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Matrilineal genealogies suggest a very low dispersal in desert rodent females

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ABSTRACT

Previous research shows little haplotype diversity in small geographic areas, such as islands and areas where physical barriers interrupt gene flow. The general pattern is the presence of a small number of haplotypes spread across sampling sites. Instead, this paper reports the presence of a large number of haplotypes (*Cytb* and COI) in the extremely small distribution area (Los Planes basin, Baja California Sur, Mexico) of the Cerralvo pocket mouse, *Chaetodipus siccus*. Haplotype zoning revealed that haplotypes considered as ancestral are located to the periphery of the distribution area, whereas derived haplotypes are located to the center of the distribution range. Most derivatives are unique haplotypes and many of them exhibit a remarkable characteristic: a separation of not more than 1.7 km between them, which prompts a genetic microstructured population. All these features suggest the presence of a strong philopatric behavior among females.

1. Introduction

Former socio-genetic studies revealed that the social systems of most mammals are characterized by a polygynous mating system, female philopatry and the associated formation of clumps of closely related females or matrilines, as well as male-biased dispersal (Clutton-Brock, 1989; Kappeler et al., 2002). Moreover, the populations of many mammal species are subdivided into behaviorally segregated breeding groups maintained by sex-biased philopatry and territorial exclusion of immigrants (Clutton-Brock, 1989; Solomon, 2003). Finally, the vast majority of mammalian species have a solitary social organization (Jones, 1993).

Phylogeography (Gao et al., 2010) is an important research field because it reveals the drivers that determine the spatial distribution of matrilines within and between closely related species. An extension of phylogeography involves understanding the roles of landscape architecture and geographic isolation in the evolutionary history of species (Neiswenter and Riddle, 2010). Mammals display a wide variety of matrilineal patterns. A star network is a common genealogical signature for species that have recently expanded their size from small numbers of founders (Avise, 2000).

The main genetic breaks in taxa distributed in North American deserts are frequently associated with mountains, plateaus, and rivers that create temporary and long-term stable barriers to dispersal (Neiswenter and Riddle, 2010). These physical features have been associated with the geographic genetic structure in a variety of taxa, including rodents (Riddle et al., 2000). Genetic signatures can be very complex in species living in areas of heavy geological or paleoclimatic activity. However, genetic structure may be less complex in populations with a high migration index or whose isolation is relatively recent, geologically speaking. A shift in genetic structure can have profound evolutionary and behavioral consequences for a given population (Bossart and Prowell, 1998). Essential population processes such as speciation (Doebeli and Dieckmann, 2003), gene flow, local extinction (Hedrick, 2001), or association of individuals (Wang et al., 2011), affect and reflect patterns of genetic substructuring. Data analysis on individual variations in mitochondrial DNA often contributes significantly to the identification of the genetic structure in populations (Avise, 2000).

The rodent family Heteromyidae comprises an almost entirely North American radiation (Hafner et al., 2007). Heteromyids have been used as model organisms for studies that involve physiological ecology, macroevolution and social behavior (Genoways and Brown, 1993; Randall, 1993), among others. Phylogenetic hypotheses based on molecular data are now available for the whole family as well as for particular clades (Neiswenter and Riddle, 2010).

Chaetodipus species for the most part appear to have a social system in which adults live alone in separate home ranges. There is a general recognition that small heteromyid mice have high index of aggressive behaviors as part of their biology (Eisenberg, 1963). Thus, field data show no evidence of social grouping in *Chaetodipus* species (Jones, 1993). Additionally, it has been reported a greater dispersal movements and larger home ranges in males than females (Jones, 1993).

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The Cerralvo pocket mouse *Chaetodipus siccus* Osgood, 1907 is part of the *arenarius* complex, which also includes the little desert pocket mouse *C. arenarius* Merriam, 1894, and the Dalquest's pocket mouse *C. ammophilus* Roth, 1976 (Álvarez-Castañeda and Rios, 2011). The distribution of *C. siccus*, originally described as a subspecies of *C. arenarius* (Patton and Álvarez-Castañeda, 1999), is limited to Cerralvo Island and Los Planes basin in Baja California Sur, Mexico. On the other hand, from the revision of the *arenarius* complex (Álvarez-Castañeda and Rios, 2011), it was possible to identify several mitochondrial haplotypes in the insular population of *C. siccus*; hence, its endemicity and genetic patterns are of great interest to conservation (Álvarez-Castañeda and Rios, 2011).

It has been proposed that arid environments restrict mobility (Solomon, 2003). This hypothesis states that extreme conditions, unpredictable and sporadic rainfall, and the pattern of food resource distribution in these environments may impose severe restrictions on dispersal. Because of this, individuals are forced to stay in their birth area, leading to philopatry. It has been documented that after a period of considerable precipitation, both activity and foraging area increase in desert species, which is proposed as an indication of dispersal (Lacey and Wieczorek, 2003).

In this study, we assess the matrilineal structure of the Cerralvo pocket mouse *Chaetodipus siccus* in 51 sample sites using mitochondrial DNA, and considering the disjunctive insular and peninsular distributions. The species, with several haplotypes, is specifically associated to the arid environment of the Baja California Peninsula (Álvarez-Castañeda and Rios, 2011). The goal was to evaluate if the increase of the sample area would increment the number of identified haplotypes, and also study the pattern of distribution of the haplotypes in relation to different microhabitats present in the *C. siccus* range.

