

Phylogeny modulates the effects of ecological conditions on group living across hystricognath rodents



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The evolution of group living in animals has been linked both to ecological and phylogenetic drivers or constraints. However, available evidence supporting each factor remains equivocal. In this study, we evaluated the influence of both scenarios across 98 species of hystricognath rodents using phylogenetic approaches that included a statistical model of trait evolution. We first estimated the hypothetical ancestral forms of several clades within the hystricognath phylogeny. Secondly, we examined evolutionary correlations between habitat conditions in terms of vegetation cover and group living to determine general macroevolutionary trends on social behaviour. Given the contrasting modes of life that characterize these rodents, we also examined whether subterranean habits influence group living. Our results support the hypothesis that group living in Old World Phiomorpha and New World Cavimorpha had an early origin. The best-fitted and well-supported model of evolution for group living was the equal rate model, implying an equal rate of gains and losses of group living. Logistic regression analyses that included phylogenetic relationships revealed significant correlation between habitats used (i.e. vegetation cover) and absence or presence of group living. The loss of group living across the phylogeny was associated with the use of closed habitat conditions. No association was found between changes in group living and subterranean mode of life. We conclude that ancestor–descendant relationships mediate the effect of changes in habitat use on the evolution of group living across hystricognath rodents.

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Ecological conditions are thought to be a major evolutionary driver of group living, or sociality (Alexander, 1974; Ebensperger & Blumstein, 2006). This tenet is based on the hypothesis that ecological conditions influence numerous fitness advantages that social animals obtain in relation to solitary living individuals, including decreased predation risk, decreased costs during building dens or refuges, increased access to resources and enhanced thermoregulation efficiency (Alexander, 1974; Bertram, 1978; Ebensperger, 2001; Ebensperger & Blumstein, 2006; Krebs & Davies, 1993). In addition, ecological conditions (e.g. population density, resource distribution, vegetation cover) may constrain animals to live in groups (Chaverri & Kunz, 2010; Dunbar & Shultz, 2007; Ebensperger & Hayes, 2008; Shultz & Dunbar, 2006). For instance, individuals in groups may increase their ability to detect and escape from predators, gain protection from predators

because of simple dilution of per capita risk, locate themselves such that other group members become more vulnerable to attacks, or even repel predators more efficiently (Bertram, 1978; Hamilton, 1971; Romey, 1997). Given that vegetation cover generally decreases prey detection by predators (Caro, 2005; Ebensperger, 2001; Ebensperger & Blumstein, 2006), species inhabiting more open, riskier habitats tend to have larger group sizes than species living in safer habitats that have more cover (Dunbar, 1989; Kleiman, 1974; Lagory, 1986). Alternatively, group living can be the consequence of limitations in breeding sites due to high population density, a patchy distribution of critical resources, or a combination of these factors (Arnold & Owens, 1998; Brown, 1987; Emlen, 1982; Johnson, Kays, Blackwell, & Macdonald, 2002; Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992; Waser, 1988).

Regardless of whether ecological conditions provide opportunities for social benefits or act as constraints, the extent to which group living across species reflects changes to past or current ecological conditions remain a topic of discussion. Species differences in group living may reflect a close functional match with differences in current ecological conditions. This hypothesis is

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

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

Available evidence supports different patterns of social evolution across different organisms. For instance, the evolution of group living in mongooses and other families of carnivores fits the NAH in that ancestors were solitary living forms that used habitats with high vegetation cover (Dalerum, 2007; Veron, Colyn, Dunham, Taylor, & Gaubert, 2004). In contrast, the evolution of group-living behaviour in other carnivores such as wolverines is more supportive of the FAH (Dalerum, Creel, & Hall, 2006). SAH on the other hand, adequately describes the evolution of group living in insect parasitoids, bees and birds (Cardinal & Danforth, 2011; Danforth, 2002; van Rhijn, 1990; Tanner, González, Matthews, Bradleigh Vinson, & Pitts, 2011; Wcislo & Danforth, 1997). Thus, macroevolutionary patterns of group living and the relative roles of ecology and phylogeny during this process are far from well established.

