



# Agonism Management Through Agonistic Vocal Signaling in Subterranean Rodents: A Neglected Factor Facilitating Sociality?

Gabriel Francescoli<sup>1</sup> · Cristian Schleich<sup>2</sup>

Received: 21 November 2017 / Accepted: 9 July 2018  
© Konrad Lorenz Institute for Evolution and Cognition Research 2018

## Abstract

Communication is inherent to social relationships. Previous papers addressed the correlation between social and communicative complexity, and the origin of sociality in rodents. In subterranean social species, as the number of animals in the same burrow increases, so do interindividual contact rates. This is because of limitations in actually used tunnel length and diameter, leading to an increasing number of agonistic situations probably resulting in time loss, threatening, and fighting with danger of injuries. To avoid this, social species are expected to have an increase in the number of particular vocalizations. Comparison of the adult vocal repertoire of 12 species (seven genera) through regression and phylogenetically independent contrasts (PIC) suggests three main conclusions: (1) social species increase their repertoire both in number and categories of vocal signals in relation to solitary species, although the coefficient was smaller in the PIC model; (2) the number of agonistic vocalizations was also different between solitary and social species, with the latter displaying higher numbers of these calls; (3) the percentage of agonistic vocalizations in relation to total repertoire was similar between social and solitary species, with no significant relationship between this parameter and the social structure. These results imply that agonistic vocalizations have also increased in number in social species, indicating the importance of these calls in the establishment of new relationships. As repertoire changes are essential to cope with new and frequent kinds of interactions sociality originates, these results suggest that at least for these organisms, communicative changes, especially at the level of agonistic signals, could be a necessary condition to fulfill in the path to the possibility of group living.

**Keywords** Agonistic signals · Communicative complexity · Social complexity · Sociality evolution · Subterranean rodents

## Introduction

Animal communication studies have raised many important issues about general evolutionary characteristics of communication systems. One of those issues is the relationship between social and communicative complexity. Communication is inherent to social relationships, because no coordinated activities nor cooperative group actions could be performed without the existence of a minimal communication system providing ways to achieve such a coordination.

Much effort has been devoted to relating social characteristics with communicative complexity, and most of it has been centered on the influence species' ecology has over the constraints and advantages of group living. Nevertheless, behavioral constraints on group living have been somehow neglected, especially when considering the role communication could play in allowing or impairing full social grouping. Summarizing their survey on social complexity as a proximate and ultimate factor in communicative complexity, Freeberg et al. (2012, p. 1797) state "(i) that social complexity may play an important role in driving communicative complexity in animal species and (ii) that further tests of this possible role will be of great interest—and are much needed—to advance our understanding of communicative evolution."

Many levels of explanation have been considered to understand the causes and evolution of sociality, and various studies indicate that a broader perspective is needed, as many constraints not yet accounted for could be influencing

✉ Gabriel Francescoli  
gabo@fcien.edu.uy

<sup>1</sup> Ethology Section, Faculty of Sciences, Universidad de la República, Montevideo, Uruguay

<sup>2</sup> IIMyC-Conicet (Institute of Marine and Coastal Research), Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

mammalian social behavior (Kappeler et al. 2013). One element that has not yet been taken into account is the possibility that communication constitutes a key factor for the development of social behavior (Avilés 1999; Ebensperger 2001; van Veelen et al. 2010). Indeed, some studies seem to indicate that sociality may not be a previous condition for communicative complexity evolution (see Ord and García-Porta 2012, and references therein).

We can think of evolution towards sociality going through a “bottleneck” in which communicative complexity must be increased in order to allow higher social complexity to develop. As far as we know, no previous paper has considered the development of a system of signals, at least a little more complex than the one solitary species have, as a required path to increased social complexity. If we consider this from a biosemiotics perspective, the idea seems a sound one, because biosemiotic theory proposes communication as a central issue in shaping many evolutionary events and pathways, and argues that the appearance of new codes (biological information and meaning) have mediated important events in evolution (Barbieri 2008).

Rodents can be identified as a group of choice to address sociality studies, not only because they are the largest mammal order, but also very variable in social, anatomical, physiological, behavioral, and ecological characteristics (Wolff and Sherman 2007). Previous papers have addressed the putative correlation between social and communicative complexity, especially using vocal communication, in some rodent groups (Blumstein and Armitage 1997; Daniel and Blumstein 1998; Blumstein 2003; Pollard and Blumstein 2012). Some of the papers dealt with social complexity opposed to environmental influence as the origin of communicative complexity (the acoustic adaptation hypothesis), while other papers tried to find a better way to measure social complexity using other characteristics than mere colony size (Blumstein and Armitage 1997; but see also Freeberg 2006 for an opposite view). Even if the papers mentioned before have used mostly fossorial rodents and alarm calls to investigate this issue, they allowed for reaching the conclusion that probably acoustic adaptation, thus the influence of the environment, could not explain communicative complexity in full (Blumstein 2003). In another batch of studies Ebensperger and colleagues (Ebensperger 1998, 2001, 2003; Ebensperger and Cofré 2001; Ebensperger and Blumstein 2006; Ebensperger and Hayes 2008) have also examined, for different rodent groups, the possible origin of sociality. These papers dealt with the advantages of group living and the origin of sociality implying, at least in many cases, that sociality arose from solitary animals grouping together and not the other way around. However, previous literature has not considered the role that communicative complexity could have played in the facilitation of group living

in rodents through the generation of extended repertoires (Lacey and Sherman 2007). This is true even for the case of hypotheses assessing burrow sharing (Ebensperger 2001; Ebensperger and Cofré 2001) or cooperation (Gromov 2017) as possible causes of grouping.

