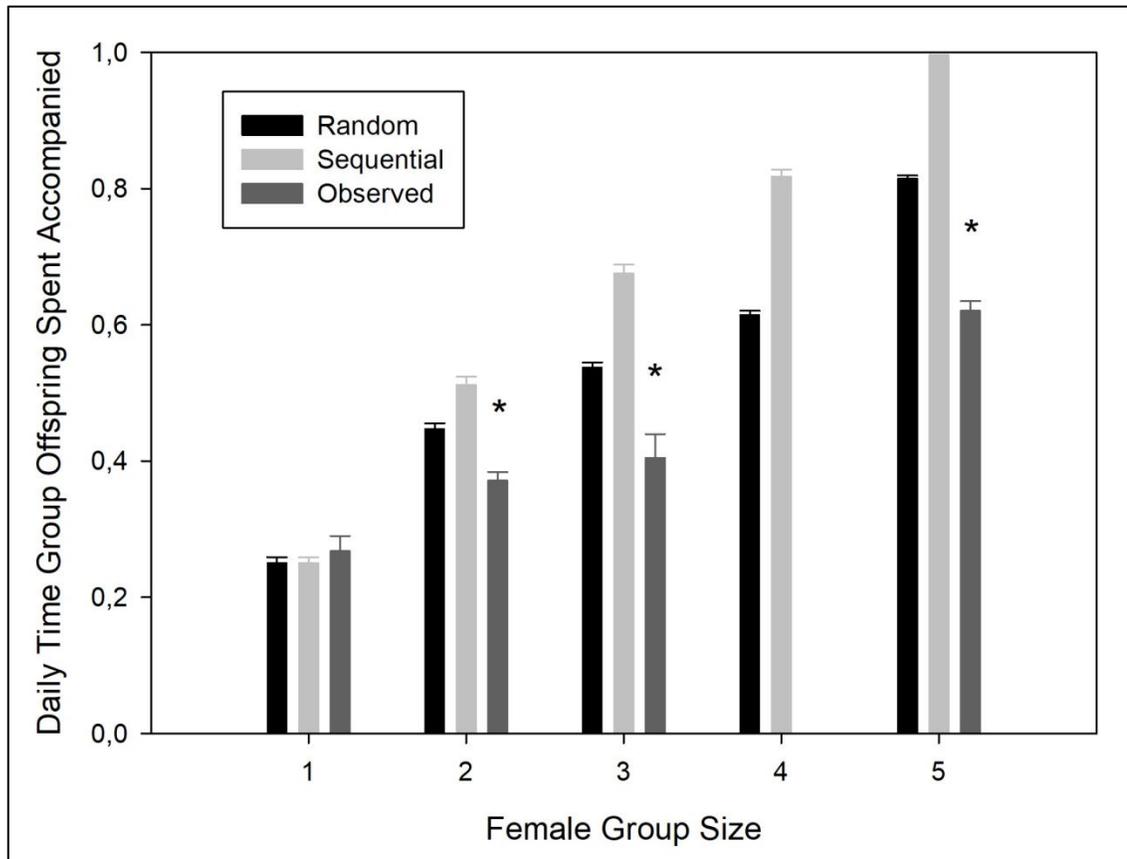
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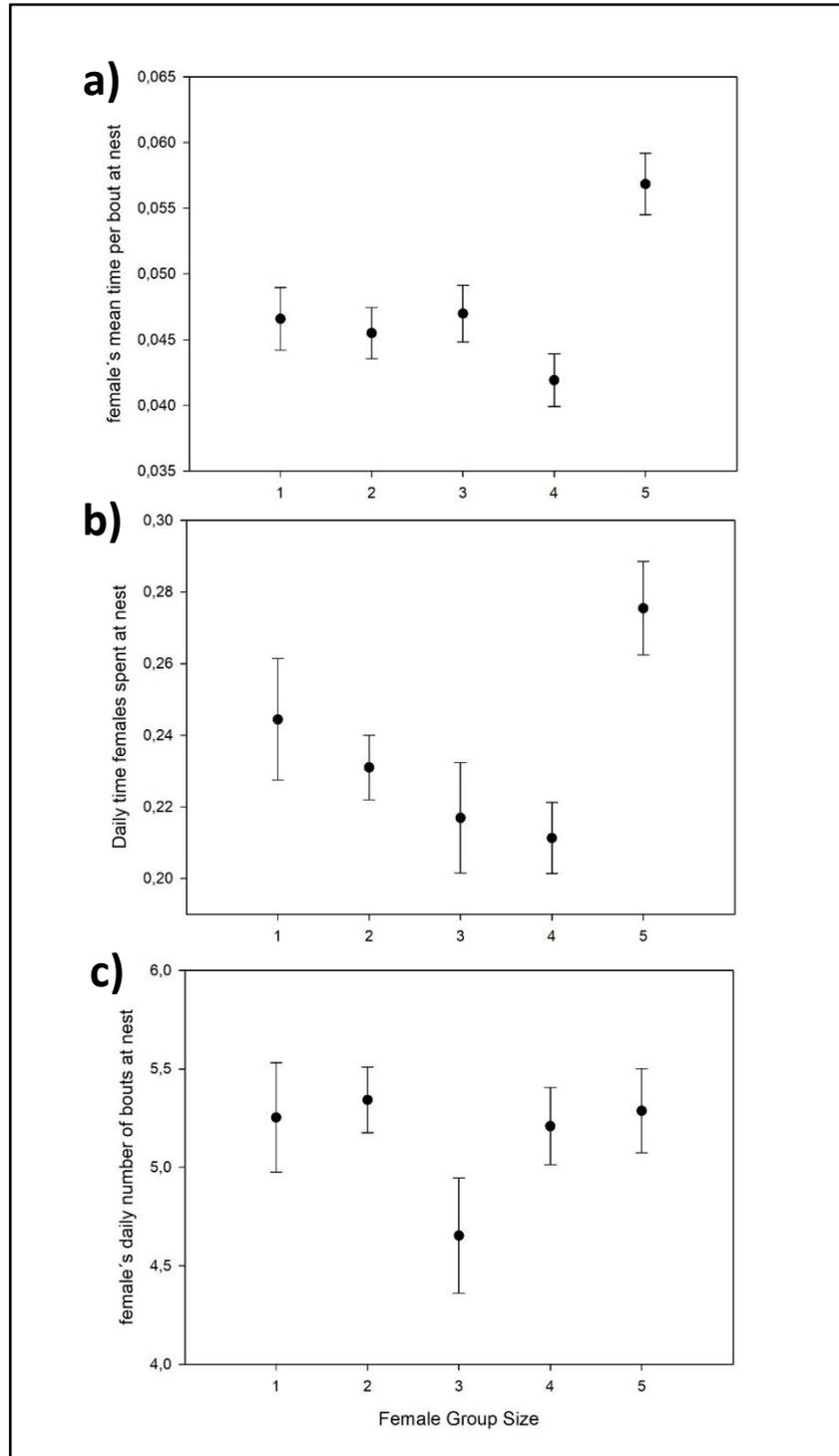
## FIGURES