Study Model

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

Lacher (1981) and Trillmich et al. (2004) suggested that ecological conditions (e.g. habitat) represent a main constraint to the evolution of group living in Caviidae (cavies, guinea-pigs and allies). Across caviomorphs, this hypothesis is supported by the observation that group size across caviomorphs is correlated with body size (larger species are more social), diurnality (diurnal species are more social) and active burrowing (burrowing species are more social) (Ebensperger & Blumstein, 2006). Given that large body size and diurnality increase conspicuousness to visual predators, these findings have been interpreted as supporting a link between predation risk, burrow digging and group living in these rodents (Ebensperger & Blumstein, 2006; Ebensperger & Cofré, 2001). On the other hand, phylogenetic effects have also been suggested to contribute to the evolution of group living in caviids (Rowe & Honeycutt, 2002).

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

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

We built a composite species-level phylogeny of African and New World hystricognath rodents to test two of the three evolutionary scenarios discussed previously: (1) group living evolved from a solitary ancestor into more complex forms of group living (i.e. the NAH); (2) group living evolved directionally from a group-living ancestor into nonsocial living forms (i.e. the SAH). The fact that relatively few studies have been conducted to quantify intra-specific variation in group living across hystricognaths did not allow us to examine the FAH model. We then estimated the evolutionary trajectories and association of group living and habitat conditions in terms of vegetation cover through the reconstruction of ancestral character state and phylogenetic logistic regression.

Finally, we focused on all nodes to examine simultaneously the extent to which phylogenetic (historical) and ecological factors (based on vegetation cover) explain the evolution of group living through the clade. In particular, an independent role of ecological factors would be supported (1) by an association between group living and vegetation cover (where social gains are correlated with use of open habitat and social losses are associated with more vegetated, covered habitat), and (2) if vegetation cover does not depend on the phylogenetic relatedness of the species considered (i.e. vegetation does not exhibit a phylogenetic signal). A modulating role of phylogenetic relationships would be supported by a similar association between group living and vegetation cover and (3) if vegetation cover exhibits a phylogenetic signal.

METHODS

Data Collection

We used the available literature and unpublished data to collect information on group living and habitat of living hystricognath rodents. A complete list of the species included in the analysis can be found in the Supplementary material (Table S1). We chose robust phylogenetic methods (i.e. based on explicit models of evolutionary change) to examine evolutionary transitions between ancestral and derived character states (see below) based on discrete variables. We examined discrete variables instead of using group size as a continuous variable in our analysis because data on hystricognath group living (particularly New World species) typically do not include quantitative estimates of group size (or typical group size), and thus, would have limited the number of species or subclades represented in our analysis. Thus, species were considered 'social' when available evidence supported that two or more adults were reported as sharing a den or burrow system (most cases) or a territory (e.g. capybaras) (Ebensperger & Blumstein, 2006). Nonsocial species were those in which individuals were typically recorded to perform their activities solitarily, including nesting. Thus, group living was categorized as a binary character: 0 = nonsocial; 1 = social. The use of these mutually exclusive social categories is supported by the observation that intraspecific variation reported in caviomorphs typically involves differences in group size rather than extreme differences between solitary and group living (Maher & Burger, 2011).

We categorized vegetation cover of the main habitat of each species as 'open', 'mixed' or 'closed'. Open habitat included grasslands, open shrublands, rocky areas with extensive bare ground and salt basins (i.e. environments with minimal vegetation cover; Shultz & Dunbar, 2006); mixed habitat included riparian, swampy and mangrove conditions; closed habitat included canebrakes, dense shrublands and forest patches (i.e. environments with relatively high vegetation cover; Shultz & Dunbar, 2006). The analysis of discrete and continuous variables was complementary and needed to discern qualitative or quantitative shifts in group living when species used new habitats (Shumway, 2008). Therefore, we also ranked vegetation cover of the habitat of each species on a scale of 1 to 7, from totally open (consisting of mostly bare ground, rank <3.5), to mixed (rank 3.5–4.9), to closed forest patches (rank ≥5–7) (Ebensperger & Blumstein, 2006).

Hystricognath rodents include subterranean species whose social behaviour may be less sensitive to vegetation cover above ground. To quantify the potential effect of this mode of life on group living, we further categorized species as subterranean or not. Species were categorized as subterranean when evidence supported that they conduct the vast majority of their life underground, foraging excursions are limited to the vicinity of burrow openings,

and they perform regular digging activities (Lessa, Vassallo, Verzi, & Mora, 2008; Smorkatcheva & Lukhtanov, 2014).

