PHYLOGEOGRAPHY OF THE SUBTERRANEAN RODENT
SPALACOPUS CYANUS (CAVIOMORPHA, OCTODONTIDAE)

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Spalacopus cyanus is a subterranean rodent inhabiting coastal and mountain habitats. Individuals from mountain populations are larger than individuals from the coast, and mountain populations have a more limited geographic range. To investigate the genetic structure and biogeography of this species, we analyzed mitochondrial DNA control region sequences. We found low levels of nucleotide diversity in comparison with other subterranean rodents. Coastal populations had higher nucleotide diversity and effective population size than mountain populations. Phylogenetic analysis using maximum parsimony and a haplotype network generated using statistical parsimony recognized 3 groups of haplotypes: northern coastal and mountain populations, central coastal populations, and southern coastal population. Consistent with the presence of unshared haplotypes, migration rates were practically 0, except from Valparaíso to Ventanas and from La Parva to Huentelauquén. We observed asymmetric migration rates from mountain to coastal populations, suggesting that this species originated in the Andean mountains. A likelihood ratio test could not reject the null hypothesis of a stable population when all sequences were grouped into a single population and when coastal populations were analyzed separately. However, a negative exponential growth parameter was estimated for mountain populations, suggesting that these populations have undergone recent demographic changes.

Key words: biogeography, Chile, Octodontidae, population genetics, South America, Spalacopus cyanus, subterranean rodents

The genetic structure of natural populations is determined by a complex interaction of ecological (e.g., population size and migration rate) and evolutionary processes (e.g., natural selection and genetic drift). Different groups of organisms show diverse types of demographic and population characteristics, which result in different levels of population genetic structure.

Subterranean rodents are characterized by having a high degree of population structure as a result of small and unconnected populations, characteristics that would promote differentiation by genetic drift (Steinberg and Patton 2000). Among subterranean species of the family Octodontidae, Spalacopus cyanus, the cururo, is a species endemic to central Chile, with coastal and mountain populations. The coastal geographic distribution is more extensive and goes from Caldera (27°03′S) to Quirihue (36°17′S), whereas mountain populations occur from Alicahue (32°19′S) to Los Cipreses (34°01′S—Torres-Mura and Contreras 1998; Fig. 1). Andean populations are phenotypically different from those of the coast, and are characterized by greater body mass (Contreras et al. 1987) as well as differences in skull and tooth morphology (Reig et al. 1972). Nevertheless, the digging apparatus (after removal of the body-size effect) showed no differences between coastal and Andean populations, even though the soil is harder where mountain populations occur (Bacigalupe et al. 2002).

Because S. cyanus feeds on bulbs of geophytes, Reig (1970) predicted a nomadic behavior for this species. In fact, Reig (1970) noted that because colonies of S. cyanus would completely exploit the resources located around their burrow system, they would soon abandon an area, moving into another.
undisturbed area. Consequently, higher levels of gene flow and genetic uniformity are predicted. However, results based on a comparison of 2 populations where the types of food resources consumed were different (subterranean roots versus aerial plant parts) showed important differences in mobility. Populations consuming slow-to-regenerate subterranean roots are mobile, whereas populations consuming quickly replenished aerial plant parts were sedentary. Accordingly, neither the nomadic nor the sedentary behavior would be a species-specific characteristic for *S. cyanus*.

At the chromosomal level, there are no differences between coastal and mountain populations, either in number or in structure of the chromosomes (Reig et al. 1972). According to Reig et al. (1972), the observed chromosomal uniformity could be explained by the proposed high vagility of the species (Reig 1970). In fact, this uniform pattern contrasts with the high chromosomal variation found in other subterranean hystricomorph rodents (e.g., *Ctenomys* and *Cryptomys*) where isolation and low vagility seem to play an important role (Tomasco 2003; Van Daele et al. 2004). However, at the allozymic level, and contra the high-vagility hypothesis, a considerable degree of demic structure has been reported in *S. cyanus* (Gallardo et al. 1992).