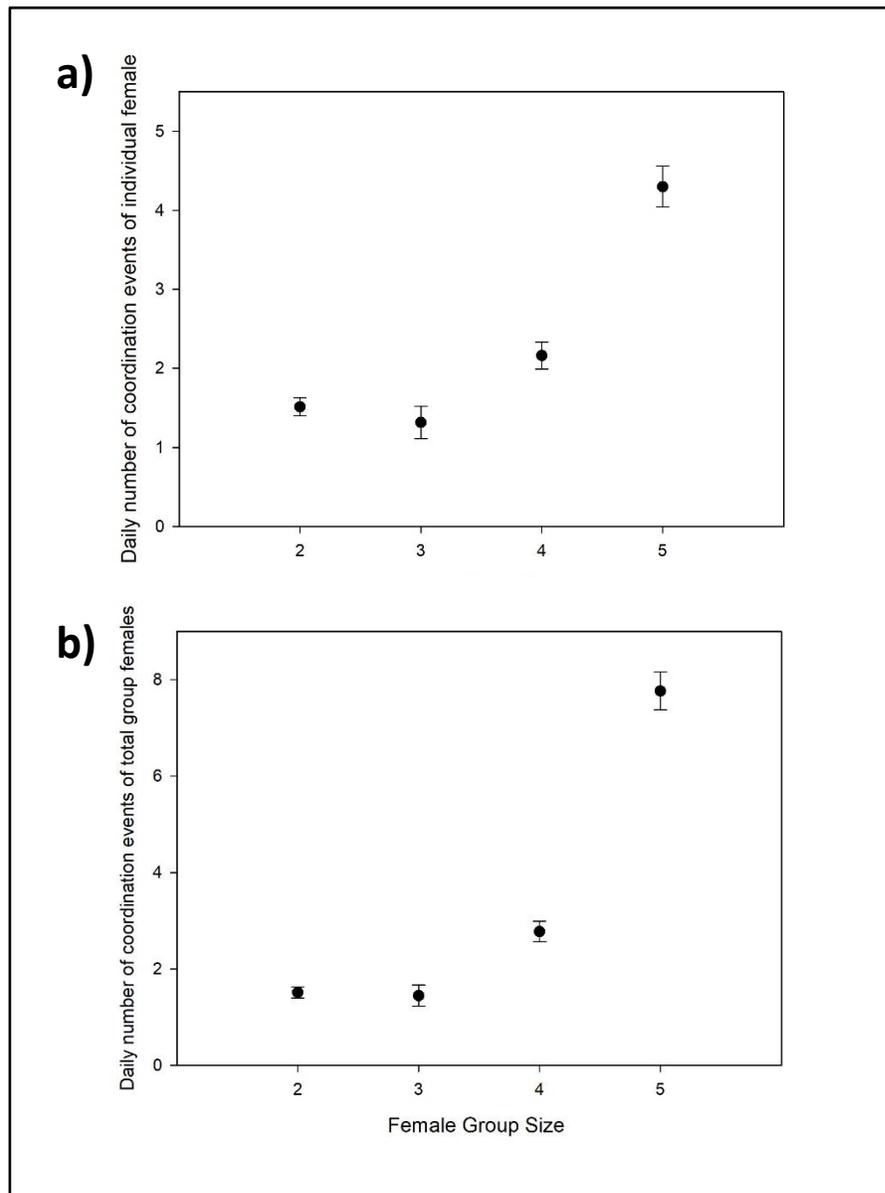
**Figure 1.** Relationship between the half-weight index (HWI), a measure of strength of nocturnal associations between group females, and genetic relatedness quantified at the (a) group-level, (b) paired female-level, and (c) individual-level analyses; and between HWI and female group size for (d) group-level, (e) paired female level, and (f) individual-level analyses.