In subterranean rodents, sociality has been proposed to vary in a continuum from solitary to eusocial forms (Lacey 2000). Usually, it is assumed that sociality evolved from solitary individuals grouping together, but in the case of subterranean rodents some authors have proposed that sociality could have been the initial condition (Burda et al. 2000). This hypothesis was challenged because in the Bathyergidae, a group of choice for subterranean rodents’ sociality studies, sociality appeared as not being an ancestral character (Walton et al. 2000; Faulkes and Bennett 2013). Recently, some papers have returned to this hypothesis to suggest that female sociality, ecological conditions, and/or neurophysiological characteristics (neuropeptides that modulate complex social behavior and social cognition) are responsible for social condition in some rodent groups (Donaldson and Young 2008; Smorkatcheva and Lukhtanov 2013; Sobrero et al. 2014), even if other researchers still support an independent origin of sociality for some of these groups (Lacey et al. 2015).

Assuming that in some species social living builds up from solitary living conditions, several hypotheses have been proposed to explain the evolution of sociality in subterranean rodents, mainly in the Bathyergidae, but sometimes applied to other families as an extension: (a) the food/aridity hypothesis (Jarvis et al. 1994); (b) the reproductive skew hypothesis (Burda 1989); (c) the historical constraints hypothesis (Burda and Kawalika 1993); and (d) the pacifistic hypothesis (Ganem and Nevo 1996; Nevo 2007). Surprisingly, when the possible origin for social living in subterranean rodents is surveyed, no communication issues are discussed (Lacey 2000) even when the pacifistic hypothesis (Nevo 2007), implying a decrease in aggressive behavior probably mediated by signaling, is considered.

In social subterranean rodents, the number of animals sharing the same burrow system increases in relation to solitary species, increasing in consequence interindividual contact rates. This situation may lead to an increase in the number of agonistic encounters that could derive in time loss by threatening and/or direct physical fighting, with the consequent danger of injuries. To avoid those consequences, and following Pollard and Blumstein (2012) in their claim that different attributes of social complexity probably drive different attributes of communicative complexity, social species are expected not only to present friendly/appeasement calls, but also an increase in the number of signals devoted to the management of agonistic behavior in the early stages of social organization (see Fig. 4 in Pollard and Blumstein 2012).

Here we propose to consider communicative complexity not only as an increase in vocal signal repertoire related to social complexity, but mainly as an increase in a particular category of vocalizations: those vocalizations dealing with the management of agonistic situations, because those vocalizations will also facilitate burrow sharing by neighboring individuals and multiple occupancy of burrows in social animals. Even if the preceding hypothesis could be considered in a general way, here it is applied to subterranean rodents for some important reasons: (1) the fact that both solitary animals and groups live in tunnel systems imposes on the animals in any social system roughly the same kind of constraints in relation to space use and crowding (frequency of interindividual contacts); (2) with regard to the opposition between environmental influence and social complexity on the determination of communicative complexity (see Blumstein 2003), environmental complexity is roughly the same for all species because of the subterranean niche being very stable (Nevo 1979), despite some changes in soil characteristics and food quality and abundance; (3) there are in the literature well described vocal repertoires or at least fair accounts of repertoire size for several species, both solitary and social, while other communication channels are not suitable for agonistic expression (chemical signals are not capable of rapid modulation that would allow for their use in agonistic encounters, visual signals cannot be used because tunnels are completely dark, and seismic signaling is only unambiguously present in two of the species studied here); and (4) previous studies on communicative complexity have mostly been performed on fossorial and/or cursorial rodents, but not on truly subterranean species (Blumstein and Armitage 1997, 1998; Daniel and Blumstein 1998; Blumstein 2003).

Therefore, the aim of this article is to propose that an increase in agonistic signal (vocal) repertoire may play a role in the development of full sociality in subterranean rodents, and eventually in other rodents and/or mammal taxa, because of the need for an effective agonism management allowing an increase in the number of individuals living together.

## Methods

For the sake of this study, we considered solitary species to be those in which only one adult individual inhabits a burrow system during its adult life, with an exception made of couples staying together for mating during short periods (only a few days). We considered social species those in which more than one adult of the same or different sex live together in the same burrow system for long periods, and usually their entire life. We also considered social complexity increasing when the number of individuals living together increases,

and communicative complexity increasing when the number of different vocal signals in adults increases.

Since definitions of agonism are often difficult to provide due to the dynamic nature of the behavior itself, in the present work we considered agonistic behavior as all patterns involved in aggression (fighting and various types of threatening) and submission (Bekoff 1981; Bekoff and Byers 1986).

We examined the adult acoustic signal repertoire of 12 species that have been studied in some detail, six social (Bathyergidae: *Fukomys anelli*, *Fukomys micklei*, *Fukomys darlingi*, *Fukomys mechowii*, *Heterocephalus glaber*; and Octodontidae: *Spalacopus cyanus*) and six solitary (Spalacidae: *Spalax ehrenbergi*; Ctenomyidae: *Ctenomys talarum*, *Ctenomys mendocinus*, *Ctenomys pearsoni*; Bathyergidae: *Heliophobius argenteocinereus*; and Geomyidae: *Geomys breviceps*).

Vocalizations were classified in six different categories (mating, agonistic, distress, contact, alarm, routine) following the classification proposed by Schleich et al. (2007) and based on the original descriptions when available. This classification seemed reasonable for characterizing different functions of the vocalizations, and was also utilized in some of the papers used as sources for this work. For some species like *F. micklei*, *H. argenteocinereus*, and *G. breviceps* original papers include some vocalizations in more than one category (DeVries and Sykes 2008; Knotková et al. 2009; Vanden Hole et al. 2014). In these cases, the criterion followed was to list the vocalizations under each of the categories for which they were cited, even if the total number seems not to coincide (see Table 1 and the note therein). The classification criterion applied has taken into account the original assignment done by the authors in their published papers and, in many cases, information extracted directly from tables built in a similar way.

