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# Demographic changes and genetic losses in populations of a subterranean rodent *(Ctenomys maulinus brunneus)* affected by a natural catastrophe

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## Abstract

Studied the demographic and genetic effects of a volcanic eruption on two local populations (Río Colorado, Las Raíces) of the fossorial rodent *Ctenomys maulinus brunneus*, in the Andes. Our data represent a unique contribution because the pre-existing demographic data and levels of genetic variation were contrasted with the changes monitored afterwards. Comparative census data of the breeding population size before and after the volcanic eruption, revealed a population decline of about 90 % in Río Colorado. An electrophoretic survey of 23 presumptive enzyme loci detected a considerable reduction of genetic variability in both populations. In Río Colorado, the proportion of polymorphic loci (P) decreased from 47.8 % to 17.4 %, and the expected heterozygosity (H) from 8.9 % to 2.8 %. In Las Raíces, P decreased from 50 % to 0 % and H from 13.2 % to 0 %. Although low genetic variability in fossorial mammals is generally assumed to reflect an adaptation to the stable subterranean niche, in some cases it may be merely the result of genetic drift.

## Introduction

Demographic bottlenecks have received significant attention since they have important evolutionary implications for assessing the genetic consequences of reduced population size (Nei and Tajima 1981; Nei et al. 1975; Chakraborty and Nei 1977). These estimates also have implications for conservation projects of mammalian species in fragmented habitats (Lande and Barrowclough 1987; Maruyama and Kimura 1980; Varvio et al. 1986) and for speciation events promoted by founder effects (Barton 1989). Genetic diversity is crucial in an evolutionary sense, and bottlenecks are the quickest means available for loosing genetic variation in natural populations through random fluctuations of population size (Leberg 1992). There is considerable theoretical support for the hypothesis that a natural population passing through a bottleneck should loose genetic variation in direct proportion to the severity of such an event (Chakraborty and Nei 1977; Maruyama and Fuerst 1985a, b; Nei et al. 1975). Despite the theoretical attention and well developed models predicting bottleneck effects (McCommas and Bryant 1990), no actual hints of both demographic and genetic data before and after a bottleneck in the wild have yet been reported. Exemplary studies in mammals (Bonnell and Selander 1974; Harwood and Hall 1990; O'Brien and Everman 1988; O'Brien et al. 1987; Packer et al. 1991) have used reduced genetic variation to infer historical bottlenecks due to the absence of previous suitable parameters. To assess the degree of demographic modifications after a volcanic eruption affecting the fossorial rodent *Ctenomys maulinus brunneus* in southern Chile, we present comparative census data. By comparing electrophoretic data from the same 23 presumptive gene loci before and after the bottleneck, we aim to test the hypothesis that bottlenecks lead to predictable decreases in allozyme variation.

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## Material and methods

Field studies were conducted in the austral summer 1986–1987, and 1991–1992, at the type locality of *C. maulinus brunneus* (Río Colorado, Malleco province, Chile, 38° 25′ S, 71° 32′ W; 1,450 m altitude) and in Cordillera Las Raíces, seven km southeast of the topotype locality (Fig. 1). Río Colorado is a flat 4 $\text{km}^2$ high Andean steppe located 3.5 km SW of the Lonquimay volcano. This area sustains a large population of *Ctenomys*, fairly isolated from other local demes by physiographic and vegetational gaps. The Holocenic Lonquimay volcano was dormant until December 1988 when its 50-year period of inactivity was interrupted by a 6-months eruptive phase (Moreno and Gardeweg 1989; Barrientos and Acevedo-Aranguiz 1992).

Pre-eruption estimates of the number of breeding individuals (N) in Río Colorado were obtained from censuses conducted within four grids differing in size, vegetation type, and plant coverage. All animals were removed from the grids, and their reproductive condition was assessed according to Gallardo and Anrique (1991).