**Figure 2.** Observed (dark gray bars), randomly expected (black bars) and sequentially expected (light gray bars) mean values of daily time that communal litters spent in the presence of one or more females (proportion of total daily time measured). Errors bars represent  $\pm$  95% confidence intervals. Asterisks denote statistically significant differences between observed values and both random and sequential expectations (mean values for each female group size). Note: observed daily time that communal litters spent accompanied for group sizes with four females could not be recorded due to a lack of these groups with all female members radiocollared (see Table S3 of Supplementary Material).



**Figure 3.** Effects of female group size on (a) mean time per bout spent by the females at the nest (proportion of total daily time measured), (b) daily time spent by the females at the nest (proportion of total daily time measured), and (c) daily number of bouts spent by the females at the nest. Error bars represent  $\pm 95\%$  confidence intervals.



**Figure 4.** Effects of female group size on mean number of daily events of coordination during attendance to offspring during daytime; (a) individual female based measures, (b) total group of females based measures. Error bars represent  $\pm$  95% confidence intervals

## TABLES

**Table 1.** Summary of data used for each level of analysis, including number of replicates (N), number of social groups, ranges for genetic relatedness, HWI (Half-Weight Index), and number of study years.

<b>Analysis Level</b>	<b>N</b>	<b>N Social Group</b>	<b>Range r</b>	<b>Range HWI</b>	<b>Years</b>
Female Group	38	38	0.005 - 0.698	0.105 - 1	6
Female Pairwise	59	38	0 - 0.819	0 - 1	6
Individual Female	84	38	0 - 0.698	0 - 1	6

**Table 2.** Results from generalized linear models explaining variation in HWI for each analysis level. These models were selected from best model rank selection show in Table S8 of Supplementary Material. Significant p values are in bold.