Phylogeny of African and New World Hystricognath Rodents

We estimated a time-calibrated phylogeny of the hystricognath rodents from DNA sequences of mitochondrial cytochrome *b* gene obtained from GenBank (see Supplementary material, Table S1). *Ctenodactylus vali* and *Massoutiera mzabi* were used as outgroups based on the recent phylogeny of Upham and Patterson (2012). The alignment was conducted in CLUSTAL W (Thompson, Higgins, & Gibson, 1994). This tree was the base for further comparative analyses.

Molecular Clock

Estimation of phylogeny and divergence times were conducted by Bayesian inference implemented in BEAST 1.8.0 (Drummond, Suchard, Xie, & Rambaut, 2012). We used the uncorrelated lognormal relaxed clock to account for lineage-specific rates of heterogeneity (Drummond, Ho, Phillips, & Rambaut, 2006) and the birth–death process as tree prior. We used the GTR + Γ model with six rate categories. We used five calibration points to date the phylogeny based on the fossil record of this clade (see Upham & Patterson, 2012). To account for uncertainty in the dates of this record, all five calibration points were set to a lognormal distribution, a step constrained the fossil data as minimum hard bounds with a soft upper bound as suggested by recent palaeontological studies (e.g. Benton, Donoghue, & Asher, 2009; Donoghue & Benton, 2007).

We conducted two independent analyses with 20 million steps, and we took samples every 1000 steps (discarding the first 1000 steps to avoid including phylogenetic trees out of the convergence zone). Convergence of chains to the stationary distribution was evaluated by inspection of the Markov-chain Monte Carlo samples in Tracer 1.5 (Drummond & Rambaut, 2007). The effective sampled size of parameters was greater than 500, indicating that independent chains were adequately sampled. Finally, both chains combined provided a final sample size of 38 000 trees. We used this tree sample to build a maximum clade credibility tree (mcc tree) with the software TreeAnnotator 1.6.1 (<http://beast.bio.ed.ac.uk/TreeAnnotator>).

Ancestral Character States and Evolutionary Transition Rates

We first evaluated the extent to which the phylogeny correctly predicted patterns of similarity in group living, habitat type (vegetation cover) and mode of life (subterranean or not) of hystricognath rodents (i.e. phylogenetic signal) using the *D* statistic (Fritz & Purvis, 2010) and the association index (AI; Parker, Rambaut, & Pybus, 2008; see details in the Supplementary material). Given that these analyses indicated that all variables had strong phylogenetic signal (see Supplementary Tables S2, S3), we used 'ape' and 'geiger' packages (Harmon, Weir, Brock, Glor, & Challenger, 2008; Paradis, Claude, & Strimmer, 2004) in R to evaluate how the origin and evolutionary transitions between categories of group living were associated with the use of different categories of habitat in terms of vegetation cover across the evolutionary history of hystricognath rodents. Ancestral state for group living was analysed with a maximum likelihood approach, using a continuous time Markov model (Pagel, 1994). We then compared two models: an equal-rates model (ER), in which a single parameter governs all evolutionary transition rates, and an all-rates-different model (ARD), where each rate is given a unique parameter. The best-fit model was determined based on Akaike's

Information Criterion (AIC) (Akaike, 1974). In particular, the model selected had the lowest AIC value and delta AIC < 3 (Burnham & Anderson, 2002). We used the same approach to examine habitat conditions in terms of vegetation cover (open, mixed, closed). We then compared ER and ARD models, adding a symmetrical model rate (SYM); that is, forward and reverse evolutionary transitions between habitat states were constrained to be equal.

Estimation of Phylogenetic Logistic Regression

We performed phylogenetic logistic regression to evaluate the extent to which group living was predicted by the rank of vegetation cover (independent ordinal predictor) and subterranean mode of life (independent discrete predictor) on all nodes of the evolutionary history of hystricognath rodents. This method is based on an evolutionary model of binary traits in which trait values switch between 0 and 1 as species evolve throughout the phylogenetic tree (Ives & Garland, 2010). This analysis was performed using a variance–covariance matrix of the species trait constructed using the composite phylogeny in the module PDAP (Midford, Garland, & Maddison, 2008) of Mesquite v2.75 (Maddison & Maddison, 2011). The phylogenetic logistic regression was run using the PLoGReg.m function written by Ives and Garland (2010). The ranks of vegetation cover were log transformed and standardized to have a mean of zero and a standard deviation of one. Under this standardization the regression coefficients represent effect sizes of the independent variables (Ives & Garland, 2010). A bootstrapping procedure involving 2500 simulations was used to generate the confidence intervals and test for statistical significance of the slope of the regression model. Convergence of model parameters was achieved in all cases after these simulations.

