



Original Investigation

Evolutionary association between subterranean lifestyle and female sociality in rodents

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ABSTRACT

Subterranean rodents are a good model system to examine adaptive evolution of social organization. Life underground has been proposed either to favor solitariness or, to the contrary, to promote sociality. In concordance with the first idea, most specialized diggers are solitary. However, group-living in several unrelated subterranean rodent species and especially eusociality in two genera of African mole-rats, the *Bathyergidae*, seem to support the second hypothesis. Thus, none of the two models is fully consistent with empirical data. Here we apply the comparative phylogenetic method to test an evolutionary correlation between fossoriality and female social strategy (solitary breeding vs breeding in group). Both characters show very strong phylogenetic signal, and we found a significant correlation between them. Subterranean lifestyle is readily acquired under female sociality. By contrast, the transition to life underground is extremely unlikely under female solitariness. Thus, not only social behavior may be affected by ecological specialization as it is widely assumed, but it can itself restrain the range of possible specializations. The rates of transition from sociality to solitariness are equal under subterranean and surface-dwelling lifestyle. Sociality loss is irreversible in subterranean lineages, unlike surface-dwelling lineages. Based on the revealed transition rates we suggest that all lineages of subterranean rodents have gone through the stage of cooperation at the beginning of their evolutionary track, whereas group-living is selected against in highly specialized diggers. An odd pattern of distribution of sociality across and within truly subterranean taxa probably derives from the influence of extrinsic factors in combination with phylogenetic inertia.

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Introduction

Group living involves some survival and/or reproductive costs to group members (Davies et al., 2012), yet it is common in many animal species. Revealing selective forces that drive individuals to lives in close association with conspecifics is a central goal of behavioral ecology. Subterranean rodents are a particularly good model system to examine adaptive evolution. The demands of living in a subterranean environment seem to have resulted in structural and functional convergence among species (McNab, 1966; Nevo, 1979, 1999; Stein, 2000). Adaptations to the underground ecotope likely affect not only anatomy and physiology of these animals, but also their behavior, including patterns of social interactions and spacing. Traditionally, life underground is thought to favor a solitary existence because low productivity of the subterranean ecotope leads to strong resource competition

while the spatial limits of a burrow system facilitate territory defense (*Territory Defence Hypothesis*, TDH – Nevo, 1979). On the contrary, the *Expansible Burrow Hypothesis* (EBH) (Alexander et al., 1991) proposes that the use of predator-free refuges, such as subterranean burrows, favors philopatry and sociality.

In concordance with TDH, most specialized diggers are solitary (Nevo, 1979; Lacey, 2000; Lacey and Ebensperger, 2007). However, group-living in several subterranean rodent species from different phylogenetic lineages (Lacey et al., 1997; Begall et al., 1999; Smorkatcheva, 1999; Evdokimov, 2001), and especially eusociality in two bathyergid genera (Jarvis, 1981; Bennett and Jarvis, 1988; Bennett, 1989; Burda, 1989, 1990; Burda and Kawalika, 1993) seem to contradict TDH and to support the EBH. Thus, neither TDH nor EBH is fully consistent with the observed pattern.

Failure in identifying the ecological correlates of behavior may be due to the influences of unaccounted environmental variables as well as phylogenetic influences (Eisenberg, 1963; Edwards and Naeem, 1993; Rendall and Di Fiore, 2007). Accordingly, there are two competing scenarios of social evolution in African mole-rats (*Bathyergidae*). *Aridity Food Distribution Hypothesis*, AFDH, proposes

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that (eu)sociality in this family evolved as an adaptation for a specific combination of environmental conditions, i.e. patchily distributed subterranean food, hard-to-excavate soils, and low and unpredictable rainfall (Lovegrove and Wissel, 1988; Jarvis et al., 1994; Faulkes et al., 1997; Bennett and Faulkes, 2000). On the other hand, Burda et al. (2000) argue that though the AFDH may explain group size dynamics as a function of the distribution and availability of resources, it is inadequate to explain the evolutionary transition from solitariness to sociality. Instead, these authors consider cooperative monogamy of social bathyergids as an ancestral trait of hystricognath rodents, and the solitariness in other genera of bathyergids as a derived trait. Sociality could have been a preadaptation to occupy the subterranean ecotope, and could have been retained or even reinforced by living underground in some lineages due to intrinsic (reproductive or physiological) rather than extrinsic (ecological) constraints (*Hypothesis of Phylogenetic Constraints*, HPC – Burda et al., 2000; Sumner et al., 2007). However, rigorous phylogenetic analysis has never been used to test these ideas.

Here, we apply phylogenetic comparative methods to test if there is an evolutionary correlation between the type of social organization (solitariness vs. living in groups) and fossoriality, and, if so, whether the direction of the relationship conforms to the predictions of TDH or EBH. Also, we use the estimated rates of evolutionary transitions between states of focal traits to discriminate between two scenarios of social evolution in the *Bathyergidae*.