<b>Analysis Level: Group</b>	<b>Predictor</b>	<b>F<sub>1,37</sub></b>	<b>p</b>
Dependent variable: HWI Group	Female Group Size	12.13	<b>0.002</b>
	r Female Group	0.040	0.840
<b>Analysis Level: Pair</b>	<b>Predictor</b>	<b>F<sub>1,58</sub></b>	<b>p</b>
Dependent variable: HWI Pair	Female Group Size	22.58	<b>&lt; 0.001</b>
	r Pair	0.400	0.532
<b>Analysis Level: Individual</b>	<b>Predictor</b>	<b>F<sub>1,83</sub></b>	<b>p</b>
Dependent variable: HWI individual	Female Group Size	42.39	<b>&lt; 0.001</b>
	r mean with Female Group	0.07	0.798

**SUPPLEMENTARY MATERIAL**

**Table S1.** Total number of social groups and male and female group members monitored during spring of each year.

<b>Year</b>	<b>Spring</b>		
	Number of social groups	Number of male group members	Number of female group members
2009	11	13	30
2010	6	10	7
2011	14	15	21
2012	11	4	20
2013	20	12	39
2014	17	16	30
2015	25	26	45
2016	22	36	49
2017	21	10	38
<b>Total</b>	147	142	279

**Table S2.** Total number of social groups of different size and the total number of females analyzed in night time approximation of communal breeding. Four females were discarded of final analysis due to that genetic relatedness was not available for them. Note: not all groups sampled had a total number of females sampled.

<b>Year</b>	<b>two-female group</b>	<b>three-female group</b>	<b>four-female group</b>	<b>five-female group</b>	<b>N females sampled</b>
2009	3	2	1	1	18
2011	2	1	-	-	6
2012	2	2	1	-	14
2013	4	5	1	-	22
2014	3	-	2	-	10
2015	6	-	2	-	18
<b>Total</b>	<b>20</b>	<b>10</b>	<b>7</b>	<b>1</b>	<b>88</b>

**Table S3.** Total number of social groups of different size and the total number of females analyzed in diurnal approximation of communal breeding. Note: not all groups sampled had a total number of females sampled. Asterisk denotes absence of totally-sampled female groups

<b>Year</b>	<b>Solitary Females</b>	<b>two-female group</b>	<b>three-female group</b>	<b>four-female group</b>	<b>five-female group</b>	<b>N Females sampled</b>
2015	-	4	-	1	-	10
2016	2	7	2	4	1	31
2017	7	5	3	-	1	29
<b>Total</b>	<b>9</b>	<b>16</b>	<b>5</b>	<b>5*</b>	<b>2</b>	<b>69</b>

**Table S4.** Total number (n = 1982) of genotyped adult and offspring degus (2009-2015).

<b>Year of study</b>	<b>Number of adult females</b>	<b>Number of adult males</b>	<b>Number of female offspring</b>	<b>Number of male offspring</b>	<b>Total</b>
2009	47	49	85	117	298
2010	10	26	18	30	84
2011	47	34	83	88	252
2012	30	27	62	64	183
2013	52	48	135	149	384
2014	71	71	99	86	327
2015	78	87	149	140	454
<b>Total</b>	<b>335</b>	<b>342</b>	<b>631</b>	<b>674</b>	<b>1982</b>

**Table S5.** Sequence, annealing temperature (Ta), size, and number of alleles of 10 microsatellite loci used to genotype degu adults and offspring.