RESULTS

The ancestral character estimation for the phylogeny nodes indicated that the most likely common ancestor of the hystricognath rodents exhibited group living (log likelihood = −41.03; proportional likelihood = 96%; Fig. 1) and used open habitat (i.e. low vegetative cover) (log likelihood = −60.92; proportional likelihood = 74 %; Fig. 2). The best-fit and well-supported model of evolution of group living was the ER, or equal rate model (evolutionary transition rate = 0.001; Table 1). Regarding evolutionary changes in habitat conditions, the best fit of the three possible models examined was the ER model (evolutionary transition rate = 0.010; Table 1), implying an equal rate of gains and losses of group living throughout hystricognath rodents.

Group living, vegetation cover and subterranean mode of life exhibited strong and statistically significant phylogenetic signal (see Supplementary Tables S2, S3). The phylogenetic logistic regression analysis revealed that the effect of vegetation cover on group living was significantly different from zero when the evolutionary relationships of species were included in the model. In particular, group living across hystricognaths was significantly predicted by lower values of vegetation cover (Table 2). In contrast, group living across hystricognaths was not predicted by whether species were subterranean or not (Table 2).

DISCUSSION

Our results support the hypothesis that the ancestor of hystricognath rodents exhibited group living, and that subsequently, group living was equally lost or regained, implying no directionality during the evolution of this aspect of social behaviour. This evolutionary pattern is inconsistent with ‘nonsocial ancestor’ and ‘social ancestor’ hypotheses. Instead, our results provide some support for

the ‘flexible ancestor’ hypothesis (FAH). The FAH states that group living evolved from a flexible ancestor (i.e. an ancestor with abilities to exhibit a variety of social organizations), and that social organization of extant species is the consequence of parallel evolution into more specialized ones through ecological constraints (sensu Dalerum, 2007). Studies examining intraspecific variation in group living are restricted to a handful of New World hystricognath species (Maher & Burger, 2011), an observation that precludes an examination of the extent to which ancestral forms were socially flexible.

An important implication of this scenario is that extant solitary living species are likely to represent a derived condition in these rodents. Similar patterns have been recorded in other animal taxa, including halictine bees (Wcislo & Danforth, 1997), communally roosting birds (Beauchamp, 1999) and some mammalian taxa, such as canids, pinnipeds or phocids (Dalerum, 2007). Intriguingly, recent evidence based on the preservation of multiple adult and subadult individuals in close proximity support the hypothesis of a group-living ancestor of modern marsupial mammals (Ladeveze, de Muizon, Beck, Germain, & Céspedes-Paz, 2011). Yet, these findings depart from patterns recorded across other mammalian taxa such as mustelids (Dalerum, 2007).

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

We did not find an effect of subterranean life on group living, implying that the response of group-living and solitary species to vegetation cover of habitat was unrelated to their subterranean habits. Numerous reports show that some African bathyergids and many ctenomyids and octodontids feed on vegetation at the ground surface (e.g. Bennett & Faulkes, 2000; Busch et al., 2000), a behaviour that exposes these animals to aerial and terrestrial predators, implying that vegetation cover may affect predation risk to these animals. However, the extent to which vegetation cover influences predation risk of subterranean and nonsubterranean rodents is not well understood.

