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Environmental factors could constrain the use of long-range vocal signals in solitary tuco-tucos (*Ctenomys*; Rodentia, Ctenomyidae) reproduction

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Abstract

Ctenomys are mainly solitary subterranean rodents. Life underground has advantages (protection against predators, environmental control and reduced competition) but also implies disadvantages (digging costs, coping with hypercapnia, physiological and sensory changes, and communication problems) that can affect the social structure. Reproduction is a critical moment in the use of the signal repertoire, because individuals should locate in space, travel to, contact and copulate with a suitable partner. Energy expenditure involved in digging (connecting) tunnels makes difficult to attain a partner burrow system, but predation risk involved in moving above ground can counterbalance it and coupled with the spatial structure of the population, can determine the best communicative strategy to contact and locate a potential partner. Vocalisations allow to communicate over longer distances an with a reduced risk, while chemical signals, mostly aimed at vomerolfaction involve proximity or direct contact with the sample odour thus making information gathering more risky. As *Ctenomys* can use different signal types to gather different types of information leading to copulation, we propose that the use of these signals would be flexible, depending mostly on population spatial structure and type of predators living in the zone. This is because differences among species and/or populations in the use and characteristics of long-range vocalisations could be induced by environmental and/or social factors. This variation could be considered as a case of phenotypic plasticity, determining communication strategies variability in reproductive context, mostly dependent on long-range communication signals and the behaviour of males.

Background information about tuco-tucos

Tuco-tucos (*Ctenomys*) are subterranean rodents endemic of southern South America (southern Perú, Bolivia, Chile, Paraguay, Argentina, Uruguay and southern Brazil), and can be found from 12°S to 54°S and from Pacific to Atlantic coasts (Francescoli et al., 2004). The genus appeared in the late Pliocene and rapidly diversified towards the species identified in the present, that can be associated to at least 8 different groups in their yet unresolved phylogeny (Parada et al., 2011). While they are extremely variable at the genetic level, and capable of living from sea level up to 4,000 m in the Andes, and from grasslands to xeric habitats, they apparently maintain the majority of their general characteristics of behaviour, morphology, and physiological adaptations (Francescoli, 2000; Francescoli et al., 2004).

The genus *Ctenomys* has more than 55 nominated species, highly variable in some characteristics, but very similar in other characteristics. This high number of species probably had their origin in factors like their subterranean lifestyle, patchy distribution, limited vagility, high territoriality, low effective number, great karyotypic variability and the characteristics of their mating system (Reig et al., 1990; Nevo, 1999; Francescoli et al., 2004).

These animals spend almost all their life inside burrows, thus they are considered truly subterranean animals (Lacey et al., 2000), but differently from other subterranean rodents they leave their burrows to forage -cutting grasses and plants- above ground and usually hoarding them or consuming them inside their tunnels. This above ground activity means that juveniles are exposed to predation when foraging and when dispersing above ground (but not all species have juveniles dispersing that way), and adults are mostly exposed when foraging outside their tunnels (Busch et al., 2000). Many reports have identified their main predators as: aerial raptors (Weir, 1974; Vassallo et al., 1994; Busch et al., 2000; Kittlein et al., 2001; Altuna and Gonzalez, 2006; Baladrón et al., 2009), terrestrial mammals as foxes, skunks and grisons (Busch et al., 2000; Lacey and Sherman, 2007); Francescoli, unpublished data), and snakes (Rosi et al., 2003). Indeed, it has been established that up to an 18% of the prey species captured by owls are *Ctenomys* individuals from various species (Busch et al., 2000).

Even if some species have been identified as social, with females living in small groups and male floaters associated to the groups (Lacey and Ebensperger, 2007; Francescoli et al., 2016), the majority of the species known until now are solitary. In solitary species, each individual occupies its own burrow system and aggressively defends it, exception made of juveniles living with their mothers before dispersing. Also, in many solitary species burrow systems are usually not interconnected (*e.g.*, *C. pearsoni*; *C. talarum*), but during the mating season male and female burrows are usually connected for a brief period to allow courtship and copulation to occur. After the end of the mating activities, connecting tunnels are sealed off (Altuna et al., 1999). In other solitary species (*e.g.*, *C. talarum*), as a laboratory study using artificial tunnel systems show, individuals get together to copulate as one of the members of the couple (frequently the male) reach the burrow system of the other by travelling above ground (Zenuto et al., 2002).