Locus	Repeat motif	Primer sequence (5'-3')	Ta (C°)	PCR product size (bp)	Number of alleles	GenBank Accession n°
OCDE1	(CTTT) <sub>7</sub> CTCT(CTTT) <sub>10</sub>	F: VIC-CTAGGTGCCAGAGACCCCTTG R: CAAAGACCCTGGGTCAATC	60	152-184	9	FJ418930
OCDE2	(CA) <sub>13</sub>	F: VIC-GTTCGAGCTGCCTAGTGAGG R: ACTGGACATGGTGGTGTGTG	64	200-214	7	FJ418931
OCDE5	(GAAA) <sub>11</sub> GAGA(GAAA) <sub>7</sub>	F: FAM-CAAAGACCCTGGGTCAATC R: CATGATTGAGCTTGCCCTCTG	58	196-228	9	FJ418934
OCDE7	(GAAA) <sub>13</sub> (GA) <sub>4</sub> *	F: FAM-CAAGCTTGTCAAAGCACAGG R: GGCAGAAAATTCTGGACAGG	64	191-229	17	FJ418936
OCDE9	(GA) <sub>23</sub>	F: FAM-CATGTAGTTTTCCAGGCACT R: TTCCTCCACTTTCTGACAAT	58	169-197	13	FJ418938
OCDE10	(TG) <sub>13</sub>	F: NED-AAGGCAGCAGTTGGGAGAACAA R: TGAGATTGTCCTTTGAGTCCACATGA	64	157-185	10	FJ418939
OCDE11	(CA) <sub>5</sub> TATA(CA) <sub>4</sub> GAGACAAATA(CA) <sub>20</sub>	F: PET-TAGGAAGGAAAGGAGCTGGA R: CAACAAGCTCGGGTGATTTA	58	164-180	8	FJ418940
OCDE12	(GT) <sub>15</sub>	F: PET-GCAGAGCTAAGGACTAAAGGTTCCA R: CCAAGTTGCTAAGAGGTCCCTTG	62	174-224	19	FJ418941
OCDE14	(GT) <sub>20</sub> (TG) <sub>2</sub>	F: FAM-GCTCTGGGGCAATCAATATTCT R: AAACCACTACTTCTGCACTGTTCCA	58	150-174	12	FJ418943
SCY3	(CA) <sub>20</sub>	F: NED-AAGTTGAGGCTAGTTGTTTG R: GATCACAGGCACCACATAC	52	125-151	12	AF250221

\*OCDE7 was originally described as (GAAA)<sub>15</sub>, a four motif repeat (Quan *et al.* 2009). However, the forward and reversal sequencing of this marker in our Molecular Facility revealed this is two motif repeat marker.

**Table S6.** Analysis of Hardy-Weinberg expectations for each locus within each study year (2009 to 2015). Data include the number of alleles ( $N_A$ ), observed heterozygosity ( $H_{obs}$ ), expected heterozygosity ( $H_{exp}$ ), Hardy-Weinberg P-value after Bonferroni Corrections (p-value), and significant deviations from Hardy-Weinberg expectations highlights (HW); Key to statistical significance: NS = not significant \* = significant at  $p < 0.05$ , \*\* = significant at  $p < 0.01$ , and \*\*\* = significant at  $p < 0.001$ . The number of genotypes used during these analyses are given in Table S4.

Locus	2009					2010				
	$N_A$	$H_{obs}$	$H_{exp}$	p-value	HW	$N_A$	$H_{obs}$	$H_{exp}$	p-value	HW
OCDE1	9	0.893	0.843	0.166	NS	8	0.798	0.783	0.240	NS
OCDE2	7	0.829	0.803	< 0.001	***	7	0.798	0.794	0.632	NS
OCDE5	9	0.872	0.843	0.151	NS	8	0.702	0.789	0.118	NS
OCDE7	13	0.842	0.874	< 0.001	***	13	0.833	0.840	0.406	NS
OCDE9	13	0.856	0.866	0.027	NS	11	0.917	0.860	< 0.001	***
OCDE10	10	0.795	0.788	0.312	NS	8	0.690	0.721	0.652	NS
OCDE11	6	0.779	0.761	0.012	NS	7	0.857	0.791	0.021	NS
OCDE12	14	0.822	0.853	0.007	NS	15	0.905	0.899	0.899	NS
OCDE14	9	0.802	0.795	0.049	NS	9	0.774	0.805	< 0.001	***
SCY3	9	0.822	0.800	0.895	NS	10	0.786	0.825	0.030	NS

**Table S6.** Continuation.

Locus	2011					2012				
	N <sub>A</sub>	H <sub>obs</sub>	H <sub>exp</sub>	p	HW	N <sub>A</sub>	H <sub>obs</sub>	H <sub>exp</sub>	p-value	HW
OCDE1	9	0.869	0.839	0.694	NS	9	0.798	0.854	< 0.001	***
OCDE2	7	0.726	0.789	0.160	NS	7	0.776	0.799	0.103	NS
OCDE5	9	0.845	0.834	0.854	NS	9	0.831	0.855	0.003	*
OCDE7	13	0.853	0.881	0.094	NS	14	0.814	0.855	0.048	NS
OCDE9	12	0.869	0.866	0.068	NS	11	0.869	0.855	0.011	NS
OCDE10	9	0.766	0.735	0.336	NS	9	0.798	0.775	0.676	NS
OCDE11	7	0.786	0.823	0.019	NS	7	0.787	0.808	0.016	NS
OCDE12	16	0.861	0.862	0.010	NS	15	0.880	0.877	0.029	NS
OCDE14	9	0.750	0.753	0.391	NS	10	0.716	0.736	0.079	NS
SCY3	11	0.841	0.826	0.087	NS	11	0.923	0.881	< 0.001	**