Site A: a 50 × 70 m grid on consolidated friable soils which had an 80–90 % cover of bunchgrass interspersed with annual plants. Site B: two grids (40 × 60 m, and 50 × 50 m) on loose volcanic sediments with a 40–50 % cover of annual plants. Site C: a single 60 × 140 m grid on loose volcanic soils which had a 20–25 % cover of annual plants. Field observations confirmed a lack of vegetation from sites B and C owing to the deposition of volcanic ash and scoria following the eruption. There was also a lack of *Ctenomys* activity except in site A where a one hectare grid was sampled in the austral summer 1991.

Pre-eruption estimates of allozymic variation obtained from proteins encoded by 23 loci of 51 pre-eruption specimens from Río Colorado and nine from Las Raíces have been previously reported (Gallardo and Köhler 1992; Gallardo and Palma 1992). The loci assayed were: isocitrate dehydrogenase (ICD-1, ICD-2, Enzyme Commision No. 1.1.1.42), malate dehydrogenase (MDH-1, MDH-2, 1.1.1.37), glutamate-oxaloacetate transaminase (GOT-1, GOT-2, 2.6.1.1), glycerol-3-

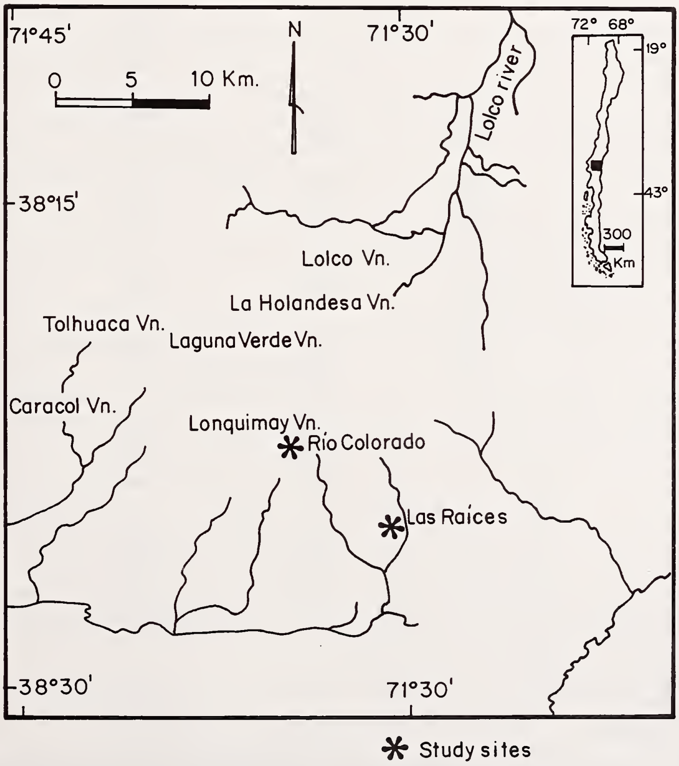

*Fig. 1.* Map of the study areas depicting the volcanoes (Vn.) that form the Lonquimay Volcanic Front in the Andes of southern Chile

*Table 1.* **Changes in gene frequencies of polymorphic loci in two populations of *Ctenomys m. brunneus* affected by the eruption of volcano Lonquimay, Chile**

Pre-eruption data for Río Colorado were obtained from Gallardo and Palma (1992), and for Las Raíces, from Gallardo and Köhler (1992)