Underground living has some advantages: protection from predators, food availability (depending on the ecosystem), control of external variables like temperature and humidity, and reduced competition. Nevertheless, it has some disadvantages that lead these animals to adapt to particular conditions like digging costs, hypercapnia, water management, or sensory and communication challenges (Reig et al., 1990; Francescoli, 2000). About the last mentioned feature, living in dark burrows prevents the use of vision for communication, so tuco-tucos have developed mainly tactile, chemical and acoustic signals to communicate with conspecifics either inside or between burrow systems. This last characteristic is especially important in solitary species, in which communicating with a putative mate to allow encounter, courtship and copulation is vital to the species survival.

Tuco-tucos do not have reduced eyes as other strictly subterranean genus, but visual communication is almost impossible inside tunnels that are completely dark. Nevertheless, there are some indications that tuco-tucos can be sensible to UV light and eventually follow urine marks using UV vision (Francescoli et al., 2016). As a consequence, these animals mostly use acoustic, chemical or tactile signals to communicate with their neighbours (competitors) and/or sexual partners.

Due to their characteristics, tactile and chemical signals are mostly bounded to an inside burrow use. As have been shown for *C. talarum* chemical signals are important once the male has entered the female tunnel (Fanjul et al., 2003; Fanjul and Zenuto, 2008a; Zenuto et al., 2004, 2007). Urine allow animals to detect the reproductive condition of a conspecific of different sex. During courtship male and female can sniff each other's genital areas, gathering more information. Chemical signals could also be important in case of accidental invasion of another individual's tunnel system. Chemical social signals seem to be mostly directed to the vomerolfactive system, thus constraining these animals to close contact sampling of the chemicals for identification, and then making difficult their use as a long-distance (inter-burrow) communication system (see Fanjul and Zenuto, 2017).

Tactile signals, mostly based on biting, grasping, licking, and whisker contact, are very important during courtship, mounting and copulation (Altuna et al., 1991; Fanjul and Zenuto, 2008b). During the very act of copulation males could also transmit tactile information to females because male's penis is armed with spines and spikes (Altuna and Lessa, 1985; Dewsbury, 1988). As tuco-tucos are induced ovulators this tactile information is very important for successful reproduction because it is thought to trigger ovulation when sperm is present, thus insuring insemination (Bennett et al., 2000; Francescoli et al., 2004).

Seismic signals have been mentioned as responsible for long-range communication in other subterranean rodents (Francescoli, 2000) but they have not been detected in tuco-tucos.

Why tuco-tuco's vocalisations are important?

Acoustic signals seem to play the main role in *Ctenomys* communication systems, and some studies explored their repertoires from both the physical and functional perspectives (Francescoli, 1999, 2001; Schleich and Busch, 2002; Francescoli and Quirici, 2010; Amaya et al., 2016). Vocal signals have a widespread usage by tuco-tucos, both in long- and short-range communicative situations (Francescoli, 1999; Schleich and Busch, 2002; Francescoli and Quirici, 2010; Amaya et al., 2016). Short-range vocalisations, are mostly related to proximity courtship and copulation (these having higher main frequencies than the long-range ones), and also with intra-tunnel aggression (these also having low main frequencies) as shown by Francescoli (1999) and Schleich and Busch (2002).

It is generally thought that vocal signals are a poor way for long-range communication in subterranean animals, but tuco-tucos seem to be the exception to this "rule." These signals are used as territorial advertising and, as suggested by field data on *C. pearsoni* (Francescoli, 2011) and by some field but mostly laboratory data in *Ctenomys* sp. "Anillaco" (Amaya et al., 2016), could encode information about location, sex and reproductive disposition of the emitter.

Many species of tuco-tucos are known to vocalise loud enough to be heard at a considerable distance outside their burrows (Francescoli, 2000, 2011; Schleich and Busch, 2002; Amaya et al., 2016); these long-range vocalisations could be used as territorial signals (Francescoli, 1999; Schleich and Busch, 2002; Amaya et al., 2016) and also inform about some sexual and reproductive characteristics of the emitter (Francescoli, 2011). In the majority of the species sampled, exception made of *Ctenomys sociabilis*, long-range vocalisations have their main frequencies in a band going from 180 to 300 Hz (Francescoli, 1999; Schleich and Busch, 2002; Francescoli and Quirici, 2010; Amaya et al., 2016) and the frequency range of their emissions is in the audible part of the sound spectrum, with no ultrasound or infrasound use yet detected.