**Table S6.** Continuation.

Locus	2013					2014				
	N <sub>A</sub>	H <sub>obs</sub>	H <sub>exp</sub>	p-value	HW	N <sub>A</sub>	H <sub>obs</sub>	H <sub>exp</sub>	p-value	HW
OCDE1	9	0.859	0.848	0.006	NS	9	0.838	0.854	0.073	NS
OCDE2	7	0.745	0.789	0.001	*	6	0.758	0.794	0.262	NS
OCDE5	9	0.862	0.846	< 0.001	**	9	0.847	0.853	0.034	NS
OCDE7	14	0.797	0.857	< 0.001	***	15	0.780	0.836	0.011	NS
OCDE9	13	0.862	0.852	0.127	NS	13	0.859	0.850	0.039	NS
OCDE10	9	0.742	0.750	0.004	*	10	0.783	0.774	0.107	NS
OCDE11	7	0.794	0.790	< 0.001	**	8	0.774	0.792	< 0.001	**
OCDE12	16	0.906	0.893	0.001	*	14	0.902	0.894	0.725	NS
OCDE14	12	0.766	0.767	0.202	NS	11	0.777	0.797	< 0.001	**
SCY3	11	0.893	0.871	0.001	*	11	0.865	0.878	< 0.001	***

**Table S6.** Continuation.

<b>Locus</b>	<b>2015</b>				
	<b>N<sub>A</sub></b>	<b>H<sub>obs</sub></b>	<b>H<sub>exp</sub></b>	<b>p-value</b>	<b>HW</b>
OCDE1	9	0.833	0.842	0.004	*
OCDE2	6	0.744	0.767	0.211	NS
OCDE5	9	0.841	0.842	0.004	*
OCDE7	15	0.835	0.851	0.040	NS
OCDE9	12	0.866	0.845	0.583	NS
OCDE10	10	0.802	0.808	0.005	NS
OCDE11	8	0.813	0.792	0.782	NS
OCDE12	17	0.921	0.903	0.027	NS
OCDE14	9	0.791	0.788	0.006	NS
SCY3	12	0.883	0.881	0.051	NS

**Table S7.** Spearman rank correlation between fixed factors included in preliminary analysis of generalized linear models with high values of variance inflation factor ( $VIF > 3$ ) and discarded to avoid collinearity.

<b>Group Analysis</b>	<b>Total Group Size - Female Group Size</b>	<b>Communal Litter Size - Litter Size per Female</b>	<b>r Total Group - r Female Group</b>
rho	0.691	0.887	0.751
p	< 0.001	< 0.001	< 0.001
<b>Pair Analysis</b>	<b>Total Group Litter Size - Litter Size pair</b>	<b>Communal Litter Size - Litter Size Coefficient of Variation</b>	<b>Female Group Size - Total Group Size</b>
rho	0.825	-0.619	0.823
p	< 0.001	< 0.001	< 0.001
<b>Individual Analysis</b>	<b>Total Group Size - Female Group Size</b>	<b>Communal Litter Size - Individual Litter Size</b>	<b>r with Total Group - r with Female Group</b>
rho	0.741	0.717	0.875
p	< 0.001	< 0.001	< 0.001

**Table S8.** Best model selected for each analysis level. This table only shows selected models per level after use the criteria of Delta AIC > 2 for discard low quality models.

