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Original investigation

Population genetic structure and historical dispersal patterns in the subterranean rodent *Ctenomys* "*chasiquensis*" from the southeastern Pampas region, Argentina

Matías Sebastián Mora[a,*], Fernando Javier Mapelli[a], Aldana López[b], María Jimena Gómez Fernández[c], Patricia Mónica Mirol[c], Marcelo Javier Kittlein[a]

[a] *Instituto de Investigaciones Marinas y Costeras, (IIMyC, CONICET), Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, CP7600 Mar del Plata, Provincia de Buenos Aires, Argentina*
[b] *Área de Recursos Naturales, CONICET INTA EEA Bariloche, CC 277 8400 Bariloche, Provincia de Río Negro, Argentina*
[c] *Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ángel Gallardo 470, Ciudad Autónoma de Buenos Aires, Argentina*

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ABSTRACT

Gene flow plays an essential role in the evolutionary history of the organisms and helps to identify those historical landscape features that most likely had affected the dispersal patterns. In this work, we assess, using mitochondrial control region DNA sequences, the historical migration patterns and population structure in *Ctenomys* "*chasiquensis*", a highly, vulnerable and endemic subterranean rodent distributed in a very small area from the central part of Argentina. We used Bayesian and maximum likelihood approaches to evaluate the effects of historical gene flow among populations. Moreover, we used Bayesian skyline plots, tests of neutrality and mismatch distributions to assess the potential changes in population size through time. Our analyses show that populations of *C.* "*chasiquensis*" are moderate structured at regional level and this population pattern is probably the result of an asymmetric historical gene flow essentially from the South-West to the North-West, further of a recent demographic population expansion in the North-West, in conjunction with an important degree of isolation in some populations over its eastern geographical range. Evidently, historical gene flow seems to have been more frequently on the West. Finally, a close relationship appears to exist between the major climatic episodes occurred during the Late Quaternary in the central region of Argentina and the main historical demographic changes inferred for *C.* "*chasiquensis*". The current distribution of *C.* "*chasiquensis*" appear to be a relicts of a more extended historical distribution in the Argentinean Pampas in the Late Pleistocene, with a perceptible population decline at the beginning of the Holocene. In this context, Bayesian demographic inferences showed a small but constant increment of population expansion of this species from approximately 90,000 to 11,000 years BP, after which a period of decrease in population size (that started in the early Holocene and continues nowadays) was observed.

Introduction

Genetic variation within and among populations is shaped by the interplay of microevolutionary forces as well as their history and current ecological conditions (Shikano et al., 2010). Natural populations occur in landscapes in which environmental features may constrain or promote movements of individuals and genes affecting, therefore, migration patterns among local populations and the resultant population structure (Manel et al., 2005). Even though dispersal has significant population level consequences, it originates as a behavioral trait at the level of individuals (Kittlein and Gaggiotti, 2008).

In general, the subterranean rodents are highly specialists to a particular habitat, which makes them a very interesting case to study population genetic structure (Mora et al., 2013). They present restricted dispersal abilities and often occupies naturally fragmented environments into demes of low effective population

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[*] Corresponding author at: Instituto de Investigaciones Marinas y Costeras, (IIMyC, CONICET), Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3250 3to piso, 7600 Mar del Plata, Argentina. Fax: +54 223 475 2426.

E-mail addresses: msmora@mdp.edu.ar (M.S. Mora), fmapelli@mdp.edu.ar (F.J. Mapelli), anushlop@gmail.com (A. López), mjgfernandez@gmail.com (M.J.G. Fernández), patricia_mirol@yahoo.com.ar (P.M. Mirol), kittlein@mdp.edu.ar (M.J. Kittlein).

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sizes. This is the case of the genus *Ctenomys* (Lessa, 2000; Mapelli et al., 2012a; Mirol et al., 2010; Mora et al., 2006, 2007) which is distributed throughout the southern cone of South America and constitutes the most speciose group of all subterranean rodents (Lessa, 2000; Reig et al., 1990).

The genus *Ctenomys* is currently composed by at least eight phylogenetic groups of species described by Parada et al. (2011). One of them is the "*mendocinus* phylogenetic group", which conform a monophyletic group currently distributed from the western portion of Argentina to the southeast of Brazil, and they are composed by seven recognized species of tuco-tucos: *Ctenomys australis*, *Ctenomys azarae, Ctenomys* "*chasiquensis*", *Ctenomys flamarioni, Ctenomys mendocinus, Ctenomys porteousi*, and *Ctenomys rionegrensis* (D'Elía et al., 1999; Massarini et al., 1991; Massarini and de Freitas, 2005; Parada et al., 2011; Slamovits et al., 2001). These species occupies well-drained sandy soils, mostly associated to the recent Quaternary sand dunes on the coastal plains of southeastern of Brazil, southwestern of Uruguay and eastern of Argentina in the case of *C. flamarioni*, *C. rionegrensis* and *C. australis* (Fernández-Stolz et al., 2007; Kittlein and Gaggiotti, 2008; Mora et al., 2006; Wlasiuk et al., 2003), or are related to the Pleistocene continental dunes and paleo-dunes from central Argentina, in the case of *C. azarae, C. mendocinus, C. porteousi* and *Ctenomys.* "*chasiquensis*" (D'Elía et al., 1999; Mapelli and Kittlein, 2009; Mapelli et al., 2012a; Massarini et al., 1991).