| Locus | Río Colorado | | Las Raíces | |
|---|---|---|---|---|
| | Pre | Post | Pre | Post |
| Sample size (n) | 51 | 58 | 9 | 23 |
| ICD-1 | | | | |
| A | 0.020 | 0.000 | | |
| B | 0.980 | 1.000 | | |
| MDH-1 | | | | |
| A | 0.971 | 1.000 | 0.944 | 1.000 |
| B | 0.029 | 0.000 | 0.056 | 0.000 |
| GOT-1 | | | | |
| A | 0.010 | 0.000 | | |
| B | 0.990 | 1.000 | | |
| GPD | | | | |
| A | 0.961 | 1.000 | | |
| B | 0.039 | 0.000 | | |
| Gd | | | | |
| A | | | 0.000 | 0.000 |
| B | | | 0.778* | 1.000 |
| C | | | 0.222 | 0.000 |
| GDH | | | | |
| A | | | 0.000 | 0.000 |
| B | | | 0.889* | 0.000 |
| C | | | 0.111 | 1.000 |
| LDH-2 | | | | |
| A | 0.843* | 1.000 | 0.889* | 1.000 |
| B | 0.157 | 0.000 | 0.111 | 0.000 |
| XDH-1 | | | | |
| A | 0.157 | 0.034 | 0.778 | 1.000 |
| B | 0.647* | 0.026* | 0.000* | 0.000 |
| C | 0.196 | 0.940 | 0.222 | 0.000 |
| PGM-2 | | | | |
| A | 0.814 | 1.000 | 0.444 | 1.000 |
| B | 0.186 | 0.000 | 0.556 | 0.000 |
| PGM-3 | | | | |
| A | 0.059 | 0.000 | 0.000 | 0.000 |
| B | 0.941 | 1.000 | 0.944 | 1.000 |
| C | 0.000 | 0.000 | 0.056 | 0.000 |
| PGI | | | | |
| A | 0.951* | 1.000 | 0.000 | 0.000 |
| B | 0.049 | 0.000 | 0.944 | 1.000 |
| C | 0.000 | 0.000 | 0.056 | 0.000 |
| PGD | | | | |
| A | 0.078 | 0.181 | 0.222 | 0.000 |
| B | 0.902* | 0.793* | 0.000* | 0.000 |
| C | 0.020 | 0.026 | 0.778 | 1.000 |
| Mean Polymorphism | 47.8 % | 17.4 % | 50.0 % | 0.0 % |
| Mean N° Allele/locus | 1.6 | 1.3 | 1.5 | 1.0 |
| Mean Heterozygosity (direct count) | 3.1 % | 0.9 % | 4.3 % | 0.0 % |
| (Hardy-Weinberg) | 8.9 % | 2.8 % | 13.2 % | 0.0 % |

* Genotypes for this locus and population deviate significantly from Hardy-Weinberg expectations.

phosphate dehydrogenase (GPD, 1.1.1.8), glucose 6-phosphate dehydrogenase (Gd, 1.1.1.49), glucose dehydrogenase (GDH, 1.1.1.47), lactate dehydrogenase (LDH-1, LDH-2, 1.1.1.27), xanthine dehydrogenase (XDH), phosphoglucomutase (PGM-2, PGM-3, 2.7.5.1.), glucose isomerase (GPI, 5.3.1.9), phosphogluconate dehydrogenase (PGD, 1.1.1.44), albumin (ALB), transferrin (TRFER), hexokinase (HK, 2.7.1.1), acid phosphatase (ACP-1, ACP-2, 3.1.3.2), and malic enzyme (ME, 1.1.1.40). Fifty eight animals from Río Colorado, and 23 from Las Raíces were live-trapped and screened for the same loci after the eruption. Tissue homogenates, buffer systems, migration conditions and mixtures were prepared according to the methods of Selander et al. (1971). Estimates of expected heterozygosity values were compared to the observed numbers and tested for significance by the nonparametric Wilcoxon two-sample test and by a t-test of arcsin transformed genetic data (Archie 1985). All computations of genetic variation were performed with Biosys-1 (Swofford and Selander 1989).

## Results

Twenty three animals captured in site A gave an estimate of 66 animals/ha. An additional estimate of 35 animals/ha was generated by pooling density data from the two grids in site B, whereas an estimate of 8.3 animals/ha was obtained from site C. Direct estimates of the breeding population size obtained from census data indicated 1930 animals before the eruption. Based on a density estimate of 20 animals/ha after the eruption in site A, the breeding population size consisted of 168 animals, which corresponds to a 91.3 % reduction in population size after the catastrophe. This estimate provided a rough approximation of the effective population size; at best, it was an upper limit, below which Ne decreases depending on departures from idealized structure (Husband and Barrett 1992).