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

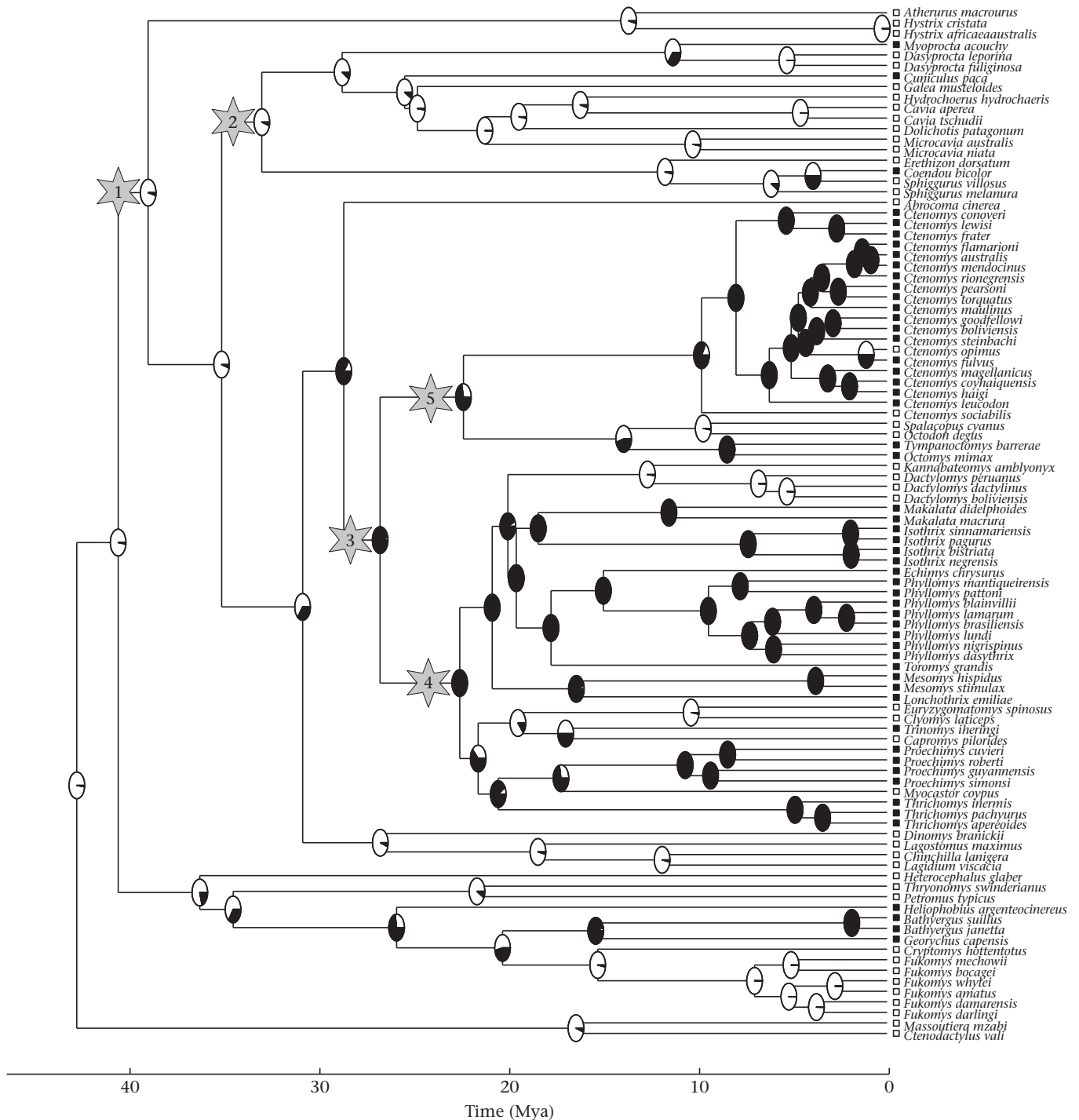


Figure 1. Reconstruction of the ancestral state of the social behaviour in hystricognath rodents. The squares next to the tips of the phylogeny represent the presence (white) or absence (black) of group living. The pie chart in the nodes of the phylogeny show the proportional likelihood of each state estimated. A star symbol is used to identify calibration points based on the fossil record of hystricognath rodents (see Upham & Patterson, 2012): 1 (*Gaudeamus*, early Oligocene 37.2–33.9 million years ago, Mya); 2 (stem cavioid, early Oligocene 33–31.5 Mya); 3 (*Sallamys*, late Oligocene 29–24.5 Mya); 4 (*Paradelphomys*, early Miocene 21–17.5 Mya); 5 (*Xenodontomys*, late Miocene 10–9 Mya).

Group living and cooperative care of offspring characterizes several species of African bathyergids, or mole-rats (Burda et al., 2000; Faulkes & Bennett, 2013). Burda et al. (2000) suggesting that this complex form of group living would have originated in these subterranean rodents from an ancestor already exhibiting group living and cooperative brood care. Thus, solitary living recorded in some species would be a derived trait, possibly as a consequence of constraints linked to a subterranean mode of life.