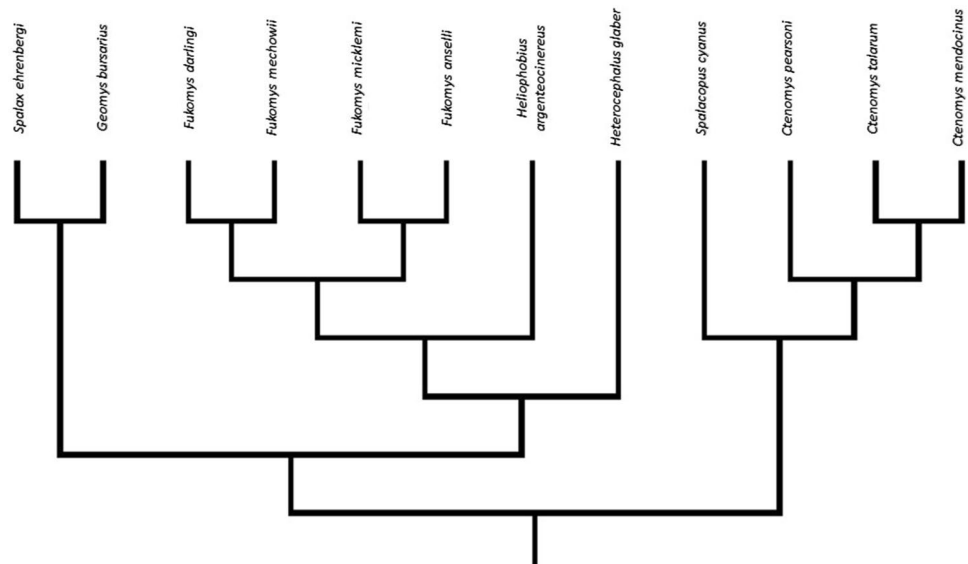
Relationships between sociality and vocal repertoire size or agonistic signals were analyzed using linear regression (using sociality as a binary variable) and phylogenetically independent contrasts (PIC), since this study involves the comparison of species closely and not closely related from the phylogenetic point of view. However, no complete valid and robust phylogenetic tree exists for all the analyzed species. Therefore, we combined partial phylogenies taken from White (2003), Voloch et al. (2013), and Luna et al. (2017) to obtain a phylogenetic tree (Fig. 1) and analyze data with PIC. Data on sociality and vocalizations were converted to phylogenetically independent standardized contrasts using the phylogenetic diversity analysis program PDAP Package (version 1.16, by Peter E. Midford, Ted Garland Jr., and Wayne P. Maddison) under the Mesquite package (version 3.31). Grafen's branch length transformation (Grafen 1992) was utilized to assign arbitrary branch lengths to the phylogenetic tree. Data about group size are reproduced from the published source papers,

**Table 1** Social status and number of signals in each category for the surveyed species

Species	Sociality	Mating	Agonistic	Distress	Contact	Alarm	Routine	Total	Sources
<i>Fukomys anselli</i>	Social	3	<u>7</u>	<u>1</u>	2	–	–	12	Credner et al. (1997)
<i>Fukomys micklemi</i>	Social	2	<u>5</u>	<u>6</u>	<u>4</u>	–	–	14	Vanden Hole et al. (2014)
<i>Fukomys darlingi</i>	Social	2	5	0	3	–	–	10	Dvořáková et al. (2016)
<i>Fukomys mechowii</i>	Social	3	<u>5</u>	<u>1</u>	<u>6</u>	1	–	14	Bednářová et al. (2013)
<i>Spalacopus cyanus</i>	Social	2	<u>3</u>	<u>1</u>	4	1	–	10	Veitl et al. (2000)
<i>Heterocephalus glaber</i>	Eusocial	1	<u>5</u>	–	1	<u>4</u>	2	12	Pepper et al. (1991), Judd and Sherman (1996), and Yosida and Okanoya (2009)
<i>Heliophobius argenteocinereus</i>	Solitary	3	<u>4</u>	<u>4</u>	–	–	–	9	Knotková et al. (2009)
<i>Spalax ehrenbergi</i>	Solitary	1	2	1	?	?	?	6	Heth et al. (1988) <sup>a</sup>
<i>Ctenomys mendocinus</i>	Solitary	?	2	–	?	?	?	4?	Francescoli, Camin, unpublished observations
<i>Ctenomys talarum</i>	Solitary	2	2	–	–	–	–	4	Schleich and Busch (2002)
<i>Ctenomys pearsoni</i>	Solitary	2	2	–	–	–	–	4	Francescoli 1999; unpublished data
<i>Geomys breviceps</i>	Solitary	<u>2</u>	<u>2</u>	–	1?	–	–	3	DeVries and Sykes (2008)

Short line=no data; ?=doubt about data; underlined signal numbers add to more than total because some vocalizations were put by authors in more than one category or display behavioral characteristics by which they can be classified under two different categories

<sup>a</sup>In *Spalax ehrenbergi* the number of vocalizations was established from the qualitative description by Heth et al. (1988), from which the emission context could be inferred for only three signals

**Fig. 1** Phylogenetic tree used to calculate PIC values

and in the case of multiple sources data were obtained from the most recent papers.

The percentages of agonistic vocalizations/total vocalizations for each species were calculated using the number of agonistic vocalizations shown in Tables 1 and 2, and the total number of vocalizations shown in Tables 1 and 3.

## Results

Results of the analysis are presented in Tables 1, 2, and 3, together with the source articles for the data. In Table 1 the number of vocalizations in each of the six categories

**Table 2** Social status and list of agonistic signals for the surveyed species

Species	Sociality	Agonistic	Sources
<i>Fukomys anelli</i>	Social	Whistle, trill, trill II, hiss, grunt I, grunt II, loud call	Credner et al. (1997)
<i>Fukomys micklemi</i>	Social	Grunt, soft call, ♂ cluck, ♂ shriek, whistle	Vanden Hole et al. (2014)
<i>Fukomys darlingi</i>	Social	Whistle, squeak, squeal, harsh, cry	Dvořáková et al. (2016)
<i>Fukomys mechowii</i>	Social	Scream, high trill, swing trill, long twitter, cry	Bednářová et al. (2013)
<i>Spalacopus cyanus</i>	Social	Cluck I, cluck II, cluck III	Veitl et al. (2000)
<i>Heterocephalus glaber</i>	Eusocial	Hiss, grunt, upsweep trill, loud chirp, scream	Pepper et al. (1991), and Yosida and Okanoya (2009)
<i>Heliophobius argenteocinereus</i>	Solitary	Squeak, scream, low cluck, hiss	Knotková et al. (2009)
<i>Spalax ehrenbergi</i>	Solitary	Attack, threat	Heth et al. (1988)
<i>Ctenomys mendocinus</i>	Solitary	S type, G type	Francescoli, Camin, unpublished observations
<i>Ctenomys talarum</i>	Solitary	Tuc-tuc, grunt	Schleich and Busch (2002)
<i>Ctenomys pearsoni</i>	Solitary	S type, G type	Francescoli (1999), unpublished data
<i>Geomys breviceps</i>	Solitary	Squeak; purr	DeVries and Sykes (2008)