In particular, *C.* "*chasiquensis*" (or Chasicó's tuco-tuco), is a form of uncertain status, initially reported only for the Chasicó Lake (Buenos Aires Province) by Contreras and Maceiras (1970) and then by Contreras (1973), but without proper taxonomic description, which makes this designation a "nomen nodum". Although the close phylogenetic relationship among all species belonging to the "*mendocinus* phylogenetic group", we consider the populations of this study as *C.* "*chasiquensis*", using the same terminology of nominal species adopted by Contreras and Maceiras (1970). Thus, the proposed distribution for this taxonomic group includes the sand-dunes that extend from the Southwest of Buenos Aires to the Southeast of La Pampa in Argentina. As other species of tuco-tucos, the Chasicó's tuco-tuco is strictly related with sandy soils, on dunes with low vegetation cover and some elevation, eluding low and flood areas. Particularly, Chasicó Lake is the biggest body water in the region, and divides the sand dune rearrangement in conspicuous sandy diagonals (Fig. 1).

The landscape is also interrupted by the presence of some small inland salt flats such as Salina Chica, Salina Colorada Chica, Salina Colorada Grande, Salinas de Jacinto Aráuz and some streams as Arroyo Chasicó, from which the homonymous lagoon arise. These topographic features constitute natural important barriers to dispersal and essentially divide the distribution of this species in three evident sandy diagonals (Fig. 1), two at the West and one at the East relative to the Chasicó Lake. The sand dunes inhabited by the Chasicó's tuco-tuco are located along the side valleys with NE-SW direction. Beyond this, there are some important differences in the eastern and western parts of the distribution of this species. The East part comprise sandy, well-drain and friable soils that occur in the higher topographic positions surrounding by few lagoons. On the contrary, the distribution of this species becomes more continuous and homogeneous westward.

In current days the natural configuration of this landscape is being lost to forestry, urban development, and the progressive advance of farming (e.g., soybean) in the region; these factors associated with the particular biological attributes of this group, might have caused a negative impact on their populations. Thus, the viability of this endemic species is also associated to the protection of the whole sand-dune environment. Considering this scenario, it is essential to know the population dynamics and dispersion patterns in species with particular restrictions in highly fragmented habitats.

Here we use a mitochondrial data to characterize the population genetic structure and historical migration patterns of *C.* "*chasiquensis*", assessing the effects of habitat configuration on the genetic structure of this endemic rodent. Thus, one of the main objectives of this work is to determine whether areas with greater environmental connectivity (located on the West of the species distribution) have shown higher levels of gene flow between populations than the most isolated populations (located in the East, where the human activity produced a strong impact over the borders of this area in current days). Alternatively, we assess the connection between the demographic changes in population sizes through time and the most important climatic changes occurred during the Late Quaternary.

Material and methods

Sampling design and habitat characteristics

Typical sand dune habitat of this species, where sampling of populations was conducted, are characterized by three major sand dunes diagonals disposed in NE-SW direction, from Lihuel Calel (in the Southwest of La Pampa) to Salitral de la Vidriera, nearby Bahia Blanca (Southeast of Buenos Aires; see Fig. 1). Some important landscape features (e.g., depressions of Salinas Grandes, Chasicó Lake and the Chasicó stream) break the nearly continuous distribution of this species on these sandy diagonals (Fig. 1). Population densities of *C.* "*chasiquensis*" are higher on these sandy diagonals compared to the surrounding environment, which are composed by a highly patchy landscape (pers. obs.). The sampling sites were chosen over this area (sediments in the diagonals are conformed by slime-sand material of eolian origin), between 20 and 40 km of distance between locations (Fig. 1). Mean annual rainfalls around the study area are ~600–700 mm with no pronounced seasonality (Zech et al., 2009).

The central region of Argentina where the study area is included comprises from the Andean foothills to the Atlantic coast between latitudes 32°–40°S, and is covered by powerful and extensive Quaternary aeolian deposits (Iriondo, 1999; Zarate and Tripaldi, 2012). Iriondo (1999) and Zárate and Tripaldi (2012) described the sandy and silty deposits (loess) covering the Pampean Plain as the "Eolian Pampean System". Thus, the sampling area is naturally included into this major aeolian unit.

Some natural barriers such as the Chasicó Lake and the Chasicó stream divided the distribution of *C.* "*chasiquensis*" between two groups of populations: the westernmost sampling sites (LCH, R1, R154, PSR, LE, LC) located at the West of Chasicó Lake, and the easternmost sampling sites (SC, LM) located at the East of this lagoon (Fig. 1). The eastern unit presents more percentage of loess and silt, and higher proportion of precipitation (with higher diversity of grassland species) in comparison to the West (Fig. 1).

It should be noted that vegetation in the eastern unit (38°38′S to 38°53′S, 63°03′W and 62°29′W) has been highly modified by clearings, cultivation, introduction of domestic livestock (especially cattle and sheep) and the occurrence of accidental and directed fires during the last century (Zárate and Tripaldi, 2012). Despite the sub humid conditions, only a tall grass steppe with some shrubs prevails, which is probably due to the intensive land use (Zech et al., 2009). In contrast, the western unit is less affected, creating a continuous sand dune habitat within the phytogeographical Argentinean regions of "Espinal" and "Monte" (Fig. 1), which constitutes a heterogeneous mosaic of landscapes, from open sand dune habitats composed by *Larrea* shrublands and dense vegetation patches of *Prosopis* woodlands to important salt flats.