Our findings that group living was likely the ancestral condition to all hystricognaths and that solitary living represents a more derived condition provide support for the overall scenario suggested by Burda et al. (2000). Yet, we did not find an overall association between subterranean life and sociality across the clade. A recent study specifically aimed to test the importance of subterranean life across all rodents showed that this mode of life is more likely to evolve from ancestors exhibiting group living (Smorkatcheva &

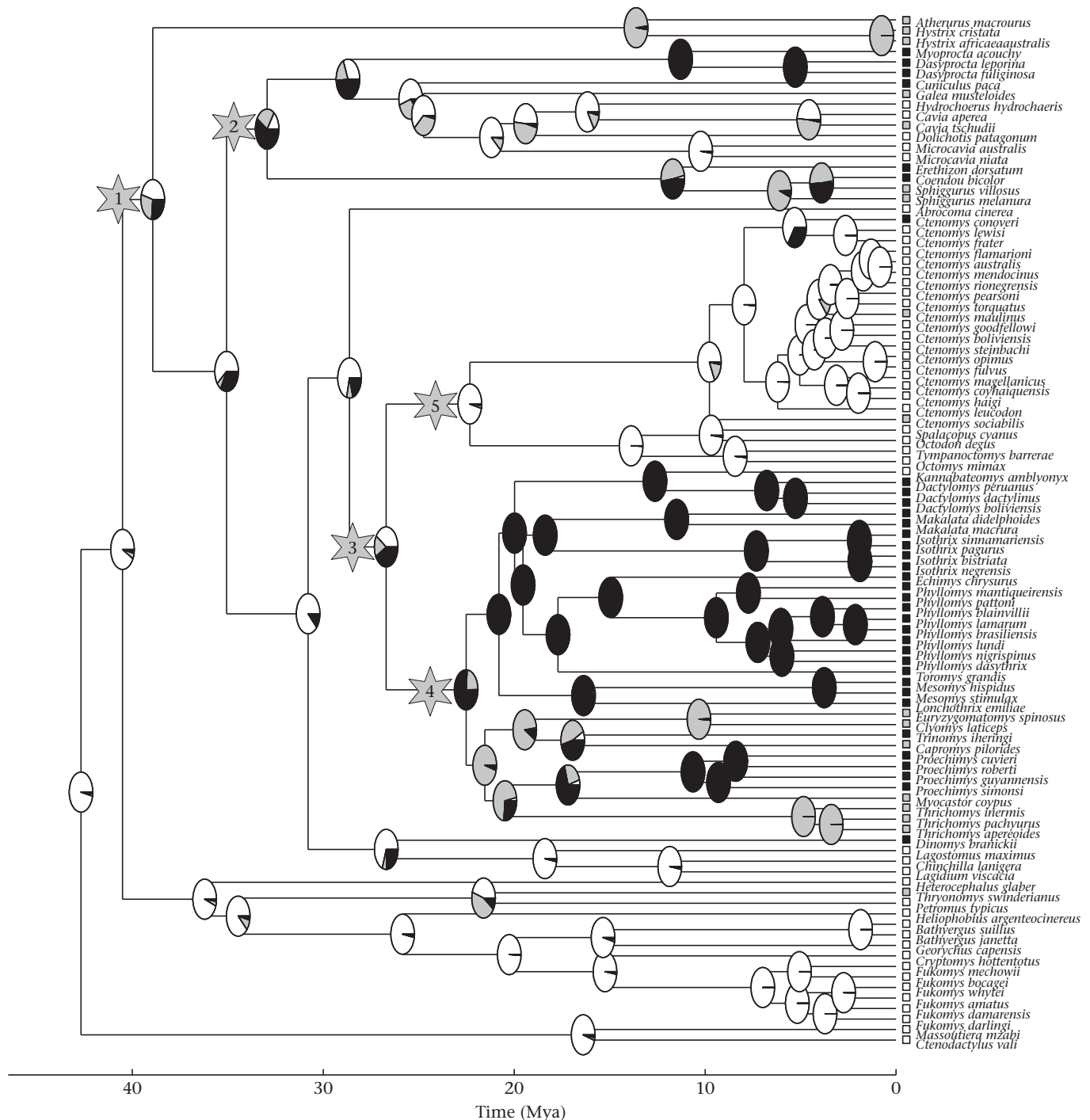


Figure 2. Reconstruction of the ancestral state of the habitat in hystricognath rodents. The squares next to the tips of the phylogeny denote the species' habitats. White: open habitat; grey: mixed habitat; black: closed habitat. The pie chart in the nodes of the phylogeny show the proportional likelihood of each state estimated. A star symbol is used to identify calibration points based on the fossil record of hystricognath rodents (see Upham & Patterson, 2012): 1 (*Gaudeamus*, early Oligocene 37.2–33.9 million years ago, Mya); 2 (stem cavioid, early Oligocene 33–31.5 Mya); 3 (*Sallamys*, late Oligocene 29–24.5 Mya); 4 (*Paradelphomys*, early Miocene 21–17.5 Mya); 5 (*Xenodontomys*, late Miocene 10–9 Mya).

Lukhtanov, 2014). Together, these findings are consistent with the notion that group living in African mole-rats represent an ancestral condition and that subterranean life is more likely a consequence rather than a cause of this trait (Burda et al., 2000).

Arrival of ancestral hystricognath rodents to the New World from Africa has not been dated precisely, and estimates range from 34 (early Oligocene) to 45 (middle Eocene) million years ago (Antoine et al., 2012; Poux, Chevret, Huchon, de Jong, & Douzery,

2006). This arrival was followed by two main events of radiation, one during the Oligocene, and another during the middle late Miocene boundary (Huchon & Douzery, 2001; Opazo, 2005; Vucetich, Verzi, & Hartenberger, 1999). Changes in renal morphology and particular modes of life such as arboreality have been suggested to have contributed to radiation of New World hystricognaths (Diaz, Ojeda, & Rezende, 2006; Galewski, Mauffrey, Leite, Patton, & Douzery, 2005). In contrast, the role of behaviour

Table 1

Comparison of model fit to group living and vegetation cover in the habitat of hystricognath rodents

Group living				Habitat			
Model	k	Log-Lh	AIC	Model	k	Log-Lh	AIC
ER	1	−41.86	85.72	ER	1	−60.36	122.73
SYM	—	—	—	SYM	3	−59.81	125.61