On the other hand, the low species diversity of the genus *Spalacopus* contrasts with the high species diversity of the genus *Ctenomys*, both of which are in the superfamily Octodontoidea. Reig (1970) and Vrba and Gould (1986) have suggested that the high species diversity of the genus *Ctenomys* relative to *Spalacopus* might result from species-level differences (e.g., gene flow and population structure) rather than different organismal adaptations. This contrast makes *S. cyanus* an interesting model species to compare with rodents of the genus *Ctenomys* to test the hypothesis that population genetic parameters are responsible for the previously proposed differences in speciation rates.

The goal of our study is to examine the genetic structure and biogeographical patterns of genetic variation in *S. cyanus*. To achieve this objective, we sequenced the mitochondrial DNA (mtDNA) control region from specimens of *S. cyanus* from coastal and mountain populations, and analyzed them from a phylogenetic and population genetic perspective.

**Materials and Methods**

**Sampling.**—Animals were trapped from 7 different populations. Five localities were located in coastal areas: La Serena (29°49′S, 71°16′W), Huentelauquén (31°33′S, 71°30′W), Ventanas (32°46′S, 71°27′W), Valparaíso (33°04′S, 71°09′W) and Quirihue (36°10′S, 72°27′W), whereas 2 localities were located in the Andean (mountain) range: La Parva (33°19′S, 70°17′W) and Lagunillas (33°36′S, 70°17′W). All of our sampled localities covered large areas and included individuals from different burrows. We thus covered almost the entire geographic range of the species (Fig. 1). Details about number of individuals, haplotype identification, haplotype frequency, and altitude are given in Table 1. Our animal collecting procedures were performed in a humane manner, following guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

**DNA extraction and amplification.**—Voucher specimens were prepared and deposited in the Colección de Flora y Fauna Profesor Patricio Sánchez Reyes, Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile. DNA was isolated following a modified protocol of Miller et al. (1988), involving treatment with sodium dodecyl sulfate, digestion with proteinase K, NaCl protein precipitation, and subsequent isopropanol precipitation of the DNA. A fragment of 611 base pairs adjacent to Pro-tRNA of the hypervariable region I of the mtDNA control region was amplified using the following primers: Tuco-Pro
Table 1.—Locality type, sample size (n_{ind}), haplotypes identification (Hap_id), haplotype frequency, and elevation (meters above sea level) of 7 populations of Spalacopus cyanus included in this study.

<table>
<thead>
<tr>
<th>Population</th>
<th>Locality type</th>
<th>n_{ind}</th>
<th>Hap_id</th>
<th>Haplotype frequency (%)</th>
<th>Elevation</th>
</tr>
</thead>
<tbody>
<tr>
<td>La Serena</td>
<td>Coastal</td>
<td>8</td>
<td>H10</td>
<td>100</td>
<td>61</td>
</tr>
<tr>
<td>Huéntelauquéén</td>
<td>Coastal</td>
<td>8</td>
<td>H8, H9, H11, H12</td>
<td>25, 12.5, 37.5, 25</td>
<td>131</td>
</tr>
<tr>
<td>Ventanas</td>
<td>Coastal</td>
<td>5</td>
<td>H1, H2, H3</td>
<td>60, 20, 20</td>
<td>31</td>
</tr>
<tr>
<td>Valparaíso</td>
<td>Coastal</td>
<td>7</td>
<td>H1, H4</td>
<td>85,7, 14,3</td>
<td>200</td>
</tr>
<tr>
<td>Quirihue</td>
<td>Coastal</td>
<td>6</td>
<td>H13</td>
<td>100</td>
<td>246</td>
</tr>
<tr>
<td>La Parva</td>
<td>Mountain</td>
<td>9</td>
<td>H5</td>
<td>100</td>
<td>2,779</td>
</tr>
<tr>
<td>Lagunillas</td>
<td>Mountain</td>
<td>8</td>
<td>H6, H7</td>
<td>50, 50</td>
<td>2,250</td>
</tr>
</tbody>
</table>