Material and methods

Data collection and character coding

We collected data about substrate utilization and female social strategy for about 280 species which constituted our preliminary dataset.

We categorized species as being either subterranean or not. We followed the definition of subterranean species used by Lessa et al. (2008). A species was considered subterranean if animals conduct the vast majority of their life underground, perform regular digging activities, and their foraging excursions are limited to the vicinity of burrow openings. Thus, our list of subterranean species includes, in addition to species exhibiting the obvious morphological specializations for digging (e.g. broad feet, enlarged forearms, incisor procumbency, massive skull, reduced visual system – Nevo, 1979; Stein, 2000), several species that have only slight modifications and usually labeled as fossorial, yet demonstrate almost subterranean habits. Within the genus *Arvicola*, *A. amphibius* and *A. scherman* were treated separately (Wilson and Reeder, 2005), the first being scored as a surface-dwelling form while the second is considered a subterranean form, on the base of nesting and foraging behavior displayed by breeding females.

We used a simple, qualitative criterion for sociality that can be unambiguously inferred from heterogeneous literature sources. We dichotomized social patterns as either strictly solitary or social. For a number of species, social behavior dramatically varies between sexes, age categories or periods of reproductive cycle. For the purpose of this study, we focused on social strategy of reproductive females. On the one hand, those factors which are expected to be responsible for the adaptive changes of social organization in subterranean rodents (strong competition for food, according to TDH, and high energy costs of tunnel construction, according to EBH) are thought to affect primary on social strategy of pregnant/lactating females. This is because food and nursery dens are the key resources for females rather than males (Eisenberg, 1966; Fleming, 1979), and because in mammals females rather than males tend to be philopatric (Dobson, 1982). On the other hand, burrow sharing by breeding female with other adult individual(s) is

a first step necessary for cooperative groups to form in fossorial or subterranean rodents. According to EBH, sociality based on philopatry and cooperation is advantageous for species using long-lasting, expansible burrows (Alexander et al., 1991), and the combination “subterranean social” is more beneficial than the combination “subterranean solitary”. Therefore, EBH predicts that if social intolerance is a conservative trait, it might hamper the transition to fossorial existence. On the contrary, TDH expects that phylogenetically inherited predisposition of a female to defend a nursing burrow from any conspecifics might facilitate the gain of subterranean lifestyle while phylogenetically inherited sociality should complicate such a transition.

Based on this argumentation, the key criterion for dividing species into two categories was whether or not a reproductive female is willing to share its nursery den with any adult conspecifics, or, for species that use no den, whether she lives in a breeding group or alone. Species was scored as solitary if females are reported to use individual nursing dens in field and/or display social intolerance in captivity.

We classify species as social if there is field evidence (in some instances, the evidence from the studies conducted in large enclosures) of either communal breeding, cooperative breeding or joint nesting by male and pregnant/lactating female. When social monogamy was inferred from spacing, but joint nesting by male and female was not clearly established, the species was referred as social if data on paternal care in captivity provided additional support.

Developing the phylogenetic trees

Modern comparative analysis requires information about phylogenetic relationships in the form of tree topology and branch length (Felsenstein, 2004). There is no published phylogeny that would include all the species from our data set. Therefore, as a first step of our research, we elaborated this phylogeny using mitochondrial *cytochrome B* gene and Bayesian approach implemented in MrBAYES, version 3.2 software (Ronquist et al., 2012). The *cytochrome B* was selected since it was the only gene sequence available for the majority of species from our initial data set. These species were included into the final dataset. Given the small number of subterranean rodents with known social strategy, we also added two subterranean species with no available *cytochrome B* sequences, *Clyomys bishop* and *Tachyoryctes macrocephalus*, using the sequences found for their closely related congeners, *Clyomys laticeps* and *Tachyoryctes splendens*. Each of these genera, *Clyomys* and *Tachyoryctes*, was represented in our analyses by single species. The replacing of one species by the close-related congener should not change the position of these genera on the phylogenetic tree. This approach has been used in such situations in comparative phylogenetic studies (e.g. Cornwallis et al., 2010).

Our final dataset included 225 rodent species (183 surface-dwelling and 42 subterranean) representing 30 families. A list of species, references and the accession numbers of the *cytochrome B* sequences are presented in the Supplementary Data, Table S1.

The *cytochrome B* sequences were downloaded from GenBank, aligned using BioEdit software (Hall, 1999) and manually edited. Alignment of the sequences was unambiguous, because no insertions or deletions occurred in the dataset. Of 1140 positions, 792 were variable and 680 were parsimony-informative.

It is well known that rodents phylogenetic reconstructions based on *cytochrome B* may not be as accurate as multi-gene analyses (Montgelard et al., 2008). Indeed, preliminary runs of Bayesian analysis showed that obtained *cytochrome B* trees were poorly resolved. At the same time, monophyly of numerous (but not all) clades of rodents is known to be strongly supported by multiple

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