ARD	2	−42.48	88.96	ARD	6	−56.85	125.70

Bold font identifies the best-fitting model; k: number of model parameters; Log-Lh: logarithm of likelihood; AIC: Akaike's Information Criterion; ER: equal-rates model; SYM: symmetric model; ARD: all-rates-different model.

Table 2

Phylogenetic logistic regression parameter estimates for the effect of vegetation cover and subterranean mode of life on the evolution of group living in hystricognath rodents

Parameters	Estimate*	SE*	Bootstrap mean†	Bootstrap CI†	P
b0 (intercept)	0.829	0.741	0.806	−0.809, 2.471	0.374
b1 (vegetation cover)	−0.972	0.348	−1.172	−2.451, −0.396	<0.00001
b2 (subterranean life)	−0.791	0.444	−0.969	−2.515, 0.267	0.138

Bold font indicates statistically significant parameter estimates.

* Parameters of logistic regression and standard errors of the estimates were obtained using the generalized estimating equations (see Ives & Garland, 2010).

† Parametric bootstrapping was performed by simulating 2500 data sets to obtain confidence intervals. Parametric bootstrapping was also used to test the null hypothesis that the regression coefficients equal zero ($H_0: b_i = 0$, two-tailed tests).

remains less understood. It has been hypothesized that behaviour may drive or inhibit adaptive ecological change (Duckworth, 2009; Mayr, 1960; Wcislo, 1989; West-Eberhard, 1989), yet the roles of different behavioural traits, including group living, remain unclear (Duckworth, 2009). Subsequent studies are needed to determine the extent to which group living and other aspects of social behaviour (e.g. cooperation during breeding and rearing) preceded or promoted subsequent adaptative change in hystricognath rodents.

To summarize, our study, based on a large taxonomic sample and a probabilistic framework, supports an association between evolutionary changes in group living, changes in habitat use and the history of ancestor–descendant relationships across hystricognath rodents. Although the importance of vegetation cover in the habitat on the evolution of group living has been examined previously (Ebensperger & Blumstein, 2006; Veron et al., 2004), no previous studies reconstructed ancestral and derived states of this factor. Our results link both factors together, and suggest that both the ecological conditions (i.e. vegetation cover) and the phylogenetic relationships of these rodents may drive group living.

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Supplementary Material

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