(5’ TTCTAATTTAATTTTCTTG 3’—Tomasco 2003) and L259 5’ ATGTCCTTCTAGCATTAAAAAGTATGCACCT 3’). The polymerase chain reaction conditions were as follows: 94°C for 2 min; 30 cycles of 94°C for 30 s, 52°C for 30 s, and 72°C for 30 s; 72°C for 2 min. Polymerase chain reaction products were purified with the QIAquick polymerase chain reaction purification kit (Qiagen, Valencia, California). Sequencing reactions were carried out using a BigDye Terminator Cycle sequencing ready reaction mix (Applied Biosystems, Foster City, California) and were run on an ABI 3100 automated sequencer (Applied Biosystems).

Statistical analyses.—Representative haplotype sequences were deposited in GenBank under accession numbers AY836562–AY836574. The alignment was performed using ClustalX (Thompson et al. 1997). We performed Tajima’s (Tajima 1989) and Fu’s (Fu 1997) test of neutrality implemented in Arlequin 2000 (Schneider et al. 2001). Haplotype relationships were reconstructed using maximum parsimony as implemented in TCS defines the parsimony limit (maximum number of differences among haplotypes as a result of single substitutions with a 95% statistical confidence), and then first connects the haplotypes with smaller differences until all haplotypes are included in a single network. On the other hand, the median joining approach implemented in network combines the minimum spanning trees within a single network, and then using the parsimony criterion; median vectors are added to the network.

In order to determine how the genetic variation was partitioned, we carried out a hierarchical analysis of molecular variance (AMOVA—Excoffier et al. 1992) implemented in Arlequin 2000 (Schneider et al. 2001). Individuals were grouped into populations, and populations into 2 different groups according to their geographic location. The coastal group included 5 populations (La Serena, Huéntelauquéén, Ventanas, Valparaíso, and Quirihue), whereas the mountain group included 2 populations (La Parva and Lagunillas).

To assess the relationships between geographic distance and migration rate between populations, we performed an isolation-by-distance analysis (Slatkin 1993), as implemented in Arlequin 2000 (Schneider et al. 2001). This program uses pairwise FST values to estimate the migration rate (≈N_e/m) and then correlates these values with the geographical distance between populations. A Mantel test was used to assess the statistical significance of the correlation. Geographic distances were obtained using the program “How far is it?” (http://www.indo.com/distance).

We used MIGRATE 1.7.3 (Beerli and Felsenstein 2001) to estimate the effective population sizes (2μN_e) and migration rates (2N_e/m) among populations. This program uses an extension of the coalescent theory to estimate parameters and a Markov chain Monte Carlo approach with Metropolis–Hasting importance sampling to search through genealogy space. We used this approximation to estimate the migration rates in both directions among all populations and their population sizes. Furthermore, in order to investigate the biogeographic origin of this species, we arranged populations into 2 groups as in the AMOVA (see above). FST estimates of effective population sizes and migration rates were used as initial values. Ten short chains with 10,000 sampled genealogies each and 3 long chains with 100,000 sampled genealogies each were run. One of every 100 reconstructed genealogies was sampled. The temperature parameters for heating the chains were set at 1.0, 1.2, 1.5, and 3.0. In order to verify the results, 4 independent runs were performed simultaneously.

To test whether there was evidence of population expansion, in addition to the Tajima and Fu tests, we used FLUCTUATE 1.4 (Kuhner et al. 1998). This program uses the same sampling procedure as MIGRATE to obtain joint estimates of the population size parameter (2μN_e) and of the exponential growth parameter g. We set up 10 short chains with sampling increments of 10 and 1,000 steps per chain, and 10 long chains with sampling increments of 10 and 20,000 steps per chain. We
provided initial unweighted pair-group method using arithmetic averages trees constructed using PAUP* 4.0b10 (Swofford 2002). We used a likelihood ratio test to determine the significance of the exponential growth rate ($g$), by comparing the log-likelihood of the model in which $g$ was set to 0 (representing a stable population) and one in which the $g$ was allowed to vary. The test statistic was calculated as twice the difference in log-likelihood scores for each model and was compared to a chi-square distribution with 1 degree of freedom. We used this approximation with all sequences grouped together and by separating them into coastal (La Serena, Huentelauquén, Ventanas, Valparaíso, and Quirihue) and mountain (La Parva and Lagunillas) groups.