There was a severe loss of electrophoretic variation in both populations following this bottleneck episode (Tab. 1). Mean polymorphism was significantly reduced; it dropped from 47.8 % to 17.4 % in Río Colorado and reached its minimum value in Las Raíces. Eighty percent of previously polymorphic loci in Río Colorado, and all variable loci in Las Raíces became monomorphic after the bottleneck. As theory predicts, the most frequent allele was more likely to become fixed, but the reverse held for loci GDH and PGM-2 in Las Raíces. Similarly, locus XDH-1, although still polymorphic in Río Colorado, changed significantly in frequency after the eruption (Tab. 1).

The difference between the pre- and post-eruption frequency of heterozygotes was highly significant ($P < 0.0056$; Tab. 2). Further indications for rejecting the null hypothesis of equality between initial and final mean heterozygosities were obtained by congruently significant results of angular-transformed data ($P < 0.004$; not shown). No analogous comparisons were conducted in the Las Raíces sample where the final absence of heterozygotes resulted from a generalized monomorphism.

*Table 2.* **Observed pre- and post-bottleneck mean heterozygosity values of polymorphic loci in *Ctenomys maulinus brunneus* (Río Colorado)**

The non parametric comparison of mean values is based on the Wilcoxon two-sample test

| Locus | Pre-bottleneck Heterozygosity | Post-bottleneck Heterozygosity |
|---|---|---|
| ICD-1 | 0.039 | 0.000 |
| MDH-1 | 0.058 | 0.000 |
| GOT-1 | 0.020 | 0.000 |
| GPD | 0.076 | 0.000 |
| LDH-2 | 0.267 | 0.000 |
| XDH-1 | 0.523 | 0.116 |
| PGM-2 | 0.306 | 0.000 |
| PGM-3 | 0.112 | 0.000 |
| PGI-1 | 0.094 | 0.000 |
| PGD | 0.182 | 0.340 |
| HK | 0.179 | 0.144 |
| ACP-2 | 0.179 | 0.051 |
| Total | 0.170 | 0.054 |
| Wilcoxon test: Z = −2.7651 | | P = 0.0056 |

## Discussion

Our estimations of density fall within the range reported for other subterranean mammals (Nevo 1979), implying a direct correlation between number of animals and food supply. Estimates ranging from 3–47 animals/ha in *C. peruanus* (Pearson 1959) to 218 animals/ha in *C. talarum* (Pearson et al. 1968) indicate the large variance of demographic attributes in the genus (Reig et al. 1990).

Theoretically, the major genetic consequence of a bottleneck involves a reduction in the number of alleles, because the variants most at risk are those in low frequency (Chakraborty and Nei 1977). This prediction, supported by our data, reached its maximum expression in the Las Raíces sample. Mean heterozygosity was also affected, especially in Las Raíces where all estimates of genetic diversity reached the most extreme minimum values. Although theory predicts a significant reduction of the number of alleles with less than 10 founders, and even fewer pioneers to affect the average heterozygosity (Chakraborty and Nei 1977; McCommas and Bryant 1990), significant losses in genetic diversity occurred with a larger number of founders, provided a slow population recovery (Lande 1987).

In connection with the genetic effects of demographic bottlenecks, deficiencies in sampling may distort the assessment of heterozygosity levels. Although these estimates appear to be more affected by the number of loci screened than by the number of individuals analyzed (Gorman and Renzi 1979). Considering that the analysis of 8–12 individuals yields, on the average, a heterozygosity estimate within 1 % of the value calculated using larger numbers of individuals, sampling biases can be confidently disregarded in our estimations (Gorman and Renzi 1979). Another possible bias stems from the assumption that losses result from the bottleneck itself (Boileau et al. 1992), with no additional genetic cost because a fast demographic recovery is expected. These predictions result in underestimates of the absolute losses, as *Ctenomys* is a k-strategist exhibiting a low instrinsic growth rate (Reig et al. 1990).