Available information shows that at least *C. flamarioni* (K. Saché pers. comm.), *C. haigi* (Pearson and Christie, 1985), *C. mendocinus* (Francescoli and Quirici, 2010), *C. pearsoni* (Francescoli, 1999), *C. peruanus* (Pearson, 1959), *C. rionegrensis* (Francescoli and Quirici, 2010), *C. sociabilis* (Francescoli and Quirici, 2010), *Ctenomys sp.* "Anillaco" (Amaya et al., 2016), *C. talarum* (Schleich and Busch, 2002), and *C. torquatus* (Francescoli and Quirici, 2010) use long-range vocalisations which are mainly low frequency, repetitive, rhythmic signals.

Some studies suggest that using low-frequency rhythmic signals could be a result of the constraints imposed by the underground environment and that propagation conditions determine rhythm-encoded information as more reliable than a frequency modulation-encoded one (Francescoli, 1999; Francescoli et al., 2012). Other views (Francescoli, unpublished data) agree with the idea that the main force determining signal design in subterranean rodent vocalisations is motivation, because when we look at the signal's quality we can see that aggressive signals are mostly harsh sounds and mating signals tend to be tonal, in accordance with the frequency characteristics highlighted by Morton (1977, 1982) to define his motivation-structural rules. Then, motivation seems to be the main force constraining signal design in subterranean rodents, but environmental constraints could be more influential in the long distance signals, maybe causing motivation-structural rules to have taken a secondary role in the design of these signals during evolution (Morton, 1982): 191–192; Francescoli, unpublished data). Indeed, there are reports of differences among species and even between different populations of the same species, at the level of copulatory mechanisms (Altuna et al., 1991); Fanjul and Zenuto, 2008b; Camín, 1999), mate searching strategies (Zenuto et al., 2004, 2007), and vocal signals (Francescoli, 2002, 2011) thus, spatial organisation and environmental constraints could influence the ways tuco-tucos communicate and/or their "choice" of modalities to communicate during reproduction (Zenuto et al., 2002; Cutrera et al., 2006; Francescoli, 1999, 2011).

Then, based on the personal work of the author and data published in the literature, the intention of this review is to establish associations among behavioural characteristics and environmental conditions during reproduction that may be responsible for modulating the use of long-range vocalisations by tuco-tucos.

Different strategies for different ecological/behavioral variables?

Reproduction is a critical moment in the use of the signal repertoire. During the initial stages of reproduction solitary animals should use medium and long distance signals allowing them to locate and obtain some information about putative partners, to orientate when contacting the partner (then lowering the energy investment to reach at them), and to select the appropriate strategy to navigate towards the partner while evading predators.

In social tuco-tucos (like *Ctenomys sociabilis*) the grouped sex are females and males spend different periods with different female groups, fertilising them and then changing group. Communicating at long distances is not an imperative because they can find reproductive partners in the same or in neighbouring groups, and communal burrow systems are usually close to one another (Lacey and Wieczorek, 2004), probably acting as information centres for reproduction (Ward and Zahavi, 1973; Galef and Wigmore, 1983).

Conversely, solitary animals live each one in one burrow system and these systems could be distant from one another depending on population's density. They need to detect and find a suitable partner of the other sex, mainly using long range signals to obtain information about who are their neighbours and where are they located, while maintaining their territories (Francescoli, 1999, 2000, 2011; Schleich and Busch, 2002).

Thus, in solitary animals and especially during the mating season, energy expenditure involved in digging (to reach a putative partner's burrow system) can be counterbalanced by predation risk involved in moving above ground (to forage and/or to attain a putative partner's burrow entrance), and coupled with the spatial structure of the population can determine the best strategy to contact a potential partner (Francescoli, 2000). This contact is made easier if animals can previously locate putative partners by means of long-range communication signals.

In view of what we know about tuco-tuco's communication, there are only two options for inter-burrow communication: a) scent marks, mostly aimed at vomerolfaction thus involving proximity or direct contact, must be deposited outside the burrow to allow location by the receiver, thus exposing both sender and receiver to predators; b) vocal signals, that are characteristic of these animals but could demand an important energetic investment (Francescoli, 2000, 2011).