**RESULTS**

The maximum-parsimony reconstruction illustrates the relationships among the 13 haplotypes recovered for *S. cyanus* (Fig. 2) with bootstrap values that ranged between 54% and 81%. We recovered 3 haplotype groups that are not resolved at their nodes: a northern coastal clade (La Serena and Huentelauquén) closely related to the mountain clade (La Parva and Lagunillas); a central coastal clade (Valparaíso and Ventanas), and a southern coastal clade (Quirihue). In the 1st group, the analysis grouped mountain haplotypes with a moderate bootstrap support as a sister group of 1 northern coastal haplotype (Hap 8) with poor support (Fig. 2). Haplotype network reconstruction using TCS and Network gave a similar topology with 3 haplotype groups (Fig. 3). In the network, mountain (La Parva and Lagunillas) and northern coastal (La Serena and Huentelauquén) haplotypes are separated by 2 mutational steps, whereas the central (Ventanas and Valparaíso) and southern coastal (Quirihue) haplotypes are separated by 6 steps from the northern and mountain populations, and 9 steps from each other (Fig. 3). With the exception of 1 haplotype that was shared between Ventanas and Valparaíso (Hap 1), all other haplotypes were restricted to a single population. Three of the 7 populations were monomorphic (Table 1), 2 from the coast (La Serena and Quirihue) and 1 from the mountains (La Parva).

![Fig. 2.—Maximum-parsimony reconstruction of haplotype relationships of *Spalacopus cyanus*. Tree was rooted with *Aconaemys fuscus* and 2 individuals of *Octodon degus*. Numbers on branches represent bootstrap support after 2,000 iterations.](Image)

![Fig. 3.—Haplotype network of the 13 haplotypes recovered from populations of *Spalacopus cyanus*. Empty circles represent different haplotypes; size is scaled to its frequency. Small black circles over connecting lines represent single mutational steps between a pair of haplotypes. A) Mountain haplotypes (La Parva and Lagunillas), B) northern coastal haplotypes (La Serena and Huentelauquén), C) southern coastal haplotypes (Quirihue), and D) central coastal haplotypes (Ventanas and Valparaíso).](Image)
Tajima and Fu neutrality tests did not detect departures from neutral expectations in any case (Table 2). Among single populations, nucleotide diversity (π) varied from 0.00094 (Valparaiso and Lagunillas) to 0.0029 (Huentelauquén; Table 2). Among groups of populations, the coastal group had around 5 times greater nucleotide diversity than the mountain group (Table 2). Variation among populations within groups accounted for 56.11% of the observed molecular variance (Table 3). Variation among groups (coastal and mountain) accounted for 38.69% (Table 3), and variation within populations accounted for the remaining 5.2% (Table 3). For ungrouped populations, estimates of migration rates were small, with the exception of migration rates from Valparaiso to Ventanas and from La Parva to Huentelauquén (4.81 and 0.93, respectively). Analysis of isolation by distance between pairs of populations was not significant. For grouped populations, analysis using MIGRATE showed an asymmetrical migration rate from mountain to coastal populations (Table 4).

The program FLUCTUATE can estimate if the model that varied the $g$ parameter fits better than the model where $g$ is not allowed to vary. When we pooled all populations, analysis using FLUCTUATE did not provide support for population expansion; the same result was observed for the coastal group (Table 5). For the mountain group, the model that estimated the exponential growth rate fit marginally better than the null hypothesis of a stable population ($P$-value close to 0.05; Table 5). Nevertheless, the exponential growth rate parameter ($g$) estimated was negative (Table 5).