Considering the small period of time that has elapsed since the bottleneck, drastic declines in heterozygosity in relation to expected values probably do not result from consanguineous matings, but from a generalized form of inbreeding associated with limited population size (Chesser and Ryman 1986). In this respect, panmictic conditions do not hold since considerable levels of intrademic genetic differentiation strongly suggest population subdivision (Gallardo unpubl. results). Thus, agonistic behaviour and limited dispersal in *Ctenomys* (Gallardo and Anrique 1991) are not consistent with the assumption of a panmixtic unit of 168 individuals, but support an explanation based on the sustained effects of drift acting on disrupted breeding assemblages.

From a conservation viewpoint, bottleneck-flush cycles are major factors contributing to species vulnerability (O'Brien and Everman 1988). Limited population sizes threaten demic persistence when a threshold density value defining mating success is reached (Lande 1987, 1988). Besides, the genetic uniformity attained through repeated bottleneck events also affects demic survival by inbreeding depression (Packer et al. 1991; Wildt et al. 1987), or by a homogeneous inmunological response to environmental disturbances (O'Brien et al. 1985).

Although current interpretations of genic and chromosomal variation patterns in *Ctenomys* emphasize a causal relationship with spatial components (Reig et al. 1990), sustained vulcanism and the tectonically-derived seismic activity in the Andes heighten a component of temporal stochasticity. In this line, previous eruptions of the Lonquimay volcano took place in 1940, 1887 and 1853 (Moreno and Gardeweg 1989). Assuming similar environmental effects, population survivorship, and a one-year generation time (Gallardo and Anrique 1991) the genetic pool of these, and probably other local populations has been altered in generations 135, 101, and 48 before the present.

While contrasting with the multiple karyotypic forms observed in the low land *Ctenomys* species (Gallardo 1991), the karyotypic uniformity reported for species from the Andes (Gallardo 1979) conflicts with the optimal conditions for chromosomal differentiation that stem from limited population size (Lande 1979, 1985; Wright 1941).

Apparently, chromosomal conservatism may be better explained by recurrent vulcanism for when extinctions and recolonizations are frequent, subpopulation divergence is prevented (Maruyama and Kimura 1980) and new colonies are likely to descend from a single ancestral deme (Wright 1941). Considering that the activity of the nearby volcanoes Antuco, Llaima and Villarrica total 36 eruptive events since 1640 (Veblen 1985), the long-term karyotypic uniformity in Andean *Ctenomys* populations appears to be coupled to the structure of the environment. Furthermore, low levels of genetic variability attained by recurrent catastrophes may imitate an adaptive response to the stable subterranean niche (Nevo 1979, 1990) although no selective pressure can counterbalance the effects of drift when populations recover from precarious levels of genetic variability (Maruyama and Fuerst 1985a, b).

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## Zusammenfassung

*Demographische Veränderungen und Verluste von genetischer Variabilität bei Populationen des grabenden Nagers (Ctenomys maulinus brunneus) als Folge einer Naturkatastrophe*

Es wurden die demographischen und genetischen Auswirkungen eines Vulkanausbruchs auf zwei lokale Populationen (Río Colorado, Las Raíces) des grabenden Nagers *Ctenomys maulinus brunneus* in den Anden untersucht. Ein Vergleich der Populationsgrößen vor und nach dem Vulkanausbruch auf der Grundlage von Zählungsergebnissen in Río Colorado ergab einen Rückgang der Individuenzahlen um etwa 90 %. Die elektrophoretische Untersuchung von 23 Enzymloci zeigte in beiden Beständen eine starke Reduktion der genetischen Variabilität. In Río Colorado sanken die Polymorphierate (P) von 47,8 % auf 17,4 % und der durchschnittliche erwartete Heterozygotiegrad von 8,9 % auf 2,8 %. In Las Raíces sanken P von 50 % auf 0 % und H von 13,2 % auf 0 %. Unsere Daten liefern einen Beitrag zu den wenigen Fällen, in welchen bei natürlichen Populationen Verluste von genetischer Variabilität direkt einem Engpaß in der Populationsgröße zugeordnet werden können. Obwohl die geringe genetische Variation bei grabenden Nagern in der Regel als Anpassung an die stabilen Lebensbedingungen der unterirdischen Nische zugeschrieben wird, kann sie in einigen Fällen lediglich auf genetische Drift zurückzuführen sein.

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