In *C. pearsoni*, long-range vocalisations, at a population level, peak twice a day at particular times during the day (Francescoli, 2011), while in *C. talarum* Mar de Cobo population male vocalisations were recorded during the crepuscular or nocturnal period (Cutrera et al., 2006). In *Ctenomys* sp. "Anillaco" animals are active mostly during the night in the laboratory, but they have been seen outside their burrows foraging at least once during the day in the field (Tomotani et al., 2012); long-range vocalisations were recorded in the laboratory during the night (mostly because of logistic reasons), but they appeared also during the day in the field (Amaya, 2017). This variability could be explained by several hypotheses suggested by Francescoli (2011): vocalisation peaks exploit daily

Table 1. Comparison of relevant characteristics of the different *Ctenomys* species and populations discussed in the text.

Species (Population)	Density	Sex ratio	Predation	Main predators	Activity
C. pearsoni	low/medium	skewed to females	generalised	foxes (odours)	during day
C. talarum (Mar de Cobo)	high	skewed to females	on juveniles	raptors (vision)	day & night
C. talarum (Necochea)	low	not skewed	on juveniles	raptors (vision)	day & night

Information sources: For *C. pearsoni* Francescoli et al., 2004; Francescoli, 2011; *Francescoli and Izquierdo,* unpublished data. For *C. talarum* Fanjul et al., 2003; Zenuto and Fanjul, 2002; Zenuto et al., 2002, 2004, 2007.

variations in surface environmental conditions enhancing sound propagation due to changes in soil temperature or humidity levels; they allow animals to gather information at more predictable moments; they facilitate location of neighbour movements; they avoid vocalising during periods when big terrestrial mammals (*i.e.*, cows, horses), are active and can interfere.

Vocal signals acting at long distances have some drawbacks because they are potential sources of Public Information (Danchin et al., 2004) that could originate eavesdropping opportunities by other individuals like conspecifics, competitors and/or predators. Long range signals needed to reach the putative partner's burrow are also energetically costly (even using low frequency sounds), and are also costlier than chemical signals because the latter are mostly based in odours present in urine and/or faeces (Zenuto and Fanjul, 2002).

In *Ctenomys pearsoni* -mostly studied in “Estancia El Relincho,” Uruguay (Francescoli, 2011)- vocalisations are thought to transfer information about spatial location of individuals, the sex of the emitter and their reproductive condition. Females vary their vocal emissions during the reproductive period (with respect to the rest of the year) by increasing the length and complexity of their vocal emissions at the beginning of the reproductive season, and later decreasing those variables as the reproductive season goes on, probably immediately after being inseminated by a male. This could difficult their location by other males, avoiding harassment and danger of injuries by males trying to reproduce with already inseminated females, and opening the possibility to some sort of sexual selection by the female (Francescoli, 1998, 1999, 2011). In addition, male vocalisations that are almost invariable and emitted during all the year (Francescoli, 2011), can be used by females for sensing the nearby males, thus being able to select the best males when they arrive to the female tunnels for courtship and mating, and also to resist non-preferred males.

The characteristics of different species and study sites (see Table 1) rise some questions about the communicative and reproductive biology of the studied tuco-tucos, specially in which concerns the use of vocal signals to locate individuals and during the initial steps of courtship in the reproductive season. This detected inter and intraspecific variability could be causing the variation of communicative strategies in reproductive context, probably depending mostly on male's behaviour, but also depending on the spatial positioning of the individuals in relation to their sex, and on males mobility strategy (subterranean or above ground) to reach the mate.

Behavioural flexibility and phenotypic plasticity

Thus, the results of our studies in Uruguay (primarily done in the field) and those carried on in Argentina (mostly in the laboratory) allow us to state that, globally speaking, *Ctenomys* would use different types of signals to collect different types of information that lead to copulation, but the type of signals used, their importance and the behaviours necessary to initiate courtship would be somehow flexible.

Energy expended in excavation, the risk of predation involved in surface movement (if this occurs), and the population spatial structure could determine the best strategy for contacting a potential partner. The resolution of reproductive events would depend on the use of signals acting at different distances and in different channels, constituting the most important communicative moments in the life of the solitary species of the genus.