**DISCUSSION**

Our mtDNA survey found 13 haplotypes among 7 populations of the subterranean rodent *S. cyanus*. Our haplotype number per population (1.86) is comparable with the results obtained for the subterranean rodent *Ctenomys pearsoni* (1.91—Tomasco 2003) and *C. rionegrensis* (1.89—Wlasiuk et al. 2003). However, these values are lower than results reported for *C. australis* (3—Mora et al. 2006). The nucleotide diversity values observed in our populations ranged from 0.00094 to 0.0028 (Table 2) and were comparable to those described for *C. australis* (Mora et al. 2006). However, these values were 6.82 times lower than those described for *C. pearsoni* (Tomasco 2003). Furthermore, if we compare our data with those obtained for another fossorial species of the genus *Spalax*, the observed differences in nucleotide diversity were even more pronounced, because the upper limit for *S. cyanus* is smaller than the lower limit for *Spalax* (Reyes et al. 2003). Additionally, the range of variation also was smaller (0.0046—0.0264 for *Spalax*—Reyes et al. 2003). On the other hand, we observed that in 3 (42.8%) of 7 populations of *Spalacopus*, only a single mtDNA haplotype was found. For *C. pearsoni*, only 1 of 11 populations had a single mtDNA haplotype (9.1%—Tomasco 2003), and for *Spalax* only 1 of 12 populations had a single mtDNA haplotype (8.3%—Reyes et al. 2003). Our low values of genetic variation also are in agreement with previous studies based on allozymes (Gallardo et al. 1992). The latter study showed that among 4 populations of *S. cyanus*, the Quirihue population was the least variable, and found that 6 of the 8 loci examined were monomorphic, whereas the Huentelauquén population showed higher levels of variation. At the chromosomal level, Reig et al. (1972) reported that 4 coastal populations and 1 mountain population (Lagunillas) showed the same karyotype (2n = 58; FN = 116) with almost no variation either in number or in structure, either within or among populations. This contrasts with the pattern observed in other subterranean hystricomorph rodents (e.g., *Ctenomys* and *Cryptomys*), where karyotypic rearrangements are extensive (Tomasco 2003; Van Daele et al. 2004). In general, populations of *S. cyanus* exhibited lower levels of genetic variation in comparison with other subterranean rodents such as those of the genus *Ctenomys*, as well as with more distantly related fossorial rodents of the genus *Spalax*.

The results of our phylogenetic analyses using maximum parsimony (Fig. 2) and the haplotype network generated using statistical parsimony (Fig. 3) were concordant and recognized 3 main haplotype groups: the northern coastal (La Serena and Huentelauquén) and mountain group (La Parva and Lagunillas), the central coastal group (Ventanas and Valparaíso), and the southern coastal group (Quirihue). Estimates of migration rates among all populations were generally low and almost all of the populations sampled had unique haplotypes. In fact, with the exception of Ventanas and Valparaíso populations ($F_{ST} = 0.11$), $F_{ST}$ values were high and ranged from 0.76 to 1.

**Table 2.**—Tajima’s (1989; $D$) and Fu’s (1997; $F$) neutrality tests for 7 populations of *Spalacopus cyanus* from central Chile. $\theta_a =$ Waterson’s theta; $\pi =$ nucleotide diversity; NS = not significant.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>$d.f.$</th>
<th>Sum of squares</th>
<th>Variance components (%)</th>
<th>$P$-statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>All populations</td>
<td>0.008</td>
<td>0.012</td>
<td>1.66 NS</td>
<td>1.86 NS</td>
</tr>
<tr>
<td>Coastal populations</td>
<td>0.0072</td>
<td>0.014</td>
<td>1.48 NS</td>
<td>1.79 NS</td>
</tr>
<tr>
<td>Mountain populations</td>
<td>0.0014</td>
<td>0.0023</td>
<td>1.76 NS</td>
<td>1.95 NS</td>
</tr>
<tr>
<td>La Parva</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>La Serena</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quirihue</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Huentelauquén</td>
<td>0.00252</td>
<td>0.00286</td>
<td>0.59 NS</td>
<td>-0.11 NS</td>
</tr>
<tr>
<td>Ventanas</td>
<td>0.00157</td>
<td>0.00164</td>
<td>0.24 NS</td>
<td>-0.48 NS</td>
</tr>
<tr>
<td>Valparaíso</td>
<td>0.00134</td>
<td>0.00094</td>
<td>-1.24 NS</td>
<td>0.86 NS</td>
</tr>
<tr>
<td>Lagunillas</td>
<td>0.00063</td>
<td>0.00094</td>
<td>1.44 NS</td>
<td>0.97 NS</td>
</tr>
</tbody>
</table>