**Table 3** Social status, total repertoire, and colony size for the surveyed species

Species	Sociality	Total repertoire	Colony size	Sources
<i>Fukomys anelli</i>	Social	12	9–20	Šklíba et al. (2012), and García Montero et al. (2016)
<i>Fukomys micklemi</i>	Social	14	Not reported	Vanden Hole et al. (2014)
<i>Fukomys darlingi</i>	Social	10	5–9	Dvořáková et al. (2016)
<i>Fukomys mechowii</i>	Social	14	10–20	Sichilima et al. (2008), and Bednářová et al. (2013)
<i>Spalacopus cyanus</i>	Social	10	15–26	Veitl et al. (2000)
<i>Heterocephalus glaber</i>	Eusocial	12	60–80	Pepper et al. (1991)
<i>Heliophobius argenteocinereus</i>	Solitary	9	1	Knotková et al. (2009)
<i>Spalax ehrenbergi</i>	Solitary	6	1	Heth et al. (1988)
<i>Ctenomys mendocinus</i>	Solitary	4?	1	Francescoli, Camin, unpublished observations
<i>Ctenomys talarum</i>	Solitary	4	1	Schleich and Busch (2002)
<i>Ctenomys pearsoni</i>	Solitary	4	1	Francescoli (1999), unpublished data
<i>Geomys breviceps</i>	Solitary	3	1	DeVries and Sykes (2008)

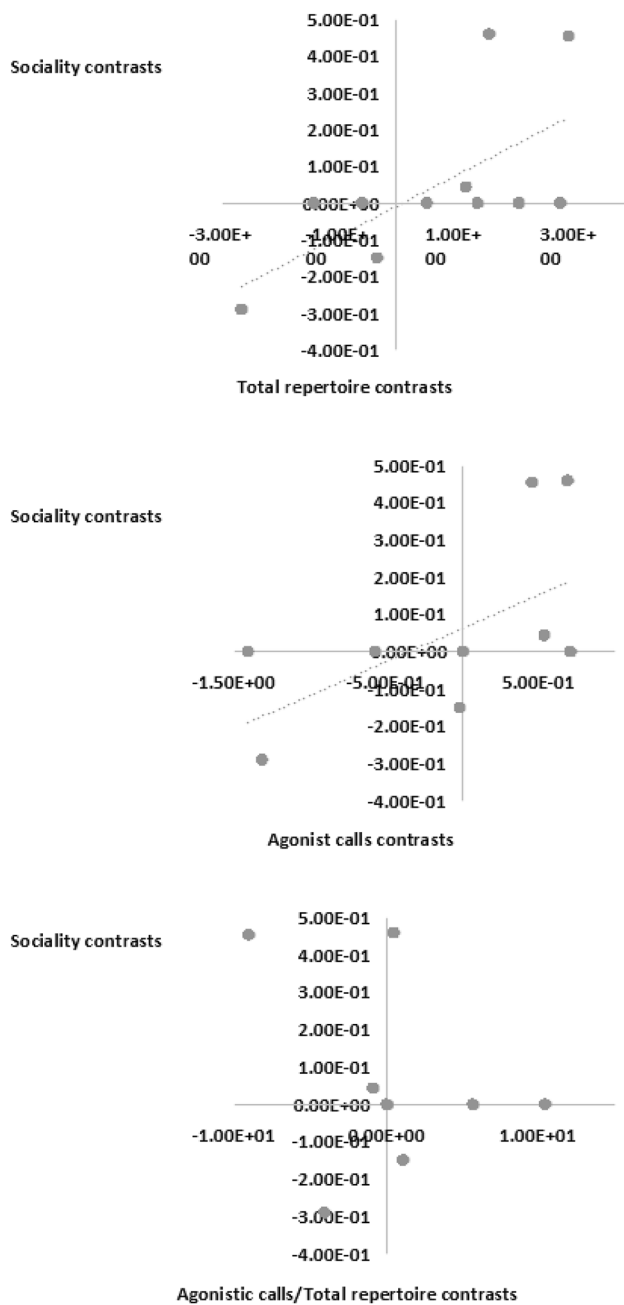
? = doubt about data

for each of the 12 species surveyed is shown. In Table 2, a detail of the agonistic vocalizations included in the study is displayed, using the names attributed to them in the original descriptions. In Table 3 the colony size of each species is shown, using the most recent data available.

Observation of the tables suggests some main results: (1) social species tend to have a vocal repertoire with increased complexity, both in vocalization numbers and categories, if compared with solitary species; (2) the percentage of agonistic vocalizations in social species in relation to the total number of vocalizations is still similar to those of the solitary species; (3) having a similar percentage of agonistic vocalizations when the total number of vocalizations in the repertoire increases and new signal categories exist, means that agonistic vocalizations have

been increased in number, thus maintaining the same general proportion.