Nevertheless, even if male behaviour is central to the definition of the flexibility limits (but see Audet and Lefebvre, 2017 about the use of the term “behavioural flexibility”), female behaviour -especially the fact of they vocalising or not- is an extremely important element. Field and laboratory studies in *Ctenomys* suggested that in *C. pearsoni, C. mendocinus*, *C. sociabilis*, *C.* sp. “Anillaco” and probably *C. torquatus* both sexes vocalise long-range signals, while in *C. talarum* and *C. haigi* only males do it (Schleich and Busch, 2002; Francescoli and Quirici, 2010). As said above, *C. pearsoni* females vary their long range signals throughout the year, vocalising more and longer signals during the initial times of the mating period and decreasing their signalling later into the reproductive season. Females of *C. talarum* do not emit long-range signals (Schleich and Busch, 2002), while in *Ctenomys* sp. “Anillaco” females seem to scarcely vocalise long-range signals (Amaya et al., 2016). A possible explanation of the difference is that population structure also differs between species in which females vocalise and those in which females do not vocalise. In *C. talarum* populations are mainly organised as an addition of groups of some female burrows around a male burrow (but this can vary among populations). In *C. pearsoni* this is not always true because, at least in the better studied populations, females are interspersed with males or many female burrows are “grouped” surrounded by some males, thus females probably need to make it easier for males to locate them by vocalising (Francescoli, 2011; Francescoli and Izquierdo, unpublished data; Zenuto et al., 2002).

In *C. talarum* from Mar de Cobo (Zenuto et al., 2002) we can expect that males -the sex that moves to the partner’s tunnel- use mostly odour markings previously detected to locate the females (that live around the males), both being sensitised by their odours. They avoid the main predators in the zone (raptors) by moving above ground probably during the night to allow easier location of odour marks outside the burrows, and avoiding the use of long-range vocalisations (not used by females) and probably better detected by raptors. The sex ratio being skewed to females and the disposition of the individuals in the population could help males to attain female burrows using mostly odours as cues, but they will need the use of sounds to repel male competitors (long-range vocalisations), and to continue the courtship when arrived to the female’s tunnel.

In *C. talarum* Necochea the fact that there are no skewed sex ratio and no monopolisation of females by dominant males -in fact no dominance are established between males- results in even numbers of males and females allowing the formation of couples without apparent competition (Zenuto et al., 2002). This is probably the reason for the absence of a clear interaction by means of olfactory or vocal signals during courtship and copulation in the laboratory tests.

In *C. pearsoni* (Francescoli, 2011; Francescoli and Izquierdo, unpublished data) we can expect that animals (mostly males, the sex that moves to the partner’s tunnel) use sounds emitted by females to locate them, because both sexes use long-range vocalisations allowing space location, and sex and reproductive state identification. They will avoid the main predators in the zone (foxes) by travelling underground during the day or night, and by avoiding the use of external scent-marks that could be easily located by mammalian predators (unlike *C. talarum* males from Mar de Cobo). Sex ratio being skewed towards females could help males to attain female burrows, because of the higher number of females in the population. Nonetheless, the disposition of the individuals in the population will probably constrain males to use acoustic information for location and evaluation of the partner’s sexual condition, these two features being evaluated at distance. Males also use long-range vocalisations to repel male competitors and to continue the courtship when arrived to the female’s tunnel, while females probably identify the male that arrives and select it, avoiding other males that can arrive too, using the information contained on their vocalisations.

Some conclusions

Even if the subterranean niche is a stable system, the species inhabiting it are not necessarily as stable as the niche, and are not similar among them. *Ctenomys* in general, and especially the solitary life species, present important differences both at the inter and intraspecific levels. Those differences are clear in the behavioural repertoire and can constrain the communicative and reproductive mechanisms, especially acoustic signals usage, because in many cases acoustic communication has a central role in these processes. Those differences are mostly determined by the external environment, and they determine local variants (adaptations, flexibility, phenotypic plasticity) in the populations.

The apparent variability suggested by the available data could occur even in different populations of the same species. This variability would manifest itself in the use of certain types of long distance signals for the detection of potential partners, in the spatial disposition of individuals according to sex, and in the male mobility strategy (underground or in the surface).

This could be a case of phenotypic plasticity, determining communication strategies variability in reproductive context, apparently depending mostly on long-range communication and the behaviour of males.

The complete understanding of the functional social structure, survival strategies in nature, and successful reproduction of *Ctenomys* is closely associated with the understanding of the signal systems involved in courtship and copulation. The understanding of these signal systems is related mostly to the variable use of vocal signals in the solitary tuco-tuco species, and also to the context in which they were developed and in which they currently function.

To test these variability and the constraints originating it, future studies should try to establish: a) if solitary tuco-tuco populations living in places with abundance of terrestrial predators do use long-range vocalisations to locate each other and connect their tunnels underground when reaching a putative partner for reproduction, and even if juveniles use underground tunnels to disperse, or b) if solitary tuco-tucos living in places with abundance of aerial predators mostly use odours to locate each other, travelling to partner's tunnels on the surface and mostly at night, and using vocalisations mostly for territorial purposes (especially the females).