* $P < 0.001$.
Moreover, our AMOVA results suggest that populations are highly structured, because more than one-half of the total molecular variance was explained among populations within localities. This pattern appears to be a general trend among other species of subterranean rodents (Steinberg and Patton 2000). Therefore, our estimates of low migration rates, high $F_{ST}$ values, and high degree of genetic structure supported by the AMOVA results, in combination with the high levels of population structure found with allozyme data (Gallardo et al. 1992) all disagree with the proposed nomadic behavior of the species (Reig 1970).

Determining the geographic origin of $S$. cyanus based on phenotypic differences has been an interesting problem. Population rearrangements recently have been used to infer biogeographical patterns using MIGRATE (Alvarez-Castañeda and Patton 2004; Zheng et al. 2003). Using this approach, estimates of migration rates in our study showed an asymmetrical pattern from mountain to coastal populations, suggesting an Andean origin of the species. It is possible that our results are biased because the main part of the estimated migration is between northern coastal and mountain populations; nonetheless, according to Beerli (2004), estimates of migration rates are not much affected by nonsampled populations. Because our mountain samples came from the middle of the distribution (Table 1), it is possible that extinct (or nonsampled) populations could be related to central coastal and southern groups. However, the Andean origin hypothesis also is supported by the fact that the genus $Spalacopus$ originated after the uplift of the Andean mountains between 1.1 and 2.7 million years ago (Honeycutt et al. 2003; Opazo 2005).

The absence of a pattern of isolation by distance in the populations we examined suggests lack of equilibrium between gene flow and genetic drift, and implies a recent colonization of parts of the current geographic range (Slatkin 1993). Our analysis using MIGRATE indicates that the more recently colonized area would be the coastal range. In addition, morphological variation in digging structures of various subterranean rodents is often correlated with soil characteristics (Lessa and Thaeler 1989). The lack of differences in the digging apparatus between mountain and coastal populations also could be explained by an Andean origin (hard soil) of the species. According to this scenario, Andean populations would have migrated to the coast (sandy soils) and retained the original adaptation to hard soils (Bacigalupe et al. 2002). An alternative explanation for the absence of an isolation-by-distance pattern could be due to the low levels of gene flow suggested by the small migration rates that result in higher levels of divergence between populations.

Our analysis of demographic change using all sequences as a single population did not reject the null hypothesis of a stable population in favor of the population expansion model. A similar result was obtained for analyses of coastal populations. In contrast, for mountain populations, the model that added the $g$ parameter was favored over a stable population hypothesis, but the estimated $g$ parameter was negative. Alvarez-Castañeda and Patton (2004) reported that the model that added the $g$ parameter had a significantly better fit in their analyses for the subterranean rodent $Thomys bottae$, but their estimated $g$ parameter supported a population expansion. The lower estimate for the mountain group in our study agrees with differences in area of the geographic ranges between mountain and coastal populations (Torres-Mura and Contreras 1998), and with the estimates of effective population size produced by MIGRATE and FLUCTUATE, where effective size of mountain populations was always smaller than that of the coastal populations. Moreover, nucleotide diversity also is lower in mountain populations than in the coastal populations.