Comparing samples of social species ( $N = 6$ ) against solitary species ( $N = 6$ ) with regression and PIC lead to the following results: (1) the total number of vocalizations in repertoire increased in social species with respect to solitary ones in both analyses, although the coefficient was smaller in the PIC model due to the presence of various species belonging to two families ( $n = 12$ ,  $r^2 = 0.77$ ,  $p < 0.001$ ;  $n = 11$ ,  $r^2 = 0.43$ ,  $p = 0.03$  for regression and PIC respectively, Fig. 2 top); (2) the number of agonistic vocalizations was also different between solitary and social species, with the latter displaying higher numbers of these calls ( $n = 12$ ,  $r^2 = 0.65$ ,  $p = 0.01$ ;  $n = 11$ ,  $r^2 = 0.35$ ,  $p = 0.05$  for regression and PIC respectively, Fig. 2



**Fig. 2** Relationships of the standardized contrasts of sociality to (top to bottom): repertoire size, number of agonistic calls, percentage of agonistic calls on total repertoire

middle); (3) the percentage of agonistic vocalizations in relation to total repertoire was similar between social and solitary species, with no significant relationship between this parameter and the social structure ( $n = 12$ ,  $r^2 = 0.07$ ,  $p = 0.38$ ;  $n = 11$ ,  $r^2 = 0.07$ ,  $p = 0.40$  for regression and PIC respectively, Fig. 2 bottom).

## Discussion

The development of communication systems was shown to accelerate with population size variations (Feigel 2008), and as a consequence, social species are expected to have more vocal signals, thus increased repertoires. Our data suggest that repertoires in subterranean rodents increase by the addition of new signals to be used in old or new contexts (new signal categories). In social populations or species the number of animals sharing the same burrow system is higher, and also interindividual contact rates are inevitably higher, because of the limitations imposed mainly by tunnel system size. Thus, as results suggest, to cope with this enhanced source of agonistic-related situations, social subterranean rodents preferentially increase the number of vocalizations devoted to agonistic behavior management, although other factors besides social structure may also account for this increment in agonistic calls.

Taking a brief look at the proportion of agonistic signals to total signals in the vocal repertoire, the numbers are quite similar in both solitary and social species, but those results could be misleading. In fact, if vocal repertoire in social animals increases, this increment occurs by the addition of new signals in new categories (categories almost nonexistent, by definition, for solitary animals, like alarm or contact; Blumstein 2007) and by the addition of new signals to old categories, those shared with solitary species (agonistic calls in our case).

Taking into account the opposition between environmental influence and social complexity in relation to the determination of communicative complexity (Blumstein 2003), if we refer to the subterranean rodents example, we have to conclude that an increase in communicative complexity is expected when new and/or more common interactions of a certain type of behavior appear in relation to those present in solitary species (Feigel 2008). Also, a decrease in number of agonistic vocalizations is expected if species that originated as social evolve to a solitary type of life (as suggested by Burda et al. 2000; Smorkatcheva and Lukhtanov 2013; Sobrero et al. 2014), indicating again that the center of the communicational change still is the agonistic vocalizations' repertoire.

Following Pollard and Blumstein (2012) in their claim that the main insight from their study is that different attributes of social complexity probably drive different attributes of communicative complexity, we expect that an increase in the number of individuals will produce an increase in repertoire diversity, but mostly an increase in vocalizations devoted to the management of agonistic situations. In this sense, Kessler et al. (2014) showed that in the gray mouse lemur (*Microcebus murinus*), a model species for solitary foragers with a social life, agonistic calls

are distinctive by matriline, and sleeping groups consist of close maternal kin, thus both genetics and social learning may have generated their acoustic signatures that apparently help reduce agonism between unfamiliar matrilineal kin. *M. murinus* vocal signatures could have facilitated a kin selection process that probably has driven the evolution of increased social complexity in these mammals (Kessler et al. 2014).

In the same line Malavasi et al. (2014) affirm that the establishment of a consortium (a group of organisms connected via sign relations) by acoustic codes allows conflict avoidance between individuals and species. So consortia, as semiotic systems, become responsible for the composition of ecosystems.

In subterranean rodents, Nevo (2007) has suggested for the *S. ehrenbergi* superspecies that aggression is polymorphic because in some species there exist individuals with different degrees of aggressiveness, called militants, intermediates, and pacifists. Depending on the number of individuals of each group in the population, animals will be more tolerant, and when the number of pacifistic individuals becomes high enough, populations will evolve into sociality. Even if this hypothesis is referred to a certain group of species in a genus (but see Ganem and Bennett 2004), we can speculate about whether this mechanism could be generalized as a sort of “barrier” to overcome in reaching sociality.

Indeed, changes in repertoires are thought to be essential in coping with new kinds of interactions originating in group living. This means that those communicative changes could be instrumental to, and probably a necessary condition for, the possibility of group living. Usually behavioral changes precede structural changes (Wilson 1980; Kappeler et al. 2013), and changes needed to achieve, for example, communal burrow construction and sharing, or communal breeding—to name only two of the putative origins of group living in rodents (Ebensperger 1998; Ebensperger and Cofré 2001; Ebensperger and Blumstein 2006; Ebensperger and Hayes 2008; Gromov 2017)—may occur in the communicative domain. Indeed, in cases in which natal philopatry and kin relationships are identified as the main mechanisms responsible for burrow sharing and the origin of social life, the need for agonism management mechanisms could not be left outside of the equation because of the important influence of parent–offspring conflict, especially in a situation of limited space as the one subterranean rodents live on. Even if Ebensperger and Hayes (2008) suggested that natal philopatry has not been the exclusive reason driving social dynamics, the previous arguments suggest that communication changes like those proposed here could at least be sort of a necessary condition organisms have to fulfill to attain full social status.