This knowledge will eventually allow the planning of conservation actions aimed at maintaining local populations that present particular genetic, morphological and/or ethological adaptations (Altuna et al., 1999; Francescoli, 2002; Francescoli and Quirici, 2010).

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Competing interests

Gabriel Francescoli declares that he has no conflict of interest.

References

Altuna C. A., Francescoli G., and Izquierdo G. (1991). Copulatory pattern of *Ctenomys pearsoni* (Rodentia, Octodontidae) from Balneario Solís, Uruguay. Mammalia. 55: 316–318.

Altuna C. A., Francescoli G., Tassino B., and 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.

Altuna C. A. and Gonzalez E. M. (2006). Owl predation on the subterranean rodent *Ctenomys* (Rodentia: Octodontidae) in Uruguay, with an assessment of relative age classes. Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo. 203: 1–5.

Altuna C. A. and Lessa E. P. (1985). Penial morphology in uruguayan species of *Ctenomys* (Rodentia, Octodontidae). Journal of Mammalogy. 66: 383–389.

Amaya J. P. (2017). Interacciones acústicas de una especie de *Ctenomys* de la provincia de La Rioja. PhD thesis, Universidad Nacional de La Plata (Argentina).

Amaya J. P., Areta J. I., Valentinuzzi V. S., and Zufiaurre E. (2016). Form and function of long-range vocalisations in a Neotropical fossorial rodent: The AnillacoTuco-Tuco (*Ctenomys* sp.). PeerJ. 4: e2559. https://doi.org/10.7717/peerj.2559.

Audet J. N. and Lefebvre L. (2017). What's flexible in behavioral flexibility? Behavioral Ecology. 28 (4): 943–947. https://doi.org/10.1093/beheco/arx007.

Baladrón A. V., Malizia A. I., and Bó M. S. (2009). Predation upon the subterranean rodent *Ctenomys talarum* (tuco-tucos) by *Buteo polyosoma* (red-backed Hawks) in coastal grasslands of Argentina. Studies on Neotropical Fauna and Environment. 44 (2): 61–65. https://doi.org/10.1080/01650520902915022.

Bennett N. C., Faulkes C. G., and Molteno A. J. (2000). Reprduction in subterranean rodents. In: Life Underground: The Biology of Subterranean Rodents, edited by Lacey E. A., Patton J. L., and Cameron G. N. Chicago: The University of Chicago Press. 145–177.

Busch C., Antinuchi C. D., del Valle J. C., Kittlein M. J., Malizia A. I., et al. (2000). Population ecology of subterranean rodents. In: Life Underground: The Biology of Subterranean Rodents, edited by Lacey E. A., Patton J. L., and Cameron G. N. Chicago: The University of Chicago Press. 183–226.

Camín S. R. (1999). Mating behaviour of *Ctenomys mendocinus* (Rodentia, Ctenomyidae). Zeitschrift für Säugetierkunde. 64: 230–238.

Cutrera A. P., Antinuchi C. D., Mora M. S., and Vassallo A. I. (2006). Home-range and activity patterns of the south american subterranean rodent *Ctenomys talarum*. Journal of Mammalogy. 87 (6): 1183–1191. https://doi.org/10.1644/05-MAMM-A-386R1.1.

Danchin E., Giraldeau L. A., Valone T. J., and Wagner R. H. (2004). Public information: From nosy neighbours to cultural evolution. Science. 305 (5683): 487–491. https://doi.org/10.1126/science.1098254.

Dewsbury D. A. (1988). Copulatory behavior as courtship communication. Ethology. 79 (3): 218–234. https://doi.org/10.1111/j.1439-0310.1988.tb00712.x.

Fanjul M. S. and Zenuto R. R. (2008a). Female reproductive responses to photoperiod and male odours in the subterranean rodent *Ctenomys talarum*. Acta Theriologica. 53 (1): 73–85. https://doi.org/10.1007/BF03194280.

Fanjul M. S. and Zenuto R. R. (2008b). Copulatory pattern of the subterranean rodent *Ctenomys talarum*. Mammalia. 72 (2): 102–108. https://doi.org/10.1515/MAMM.2008.026.

Fanjul M. S. and Zenuto R. R. (2017). Female choice, male dominance and condition-related traits in the polygynous subterranean rodent *Ctenomys talarum*. Behavioural Processes. 142: 46–55. https://doi.org/10.1016/j.beproc.2017.05.019.