Further support for the mountain origin of $S$. cyanus is found in the altitudinal distribution of several species of $Aconaemys$.
(Gallardo and Mondaca 2002). Because the distribution of *S. cyanus* is more restricted in the mountains than in the coastal range (Torres-Mura and Contreras 1998), and because *A. porteri*, which groups together with *S. cyanus* (Honeycutt et al. 2003), has the southernmost distribution of all *Aconaemys* species (Gallardo and Mondaca 2002), the mountain distribution of *S. cyanus* should have been more widespread in the past. Mountain populations may have experienced a geographic range contraction, which is consistent with the negative *g* values obtained for our exponential growth parameter, smaller population sizes, and lower genetic diversity.

In general, subterranean rodents have structured populations as a result of small population sizes and limited migration rates (Alvarez-Castañeda and Patton 2004; Steinberg and Patton 2000; Wlasiuk et al. 2003). Consequently, genetic drift plays an important role in shaping the genetic attributes of natural populations (Alvarez-Castañeda and Patton 2004; Gallardo et al. 1992). Furthermore, larger geographic ranges, where broad types of habitats are occupied, are ideal conditions that may promote speciation. Therefore, the stasis of the genus *Spalacopus* contrasts with the >60 species of the subterranean genus *Ctenomys*, both members of the same superfamily. Reig (1970) and Vrba and Gould (1986) have postulated that the high species diversity of the genus *Ctenomys* relative to *Spalacopus* might result from species-level differences (e.g., gene flow and population structure) rather than different organismic adaptations. According to these authors, differences in population structure lead to different probabilities of speciation. The hypothesis of species-level selection has been tested by looking at different rates of diversification between the families Ctenomyidae and Octodontidae (Castillo et al. 2005; Lessa and Cook 1998). Their results suggest a rapid process of diversification in tuco-tucos; however, this analysis does not address the cause of the difference in the speciation rate. Our results do not support this species-level differences hypothesis because the population genetic structure of *S. cyanus* is different in comparison with the available data for *C. rionegrensis* (Wlasiuk et al. 2003) and *C. pearsorn* (Tomasco 2003) and in general for other subterranean rodents. It is possible that the stasis observed in *Spalacopus* is partly the result of the limited geographic range occupied by this species. Further studies examining the population genetics and biogeography of other *Aconaemys* species would improve our knowledge of this biogeographic scenario.

**RESUMEN**

*Spalacopus cyanus* es un roedor subterráneo que habita ambientes costeros y montañosos. Individuos de poblaciones montañosas tienen mayor masa corporal que los individuos de poblaciones costeras, por otro lado también presentan un rango de distribución más restringido. En este trabajo nosotros investigamos la genética de poblaciones y la biogeografía de esta especie en su rango de distribución utilizando secuencias de la región control del ADN mitocondrial. Nosotras encontramos valores de diversidad nucleotídica menores en comparación con otros roedores subterráneos. En general las poblaciones de la costa presentaron una mayor diversidad nucleotídica que las poblaciones de montaña. El análisis filogenético usando parsimonia recobra la monofilia de la especie y en acuerdo con los resultados de redes de haplotipos recobra 3 grupos: las poblaciones del norte y montaña; las poblaciones centro-costa y la población sur-costa. De acuerdo con la presencia de haplotipos no compartidos, las tasas de migración fueron prácticamente cero, excepto entre las poblaciones de Valparaíso y Ventanas y entre La Parva y Huventelaquí. Agrupando las poblaciones de costa en un solo grupo y las de montaña en otro, nosotros observamos migración asimétrica desde las poblaciones de montaña hacia las poblaciones costeras, sugeriendo un origen Andino para la especie. La prueba de razones de verosimilitudes no pudo rechazar la hipótesis nula de estabilidad poblacional cuando todas las secuencias fueron agrupadas, y tampoco cuando las poblaciones costeras fueron analizadas como grupo. Sin embargo, un valor negativo para el parámetro de crecimiento poblacional fue estimado para las poblaciones de montaña, sugiriendo que estas poblaciones han tenido cambios demográficos recientes.

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