Cooperative communication systems could have evolved from simpler systems like parent–pup communication

signals, because in many rodent species parents and pups need to live together (and/or have at least a common refuge) during pup development time. We can speculate about communication among parents and pups being an important factor in protosocial behavior development. This line of reasoning is related to results obtained by Blumstein et al. (2009) which showed that in *Marmota flaviventris* yearling females that had more interactions with adults (mostly relatives) were more likely to remain in the group. These results were also supportive of the social cohesion hypothesis (Bekoff 1977) predicting that individuals who socialized with others were less likely to disperse. Moreover, in solitary subterranean rodents mothers are charged with pup care for a variable period until weaning (i.e., up to two or three months in *Ctenomys* and *Heliophobius*; Altuna et al. 1999; Cutrera et al. 2003; Sumbera et al. 2007), while in social species pups are tended for mostly by females but also have contact with males (*Ctenomys sociabilis*, Izquierdo and Lacey 2008; other subterranean rodents, Busch et al. 2000; Bennett et al. 2000). These data show that in the majority of subterranean rodent species studied, even with different social systems, females have an important role in raising young and communicating with them, and also in regulating pup stress reactions that are very important in controlling social relationships, as occurs in other mammals (Sachser et al. 1998; Love et al. 2013). Tolerance differences between males and females have previously been found in *S. ehrenbergi* (Zuri et al. 1998), a solitary subterranean rodent, suggesting that females are more prepared for tolerance to other individuals than males. Tolerance differences have also been found by Ganem and Bennett (2004) in females of four species of African mole rats with different degrees of sociality, in which individuals of the social species develop tolerance to unfamiliar individuals while managing stress, as suggested by the performed experiments. These tolerance differences can be related to the ideas expressed in the pacifistic hypothesis by Ganem and Nevo (1996) and Nevo (2007). In other mammals with social and communicative variability females are also considered the sex in which the impact of changes at those levels will be more clear (Bouchet et al. 2013).

All these facts suggest that females could be acting as an anchor to socialization and social evolution processes, as well as in communication evolution in subterranean rodents, by inducing social tolerance and stress reduction in pups through agonism management vocalizations, and eventually avoiding dispersal by the young. These processes putatively fall into the domain of niche construction theory and also possibly into the EvoDevo perspective (Laland et al. 2008; Scott-Phillips et al. 2013; Laland 2014; Peterson and Müller 2016, and references therein) in the sense that changes in the mother–pup relationship coupled with changes in the communication repertoire in a physically restricted and subject-constructed environment could have channeled the evolution

of social living in subterranean rodents, and maybe also in other rodent or mammal groups.

As repertoire changes are essential to cope with new and frequent kinds of interactions “proto-sociality” originates; results suggest that communicative changes could be a necessary condition to the possibility of group living. Communicative changes are mostly effective on the agonistic vocalizations part of the repertoire, because these vocalizations are the ones that will allow individuals to manage aggressive and submissive behaviors crucial to attaining group living and, eventually, cooperation in a more integrated social group. These results also suggest that agonistic signals abundance could be a good predictive measure of the frequency of interactions among individuals, thus a proxy to social complexity, understood as an increased number of individuals living together.

**Acknowledgements** GF wants to thank CSIC (Universidad de la República, Uruguay) for support through the Dedicación Total program and ANII (Uruguay) for support through the Sistema Nacional de Investigadores program.

## References

- Altuna CA, Francescoli G, Tassino B, Izquierdo G (1999) Ecoetología y conservación de mamíferos subterráneos de distribución restringida: el caso de *Ctenomys pearsoni* (Rodentia, Octodontidae) en el Uruguay. *Etología* 7:47–54
- Avilés L (1999) Cooperation and non-linear dynamics: an ecological perspective on the evolution of sociality. *Evol Ecol Res* 1:459–477
- Barbieri M (2008) What is Biosemiotics? *Biosemiotics* 1:1–3
- Bednářová R, Hrouzková-Knotková E, Burda H et al (2013) Vocalizations of the giant mole-rat (*Fukomys mechowii*), a subterranean rodent with the richest vocal repertoire. *Bioacoustics* 22:87–107