Fanjul M. S., Zenuto R. R., and Busch C. (2003). Use of olfaction for sexual recognition in the subterranean rodent *Ctenomys talarum*. Acta Theriologica. 48 (1): 35–46. https://doi.org/10.1007/BF03194264.

Francescoli G. (1998). La comunicación acústica en poblaciones de *Ctenomys* (Rodentia, Octosdontidae) de Uruguay, con algunas consideraciones sobre el uso del canal "vibratorio" en los roedores subterráneos. PhD thesis, PEDECIBA- Facultad de Ciencias, UdelaR.

Francescoli G. (1999). A preliminary report on the acousticcommunication in Uruguayan *Ctenomys* (Rodentia, Octodontidae): Basic sound types. Bioacoustics. 10 (2–3): 203–218. https://doi.org/10.1080/09524622.1999.9753431.

Francescoli G. (2000). Sensory capabilities and communication in subterranean rodents. In: Life Underground: The Biology of Subterranean Rodents, edited by Lacey E. A., Patton J. L., and Cameron G. N. Chicago: The University of Chicago Press. 111–144.

Francescoli G. (2001). Vocal signals from *Ctenomys pearsoni* pups. Acta Theriologica. 46 (3): 327–330.

Francescoli G. (2002). Geographic variation in vocal signals of *Ctenomys pearsoni*. Acta Theriologica. 47 (1): 35–44. https://doi.org/10.1007/BF03193564.

Francescoli G. (2011). Tuco-tucos' vocalization output varies seasonally (*Ctenomys pearsoni*; Rodentia, Ctenomyidae): implications for reproductive signaling. Acta Ethologica. 14 (1):1–6. https://doi.org/10.1007/s10211-010-0083-4.

Francescoli G., Izquierdo G., Tassino B., and Altuna C. A. (2004). Tuco-tucos (Ctenomyidae). In: Grzimek's Animal Life Encyclopedia. Volume 16 (Mammals V), edited by Kleiman D. G., Geist V., Hutchins M., and McDade M. C. Michigan: Gale Group. 425–431.

Francescoli G., Nogueira S., and Schleich C. (2016). Mechanisms of social communication. In: Sociobiology of Caviomorph Rodents: An Integrative View, edited by Ebensperger L. and Hayes L. Oxford: Wiley-Blackwell. 147–172.

Francescoli G. and Quirici V. (2010). Two different vocalization patterns in *Ctenomys* (Rodentia, Ctenomyidae) territorial signals. Mastozoologia Neotropical. 17: 141–145.

Francescoli G., Quirici V., and Sobrero R. (2012). Patterns of variation in the tympanic bullae of tuco-tucos (Rodentia, Ctenomyidae, *Ctenomys*). Acta Theriologica. 57 (2): 153–163. https://doi.org/10.1007/s13364-011-0064-7.

Galef B. G. and Wigmore S. W. (1983). Transfer of information concerning distant foods: A laboratory investigation of the "information-centre" hypothesis. Animal Behaviour. 31 (3): 748–758. https://doi.org/10.1016/S0003-3472(83)80232-2.

Kittlein M. J., Vassallo A. I., and Busch C. (2001). Differential predation upon sex and age classes of tuco-tucos (*Ctenomys talarum*, Rodentia: Octodontidae) by owls. Mammalian Biology. 66: 281–289.

Lacey E. A. and Ebensperger L. (2007). Social structure in Octodontid and Ctenomyid rodents. In: Rodent Societies, edited by Wolff J. O. and Sherman P. W. Chicago: The University of Chicago Press. 403–415.

Lacey E. A., Patton J. L., and Cameron G. N. (2000). Introduction. In: Life Underground: The Biology of Subterranean Rodents, edited by Lacey E. A., Patton J. L., and Cameron G. N. Chicago: The University of Chicago Press. 1–14.

Lacey E. A. and Sherman P. W. (2007). The ecology of sociality in rodents. In: Rodent Societies, edited by Wolff J. O. and Sherman P. W. Chicago: The University of Chicago Press. 243–254.

Lacey E. A. and Wieczorek J. R. (2004). Kinship in colonial tuco-tucos: Evidence from group composition and population structure. Behavioral Ecology. 15 (6): 988–996. https://doi.org/10.1093/beheco/arh104.