<b>Model Group Analysis</b>	<b>gl</b>	<b>AIC</b>	<b>Delta AIC</b>	<b>Akaike weight</b>	<b>Evidence ratio</b>
Female Group Size	1	-7.11	0	0.483	1
Female Group Size + r Female	2	-5.19	1.92	0.185	0.383
Female Group Size + Communal Litter Size	2	-5.18	1.927	0.184	0.382
<b>Model Pair Analysis</b>	<b>gl</b>	<b>AIC</b>	<b>Delta AIC</b>	<b>Akaike weight</b>	<b>Evidence ratio</b>
Female Group Size	1	18.4	0	0.483	1
Female Group Size + Litter Size Pair	2	19.9	1.503	0.228	0.472
Female Group Size + r Pair	2	20.32	1.927	0.184	0.381
<b>Model Individual Analysis</b>	<b>gl</b>	<b>AIC</b>	<b>Delta AIC</b>	<b>Akaike weight</b>	<b>Evidence ratio</b>
Female Group Size / ID Group + Year	7	-16.76	0	0.237	1
Female Group Size	1	-15.91	0.851	0.155	0.654
Female Group Size + Litter Size Ratio / ID Group + Year	8	-15.3	1.464	0.114	0.481
Female Group Size + r with Female Group / ID Group + Year	8	-14,8702	1.889	0.092	0.389

**Table S9.** Summary of generalized linear modelling (GLM) steps for nighttime approach on communal breeding.

GLM Nighttime Approach				
Step		Individual level	Pairwise level	Group level
Full model examined	Response variable	HWI individual	HWI pairwise	HWI group
	Fixed factors	Mean relatedness with total group Mean relatedness with female group Total group size Female group size Male group size Total group litter size Litter size ratio (female/total group) Litter size	Pairwise relatedness Total group size Female group size Male group size Total group litter size Pair litter size Litter size coefficient of variation between pair	Mean group relatedness Mean female group relatedness Total group size Female group size Male group size Total group litter size Litter size per female
	Random factors	Year Id group	Year Id group Id female	Year Id group
Collinearity evaluation				
Model selection (AIC ranking)	Fixed factors retained	Mean relatedness with female group Female group size Litter size ratio (female/total group)	Pairwise relatedness Female group size Pair litter size	Mean female group relatedness Female group size Total group litter size
<b>Final model selected</b>		<b>Mean relatedness with female group + Female group size</b>	<b>Pairwise relatedness + Female group size</b>	<b>Mean female group relatedness + Female group size</b>

**Table S10.** Summary of generalized linear modelling (GLM) steps for daytime approach on communal breeding.

<b>GLM Daytime</b>	
Response variable	Daily time proportion with offspring attended by at least one female Number of daily bouts spent underground by females Total daily time spent underground by females Number of daily coordination events per female Number of daily coordination events per total female group Mean time spent underground by female per bout
Fixed factors	Female group size Total group size Male group size
Random factors	Year ID group ID female
Collinearity evaluation	
Final model selected	Female group size / Year + ID group + ID female

## Parentage Analysis in Cervus Software

Maternity and paternity were estimated using CERVUS 3.0.7 software (Marshall *et al.* 1998). To do so, we checked each offspring against all potential mothers and fathers in the population as trios in the population. Confidence calculations were obtained using the LOD score option. Simulations were run for 10,000 cycles using allele frequency data from the entire population, with a genotyping error rate of 1% and under the assumption that 90% of the population was sampled. Parent pair with sexes known assignment analyses were conducted using strict (95%) confidence levels. Maternities and paternities were inferred after individual offspring, potential mothers and potential fathers were examined as trios in the population. Assigned trios were accepted when the following conditions were met: (1) the LOD score of the mother-father-offspring trio listed was positive, and (2) the mother-father-offspring trio confidence level was significant. Within trios maternity assignments that met these two criteria were then checked against two additional criteria, one based on location of offspring capture and another, based on weight differences within putative litters. This additional verification was needed because overall level of genetic relatedness in the study population was high, a condition that raises the probability of errors in software-based estimations. Regarding location of offspring capture (criteria 3), offspring weighting <50 g that were assigned to a putative mother were accepted only if the putative mother and the offspring were both caught in the same burrow system; for larger and relatively more mobile offspring (i.e., weighting 50-75 g), mother-offspring pairs were accepted only when capture locations of the offspring and the putative mother were within <40 m (40 m represents the mean radius of adult degus' home range (Quirici *et al.* 2010)). We did not use location of offspring capture (criteria 3) for