- Bekoff M (1977) Mammalian dispersal and the ontogeny of individual behavioral phenotypes. *Am Nat* 111:715–732
- Bekoff M (1981) Development of agonistic behaviour: ethological and ecological aspect. In: Brain PF, Benton D (eds) *Multidisciplinary approaches to aggression research*. Elsevier, Amsterdam, pp 161–178
- Bekoff M, Byers JA (1986) The development of behavior from evolutionary and ecological perspectives in mammals and birds. In: Hecht M, Wallace B, Prance GT (eds) *Evolutionary biology*, (vol 19). Plenum Press, Boston, pp 215–286
- Bennett NC, Faulkes CG, Molteno AJ (2000) Reproduction in subterranean rodents. In: Lacey EA, Patton JL, Cameron GN (eds) *Life underground. The biology of subterranean rodents*. University of Chicago Press, Chicago, pp 145–177
- Blumstein DT (2003) Social complexity but not the acoustic environment is responsible for the evolution of complex alarm communication. In: Ramousse R, Allainé D, Le Berre M (eds) *Adaptive strategies and diversity in marmots*. International Network on Marmots, Villeurbanne, pp 31–38
- Blumstein DT (2007) The evolution of alarm communication in rodents: structure, function, and the puzzle of apparently altruistic calling. In: Wolff JO, Sherman PW (eds) *Rodent societies*. University of Chicago Press, Chicago, pp 317–327
- Blumstein DT, Armitage KB (1997) Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *Am Nat* 150:179–200
- Blumstein DT, Armitage KB (1998) Life history consequences of social complexity: a comparative study of ground-dwelling sciurids. *Behav Ecol* 9:8–19
- Blumstein DT, Wey TW, Tang K (2009) A test of the social cohesion hypothesis: interactive female marmots remain at home. *Proc R Soc Lond B* 276:3007–3012
- Bouchet H, Blois-Heulin C, Lemasson A (2013) Social complexity parallels vocal complexity: a comparison of three non-human primate species. *Front Psychol*. <https://doi.org/10.3389/fpsyg.2013.00390>
- Burda H (1989) Relationships among rodent taxa, as indicated by reproductive biology. *J Zool Syst Evol Res* 27:49–50
- Burda H, Kawalika M (1993) Evolution of eusociality in the Bathyergidae: the case of the giant mole-rat (*Cryptomys mechowii*). *Naturwissenschaften* 80:235–237
- Burda H, Honeycutt RL, Begall S et al (2000) Are naked and common mole-rats eusocial and if so, why? *Behav Ecol Sociobiol* 47:293–303
- Busch C, Antinuchi CD, del Valle JC et al (2000) Spatial and social systems of subterranean rodents. In: Lacey EA, Patton JL, Cameron GN (eds) *Life underground: the biology of subterranean rodents*. University of Chicago Press, Chicago, pp 183–226
- Credner S, Burda H, Ludescher F (1997) Acoustic communication underground: vocalization characteristics in subterranean social mole-rats (*Cryptomys* sp., Bathyergidae). *J Comp Physiol A* 180:245–255
- Cutrer AP, Antinuchi CD, Busch C (2003) Thermoregulatory development in pups of the subterranean rodent *Ctenomys talarum*. *Physiol Behav* 79:321–330
- Daniel JC, Blumstein DT (1998) A test of the acoustic adaptation hypothesis in four species of marmots. *Anim Behav* 56:1517–1528
- DeVries MS, Sykes RS (2008) Vocalisations of a North American subterranean rodent *Geomys breviceps*. *Bioacoustics* 18:1–15
- Donaldson ZR, Young LJ (2008) Oxytocin, vasopressin, and the neurogenetics of sociality. *Science* 332:900–904
- Dvořáková V, Hrouzková E, Šumbera R (2016) Vocal repertoire of the Mashona mole-rat (*Fukomys darlingi*) and how it compares with other mole-rats. *Bioacoustics*. <https://doi.org/10.1080/09524622.2016.1141117>
- Ebensperger LA (1998) Sociality in rodents: the New World fossorial hystricognaths as study models. *Rev Chil Hist Nat* 71:65–77
- Ebensperger LA (2001) A review of the evolutionary causes of rodent group-living. *Acta Theriol* 46:115–144
- Ebensperger LA (2003) Restricciones fisiológicas y evolución de la sociabilidad en roedores. In: Bozinovic F (ed) *Fisiología ecológica y evolutiva*. Ediciones Universidad Católica de Chile, Santiago, pp 463–480
- Ebensperger LA, Blumstein DT (2006) Sociality in New World hystricognath rodents is linked to predators and burrow digging. *Behav Ecol* 17:410–418
- Ebensperger LA, Cofré H (2001) On the evolution of group-living in the New World cursorial hystricognath rodents. *Behav Ecol* 12:227–236
- Ebensperger LA, Hayes LD (2008) On the dynamics of rodent social groups. *Behav Process* 79:85–92
- Faulkes CG, Bennett NC (2013) Plasticity and constraints on social evolution in African mole-rats: ultimate and proximate factors. *Phil Trans R Soc B* 368:20120347
- Feigel A (2008) Essential conditions for evolution of communication within species. *J Theor Biol* 254:768–774
- Francescoli G (1999) A preliminary report on the acoustic communication in uruguayan *Ctenomys* (Rodentia, Octodontidae): basic sound types. *Bioacoustics* 10:203–218
- Freeberg TM (2006) Social complexity can drive vocal complexity? Group size influences vocal information in Carolina Chickadees. *Psychol Sci* 17:557–561