2. Materials and methods

2.1. Sample collection

We surveyed 51 localities throughout the potential range of *C. siccus* (Fig. 1). The study was carried out in federal zones with the authorization of the Dirección General de Vida Silvestre (General Direction of Wildlife) of the Mexican government. Only the Isla Cerralvo population is designated as protected, and therefore the sample size of this locality is small and was approved by the authority. Specimens were collected using the linear transect method with Sherman live traps for rodents, and were sacrified by chloroform anesthesia. In all instances, animals were handled following the recommendations of the American Society of Mammalogists (Sikes and Gannon, 2011) and the Mexican government guidelines to conduct scientific research in animals. Voucher specimens and tissue samples were deposited in the Mammals Collection of the *Centro de Investigaciones Biológicas del Noroeste* (CIB) certified by the Mexican government. Details of voucher numbers, georeferenced localities and GenBank accession numbers are provided in the appendix.

2.2. Geographic areas

The habitat descriptions made for the *arenarius* complex state that the presence of these species are related to flat and sandy soil areas and are less common on slopes and ridges (Huey, 1964). Mounds and burrows of *C. siccus* on Cerralvo Island were found far up arroyos having a sandy floor, suggesting sandy soil is a more significant aspect of the habitat than is a flat, open environments (Banks, 1964). The distribution range of *C. siccus* in southern Baja California Sur, Mexico was divided into four zones: 1) central mainland area, 2) peripheral mainland area, 3) salty soil area and 4) Cerralvo Island. Mainland regions were delineated based on the percent slope of the terrain, type of soil, and absence/presence of the spiny pocket mouse *C. spinatus*, which is associated with rocky soil in contrast to *C. siccus*, which is more abundant in sandy areas. Central areas are characterized by a sandy plain, an average slope of 1.65% (0.92°), and the absence of *C. spinatus*; the former topographic features represent the optimal conditions for species in the *arenarius* complex (Banks, 1964). The peripheral mainland consists of rocky soil or sandy areas with rocky soil patches, an average slope of 1.9% (1.06°), and the presence of *C. spinatus*. This area was suboptimal for the *C. arenarius* species group. The salty soil area consisted of flood-prone sandy plains and coastal dunes with halophyte patches, an average slope of 0.37% (0.21°), and the presence of *C. siccus* only. The presence of *C. siccus* in Cerralvo Island was considered to be related to sandy plains.

2.3. Laboratory procedures

Genomic DNA was extracted from muscle tissue (kept at −20 °C in 90% ethanol) using the DNAease Kit (QIAGEN Inc., Valencia, CA). Fragments of ca. 800 and 650 base-pairs of the mitochondrial genes cytochrome *b* (*Cytb*) and cytochrome *c* oxidase subunit I (COI) were amplified using the primer pairs MVZ05/MVZ16 (da Silva and Patton, 1993) and M13-tailed vertebrate primer cocktails (Ivanova and Grainger, 2007), respectively. The following conditions for initial double-strand amplifications for *Cytb* were used: 12.5 μL (10 ng) template, 4.4 μL ddH_2O, 2.5 μL of each primer (10 nM), 0.474 μL (0.4 nM) dNTPs, 0.5 μL (3 mM) $MgCl_2$, 0.125 μL Taq polymerase, and 1x Taq buffer to a final volume of 25 μL. The conditions for PCR amplification of COI follow the protocol of the Canadian Center for DNA Barcoding (Ivanova and Grainger, 2007). The amplification conditions consisted of an initial denaturation at 94 °C (3 min for *Cytb* and 1 min for COI) followed by denaturation at 94 °C (37 cycles of 45 s for *Cytb* and 5 cycles of 30 s for COI), annealing at 50 °C (1 min for *Cytb* and 40 s for COI), and final extension at 72 °C (1 min for *Cytb* and 10 min for COI). Double-strand DNA (*Cytb*) was cleaned using the QIAquick PCR Purification Kit (QIAGEN). In the case of COI we did not clean up PCR products and proceeded directly to sequencing (Ivanova and Grainger, 2007). Templates were cycle-sequenced with the same primers using the d-Rhodamine Dye and the Big Dye Terminator Kits. Sequencing was performed on an ABI 377 automated sequencer following the manufacturer's protocols.

Genetic variation levels within *C. siccus* were measured in terms of the number of polymorphic sites, nucleotide diversity (Φ per nucleotide site, i.e., the probability that two randomly chosen homologous nucleotides differ; Nei, 1987), haplotype diversity (*h*), and number of private haplotypes, using ARLEQUIN v.3.0 (Excoffier et al., 2005). Non-redundant haplotypes were deposited in GenBank (for accession numbers, see Appendix 1 and 2).

Nucleotide sequences were aligned using the SEQUENCHER v.3.1 (Gene Codes Corp., Ann Arbor, Michigan), visually inspected, and translated into amino acids for alignment confirmation. Missing data were coded with a question mark. Non-redundant haplotypes were assessed with COLLAPSE v.1.1 (http://darwin.uvigo.es).

3. Results

3.1. Samples

C. siccus was observed in 34 of the 51 localities sampled. A total of 153 specimens were used for the genetic analyses, with a maximum of five specimens per locality (Fig. 1, Appendix 1). The estimated range of *C. siccus* in the mainland was ~270 km^2 based on the analyses of 51 localities, and ~0.77 km^2 on Cerralvo Island (Fig. 1).

3.2. Genetic variation

Fifty six haplotypes of *Cytb* ($h = 0.943 \pm 0.009$; $\pi = 0.005 \pm 0.002$) and seventeen of COI ($h = 0.628 \pm 0.039$; $\pi = 0.004 \pm 0.002$) were identified in the 153 specimens. The *Cytb*