potentially dispersing offspring that weighted  $>70$  g (Quirici *et al.* 2011b). We needed to consider criteria 4 whenever mother-offspring assignments occasionally (2.5 % of all mother-offspring assignments examined) included an offspring whose body weight was clearly heavier or lighter than that of all other offspring already assigned to the same putative mother. We accepted this assignment only if the difference in body weight between the offspring in question and the heaviest or lightest offspring already assigned to the focal female was included in a reference 95% confidence interval. Reference 95% confidence intervals were calculated from 25 litters of known age and body weight reared under laboratory conditions (L. Correa, unpublished observations). We did not use this criterion when putative mothers had only 1 offspring assigned previously. Offspring meeting additional criteria 3 and 4 were accepted as offspring of the mother assigned by the software (criteria 1 and 2) whenever the offspring-mother pair had 0, 1 or 2 mismatches in their genotypes. In these cases, we assumed that 1 mismatch came from the mother and the other came from the offspring. All offspring that met criteria 1 and 2, but not 3 and 4, were re-examined against the second most likely putative mother and father assigned by CERVUS as a trio. Then, we verified how this second most likely mother-father-offspring trio met criteria 3 and 4. We iterated this procedure until criteria 3 and 4 were met. The father associated with the most likely mother accepted during this process was retained unless a criterion 2 was not met. Thus, paternity estimates within trios were all based on criteria 1 and 2 exclusively. We based this decision on the observation that group males seem more mobile and that paternal seems of less relevance than maternal care in degus. All 10 loci selected had a combined exclusion probability of 99.9% for each study year when neither parent was previously known.

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## GENERAL CONCLUSIONS

An important amount of evidence states kin selection is a relevant mechanism underlying the evolution of cooperation. In particular, the monogamy hypothesis argues that social monogamy is a requisite for the evolution of cooperative societies, especially those exhibiting cooperative breeding. While the monogamy hypothesis has received some support in mammals, social monogamy is not the dominant mating system; however, it is more widespread within some taxa such as the Hystricognathi. These rodents also exhibit high levels of sociality and cooperation. Findings reported in Chapter 1 strongly supported the monogamy hypothesis and kin selection as main evolutionary forces driving group-living and cooperation in these rodents. Specifically, I detected that the evolution of group-living, cooperation in the context of breeding (cooperative breeding and communal rearing), and the prevalent mating system were highly correlated. Social monogamy preceded transitions to group-living and cooperation in the context of breeding. Ancestors probably exhibited social monogamy, group-living, reproductive cooperation and other forms of cooperation. Together, these findings confirmed that Hystricognathi evolved from social ancestors that exhibited social monogamy, or relatively low levels of promiscuity. Furthermore, I found that other forms of cooperative behavior also evolved early, implying that relatively high levels of cooperation and group-living were associated with the origin of these rodents.

On the other hand, findings from Chapter 2 strongly indicate that the role of kin selected benefits in maintaining group-living and cooperation in some descendant species within hystricognath rodents may be less important. Specifically, I examined communal

rearing in the group-living rodent *Octodon degus* and showed that genetic relatedness does not influence association strength among lactating females within social groups based on communal nesting during nighttime. Additionally, I found that overall, attendance of lactating females to communal litters during daytime did not fit expectations based on complete coordination, but that females may exhibit some coordination during the short-term in their daytime activity. The observation that attendance of females to communal litters increased with number of females per group supports that offspring reared communally benefit directly through enhanced care, which might include a more continuous supply of milk. These group-size effects on offspring attendance imply direct benefits may be more important derived from communal rearing. These findings in degus agree with those of Chapter 1, and where kin selection coupled to monogamy were important during the origin of group-living and cooperation in Hystricognathi. Degus and the other living octodontids represent a derived clade that include social, but also solitary living species, and where the dominant mating system of degus is promiscuity. Thus, in a scenario in which kin selection (through the monogamy hypothesis) drove the early origin of group-living and multiple forms of cooperation in these rodents, communal rearing in female degus might represent a conserved social behavior trait. In contrast, current patterns of within-group kinship may represent a derived condition.

Overall, a main message of this study is that phylogenetic comparative approaches and findings (Chapter 1) can inform relevant factors to be targeted by subsequent studies addressing the underlying mechanisms involved, in this case, social and cooperative behaviors in hystricognath rodents. Thus, degu's social system and its cooperative behavior are well predicted by the position of this species in the phylogenetic-evolutionary context of

hystrognaths (see Figure 7, Table 3 and Table S4 of Chapter 1). Additional studies focused on other potentially informative hystricognaths species are required to confirm whether findings of Chapter 1 can be established as a predictive model for the study of sociality and evolution in this group of rodents.