- Freeberg TM, Dunbar RIM, Ord TJ (2012) Social complexity as a proximate and ultimate factor in communicative complexity. *Phil Trans R Soc B* 367:1785–1801
- Ganem G, Bennett NC (2004) Tolerance to unfamiliar conspecifics varies with social organization in female African mole-rats. *Physiol Behav* 82:555–562
- Ganem G, Nevo E (1996) Ecophysiological constraints associated with aggression and evolution toward pacifism in *Spalax ehrenbergi*. *Behav Ecol Sociobiol* 38:245–252
- García Montero A, Vole C, Burda H et al (2016) Non-breeding eusocial mole-rats produce viable sperm - spermogram and functional testicular morphology of *Fukomys anselli* PLoS ONE 11(3):e0150112. <https://doi.org/10.1371/journal.pone.0150112>
- Grafen A (1992) The uniqueness of phylogenetic regression. *J Theor Biol* 156:405–423
- Gromov VS (2017) The spatial-and-ethological population structure, cooperation, and the evolution of sociality in rodents. *Behaviour* 154:609–649
- Heth G, Frankenberg E, Nevo E (1988) “Courtship” call of subterranean mole rats (*Spalax ehrenbergi*): physical analysis. *J Mammal* 69:121–125
- Izquierdo G, Lacey EA (2008) Effects of group size on nest attendance in the communally breeding colonial tuco-tuco. *Mamm Biol* 73:438–443
- Jarvis JUM, O’Riain MJ, Bennett NC, Sherman PW (1994) Mammalian eusociality: a family affair. *Trends Ecol Evol* 9:47–51
- Judd TM, Sherman PW (1996) Naked mole-rats recruit colony mates to food sources. *Anim Behav* 52:957–969
- Kappeler PM, Barrett L, Blumstein DT, Clutton-Brock TH (2013) Constraints and flexibility in mammalian social behaviour: introduction and synthesis. *Philos Trans R Soc B* 368:2012.0337
- Kessler SE, Radespiel U, Hasiniaina AIF et al (2014) Modeling the origins of mammalian sociality: moderate evidence for matrilineal signatures in mouse lemur vocalizations. *Front Zool*. <https://doi.org/10.1186/1742-9994-11-14>
- Knotková E, Veitl S, Šumbera R et al (2009) Vocalisations of the silvery mole-rat: comparison of vocal repertoires in subterranean rodents with different social systems. *Bioacoustics* 18:241–257
- Lacey EA (2000) Spatial and social systems of subterranean rodents. In: Lacey EA, Patton JL, Cameron GN (eds) *Life underground: the biology of subterranean rodents*. University of Chicago Press, Chicago, pp 257–296
- Lacey EA, Sherman PW (2007) The ecology of sociality in rodents. In: Wolff JO, Sherman PW (eds) *Rodent societies*. University of Chicago Press, Chicago, pp 243–254
- Lacey EA, Cuello PA, Tammine MN et al (2015) Estructura social en los tuco-tucos: mucho más variable de lo esperado. In: XXVIII Jornadas Argentinas de Mastozoología, Santa Fé (Argentina), November 2015
- Laland K (2014) On evolutionary causes and evolutionary processes. *Behav Process*. <https://doi.org/10.1016/j.beproc.2014.05.008>
- Laland KN, Odling-Smee J, Gilbert SF (2008) EvoDevo and niche construction: building bridges. *J Exp Zool* 310B:549–566
- Love OP, McGowan P, Sheriff MJ (2013) Maternal adversity and ecological stressors in natural populations: the role of stress axis programming in individuals, with implications for populations and communities. *Funct Ecol* 27:81–92
- Luna F, Naya H, Naya DE (2017) Understanding evolutionary variation in basal metabolic rate: analysis in subterranean rodents. *Comp Biochem Physiol A* 151:87–94
- Malavasi R, Kull K, Farina A (2014) The acoustic codes: how animal sign processes create sound-topes and consortia via conflict avoidance. *Biosemiotics*. <https://doi.org/10.1007/s12304-013-9177-5>
- Nevo E (1979) Adaptive convergence and divergence of subterranean mammals. *Annu Rev Ecol Syst* 10:269–308
- Nevo E (2007) Evolution of pacifism and sociality in blind mole-rats. In: Wolff JO, Sherman PW (eds) *Rodent societies*. University of Chicago Press, Chicago, pp 291–302
- Ord TJ, García-Porta J (2012) Is sociality required for the evolution of communicative complexity? Evidence weighed against alternative hypotheses in diverse taxonomic groups. *Philos Trans R Soc B* 367:1811–1828
- Pepper JW, Braude SH, Lacey EA, Sherman PW (1991) Vocalizations of the naked mole-rat. In: Sherman PW, Jarvis JUM, Alexander RD (eds) *The biology of the naked mole-rat*. Princeton University Press, Princeton, pp 243–274
- Peterson T, Müller GB (2016) Phenotypic novelty in EvoDevo: the distinction between continuous and discontinuous variation and its importance in evolutionary theory. *Evol Biol* 43:314–335
- Pollard KA, Blumstein DT (2012) Evolving communicative complexity: insights from rodents and beyond. *Philos Trans R Soc B* 367:1869–1878
- Sachser N, Dürschlag M, Hirzel D (1998) Social relationships and the management of stress. *Psychoneuroendocrinology* 23:891–904
- Schleich CE, Busch C (2002) Acoustic signals of a solitary subterranean rodent *Ctenomys talarum* (Rodentia: Ctenomyidae): physical characteristics and behavioural correlates. *J Ethol* 20:123–131
- Schleich CE, Veitl S, Knotková E, Begall S (2007) Acoustic communication in subterranean rodents. In: Begall S, Schleich CE, Burda H (eds) *Subterranean rodents: news from underground*. Springer, Berlin, pp 113–127
- Scott-Phillips TC, Laland K, Shuker DM et al (2013) The niche construction perspective: a critical appraisal. *Evolution* 68:1231–1243
- Sichilima AM, Faulkes CG, Bennett NC (2008) Field evidence for a seasonality of reproduction and colony size in the Afrotropical giant mole-rat *Fukomys mechowii* (Rodentia: Bathyergidae). *Afr Ecol* 43:144–149
- Šklíba J, Mazoch V, Patzenhauerová H et al (2012) A maze-lovers dream: burrow architecture, natural history and habitat characteristics of Ansell’s mole-rat (*Fukomys anselli*). *Mamm Biol* 77:420–427
- Smorkatcheva AV, Lukhtanov VA (2013) Evolutionary association between subterranean lifestyle and female sociality in rodents. *Mamm Biol*. <https://doi.org/10.1016/j.mambio.2013.08.011>
- Sobrero R, Inostroza-Michael O, Hernández CE, Ebensperger LA (2014) Phylogeny modulates the effects of ecological conditions on group living across hystricognath rodents. *Anim Behav* 94:27–34
- Sumera R, Chitaukali WN, Burda H (2007) Biology of the Silvery mole-rat (*Heliophobius argenteocinereus*). Why study a neglected subterranean rodent species? In: Begall S, Schleich CE, Burda H (eds) *Subterranean rodents: news from underground*. Springer, Berlin, pp 221–236
- van Veelen M, García J, Avilés L (2010) It takes grouping and cooperation to get sociality. *J Theor Biol* 264:1240–1253
- Vanden Hole C, Van Daele PAAG, Desmet N et al (2014) Does sociality imply a complex vocal communication system? A case study for *Fukomys micklemei* (Bathyergidae, Rodentia). *Bioacoustics* 23:143–160
- Veitl S, Begall S, Burda H (2000) Ecological determinants of vocalisation parameters: the case of the Coruro *Spalacopus cyanus* (Octodontidae), a fossorial social rodent. *Bioacoustics* 11:129–148
- Voloch CM, Vilela JF, Loss-Oliveira L, Schrago CG (2013) Phylogeny and chronology of the major lineages of New World hystricognath rodents: insights on the biogeography of the Eocene/Oligocene arrival of mammals in South America. *BMC Res Notes*. <https://doi.org/10.1186/1756-0500-6-160>
- Walton AH, Nedbal MA, Honeycutt RL (2000) Evidence from intron 1 of the nuclear transthyretin (Prealbumin) gene for the phylogeny of African mole-rats (Bathyergidae). *Mol Phylogenet Evol* 16:467–474

- White CR (2003) The influence of foraging mode and arid adaptation on the basal metabolic rates of burrowing mammals. *Physiol Biochem Zool* 76:122–134
- Wilson EO (1980) *Sociobiología: la nueva síntesis*. Omega, Barcelona
- Wolff JO, Sherman PW (2007) Rodent societies as model systems. In: Wolff JO, Sherman PW (eds) *Rodent societies*. University of Chicago Press, Chicago, pp 3–7
- Yosida S, Okanoya K (2009) Naked mole-rat is sensitive to social hierarchy encoded in antiphonal vocalization. *Ethology* 115:823–831
- Zuri I, Gottreich A, Terkel J (1998) Social stress in neighbouring and encountering blind mole-rats (*Spalax ehrenbergi*). *Physiol Behav* 64:611–620