Morton E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. American Naturalist. 111: 855–869. https://doi.org/10.1086/283219.

Morton E. S. (1982). Grading, discreteness, redundancy, and motivation-structural rules. In: Acoustic Communication in Birds. Volume 1, edited by Kroodsma D. R. and Miller E. H. New York: Academic Press. 183–212.

Nevo E. (1999). Mosaic Evolution of Subterranean Mammals. New York: Oxford University Press.

Parada A., D'Elía G., Bidau C. J., and Lessa E. P. (2011). Species groups and the evolutionary diversification of tuco-tucos, genus *Ctenomys* (Rodentia: Ctenomyidae). Journal of Mammalogy. 92 (3): 671–682. https://doi.org/10.1644/10-MAMM-A-121.1.

Pearson O. P. (1959). Biology of the Subterranean Rodents, *Ctenomys*, in Peru. Memorias del Museo de Historia Natural "Javier Prado". Peru: Universidad Nacional Mayor de San Marcos. 9: 1–56.

Pearson O. P. and Christie M. I. (1985). Los tuco-tucos (genéro *Ctenomys*) de los Parques Nacionales Lanin y Nahuel Huapi, Argentina. Historia Natural. 5: 337–344.

Reig O. A., Busch C., Ortells M. O., and Contreras J. R. (1990). An overview of evolution, systematics, population biology, cytogenetics, molecular biology and speciation in *Ctenomys*. In: Evolution of Subterranean Mammals at the Organismal and Molecular Levels, edited by Nevo E. and Reig O. A. New York: Wiley-Liss. 71–76.

Rosi M. I., Cona M. I., Videla F., Puig S., Monge S. A., et al. (2003). Diet selection by the fossorial rodent *Ctenomys mendocinus* inhabiting an environment with low food availability (Mendoza, Argentina). Studies on Neotropical Fauna and Environment. 38 (3): 159–166. https://doi.org/10.1076/snfe.38.3.159.28168.

Schleich C. E. and Busch C. (2002). Acoustic signals of a solitary subterranean rodent *Ctenomys talarum* (Rodentia: Ctenomyidae): Physical characteristics and behavioural correlates. Journal of Ethology. 20 (2): 123–131. https://doi.org/10.1007/s10164-002-0064-9.

Tomotani B. M., Flores D. E. F. L., Tachinardi P., Paliza J. D., Oda G. A., et al. (2012). Field and laboratory studies provide insights into the meaning of day-time activity in a subterranean rodent (*Ctenomys* aff. *knighti*), the Tuco-Tuco. PLoS ONE. 7 (5): e37918. https://doi.org/10.1371/journal.pone.0037918.

Vassallo A. I., Kittlein M. J., and Busch C. (1994). Owl predation on two sympatric species of tuco-tucos (Rodentia: Octodontidae). Journal of Mammalogy. 75 (3): 725–732. https://doi.org/10.2307/1382522.

Ward P. and Zahavi A. (1973). The importance of certain assemblages of birds as "information-centres" for food-finding. Ibis. 115 (4): 517–534. https://doi.org/10.1111/j.1474-919X.1973.tb01990.x.

Weir B. J. (1974). The tuco-tuco and plains vizcacha. Symposia of the Zoological Society of London. 34: 13–130.

Zenuto R. R., Estavillo C., and Fanjul M. S. (2007). Familiarity and mating behavior in the subterranean rodent *Ctenomys talarum* (tuco-tuco). Canadian Journal of Zoology. 85 (9): 944–955. https://doi.org/10.1139/Z07-078.

Zenuto R. R. and Fanjul M. S. (2002). Olfactory discrimination of individual scents in the subterranean rodent *Ctenomys talarum* (tuco-tuco). Ethology. 108: 629–641. https://doi.org/10.1046/j.1439-0310.2002.00808.x.

Zenuto R. R., Fanjul M. S., and Busch C. (2004). Use of chemical communication by the subterranean rodent *Ctenomys talarum* (tuco-tuco) during the breeding season. Journal of Chemical Ecology. 30 (11): 2111–2126. https://doi.org/10.1023/B:JOEC.0000048777.42945.e4.

Zenuto R. R., Vassallo A. I., and Busch C. (2002). Comportamiento social y reproductivo del roedor subterráneo solitario *Ctenomys talarum* (Rodentia: Ctenomyidae) en condiciones de semicautiverio. Revista Chilena de Historia Natural. 75: 165–177. https://doi.org/10.4067/S0716-078X2002000100016.