DISMINUCIÓN EN TAMAÑO POBLACIONAL Y ASIMETRÍA FLUCTUANTE EN *OCTODON BRIDGESI* (RODENTIA), TAXÓN ESPECIALISTA DE HÁBITAT

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CAPÍTULO 1

INTRODUCCIÓN GENERAL:

A MORPHOLOGICAL PATH TO EXTINCTION VORTICES[1]

Una vía morfológica para los vértices de extinción

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[1] Para ser publicado como: Saavedra B. A morphological path to extinction vortices.

RESUMEN

El estudio del número mínimo de individuos necesarios para asegurar la sobrevivencia de la población llevó a la proposición de los vértices de extinción. Estos vértices quedan definidos por tres componentes generales que son el ambiente, la estructura y adecuación de la población y el fenotipo poblacional. Éstos contienen a su vez todos los aspectos que deben ser analizados cuando una población enfrenta una reducción en su tamaño poblacional. Entre los componentes fenotípicos, la morfología ha sido escasamente integrada al estudio de estos procesos de extinción. A pesar que ella es un nexo obvio entre el organismo y su ambiente, la cual sufre modificaciones espaciales y temporales que afectan la adecuación biológica. Estudios poblacionales teóricos y empíricos hechos en poblaciones pequeñas normalmente suponen homogeneidad morfológica entre los individuos, ignorando que la variación morfológica puede determinar diferencias en reproducción y sobrevivencia, contribuyendo directa o indirectamente a la persistencia de la población. Aquí propongo la incorporación de la asimetría fluctuante, como un componente morfológico del proceso de extinción, para ser incluida en estudios tanto teóricos como empíricos de viabilidad poblacional.

ABSTRACT

The study of the minimum number of individuals necessary to assure population survival led to the proposition of extinction vortices. These vortices are defined by three general

components: Environment, Population Structure and Fitness, and Population Phenotype that contain the main aspects to be analyzed when a population faces a size reduction. Among phenotypic components, morphology has seldom being integrated to the global analysis of extinction. Morphology is an obvious link among organism and environment that changes in space and time, and affects fitness. Theoretical and empirical population studies on endangered small population, usually assume morphological homogeneity among individuals, ignoring that morphological variation can determine differences in reproduction and survival, contributing directly to overall population's persistence. Here we propose the incorporation of fluctuating asymmetry, as a morphological component of the extinction process, to be included in theoretical as well as empirical studies for population viability.

EXTINCTION VORTICES

Morphology constitutes a significant feature of organisms that has been relevant for the development of significant theories in evolution and ecology (Ricklefs & Miles 1994). Morphology is an obvious link among the organism and its environment, that changes in space and time, influencing individual fitness (Wainwright 1994). Theoretical and empirical population studies on endangered populations usually assume morphological homogeneity among individuals (e.g. Pimm 1991), ignoring that morphological variation can determine differences in reproduction and survival, contributing directly to overall population's persistence. Here, I advance that morphological variation among individuals can determine reductions in reproductive population size, increasing vulnerability to extinction of small and endangered populations.

Combining all factors that can affect population's persistence, Gilpin & Soulé (1986) defined three major components to analyze the vulnerability of small populations: Environment, Population Structure/Fitness, and Population Phenotype. The Environment is characterized by habitat quantity and quality available for the population, and Population Phenotype is characterized by the morphology, physiology or behaviour of the population. Both fields interact and determine Population Structure/Fitness field, that comprehends the dynamic consequences of population structure and environment interactions. When a population faces a size reduction, these components interact synergistically, causing increased instability and more rapid decline in population size, augmenting its vulnerability to extinction. They called these processes the extinction vortices, and defined four vortices that involved populations of reduced size, along with subsequent reductions of effective size and reduced population's growth rate. Population viability analysis are based in these extinction vortices, and have received theoretical (e.g. Soulé 1987), as well as empirical development (e.g. Lindenmayer & Lacy 1995). These vortices have been explicitly used in population management to advance the probability of persistence in time of small populations, and are based on the analyses of identifiable threats to small population's survival (Lacy 2000). Population viability models attempt to make accurate predictions, although they have been considered in general optimistic (Brook 2000, Brook et al. 2000), since they do not include all potential threats that can affect a small population's survival.

Individual phenotype, explicitly suggested as a pivotal field for the persistence of small populations (Gilpin and Soulé 1986), normally has been neglected in studies of extinction (Reed 1999, Lacy 2000). Morphology, the most tangible component of the phenotype field has not been integrated to the global analysis of extinction probability of small populations, a fact reflected in the null representation of morphology in theoretical and simulation models that examine the fate of small populations (Lacy 2000). The definition of morphology as a static attribute, "that can be stored in museums" (Gilpin and Soulé 1986), probably lead to the overlooking of the role this property can play in the extinction process of endangered populations. Nevertheless, morphology varies, changing among individuals and populations. This variability can affect not only individual destiny in the short term, but also long lasting persistence of small populations.

FLUCTUATING ASYMMETRY

The morphology of an individual can be characterized by its asymmetry. In bilateral organisms, the ideal pattern corresponds to perfect symmetry (Van Valen 1962). There are several deviants from this ideal design, which have been described as directional asymmetry, antisymmetry and fluctuating asymmetry (Van Valen 1962, Palmer 1996). Fluctuating asymmetry (FA) is one ubiquitous asymmetry determined by small random deviations in size or number among left and right sides of an individual. FA has been regarded as a comprehensive variable that contains information related to genetic quality, along with environmental condition of populations (Parsons 1992, Nosil & Reimchen 2001), with elevated levels of FA associated with reduced genetic variability and environmental quality (Møller & Swaddle 1997). Lower genetic variability determines an imperfect control of developmental processes, increasing FA (e.g. Mitton 1978, Handford 1980, Mitton & Grant 1984). Along with genetic stress, stressing environments also trigger defective development, with consequent increments in FA (Leary & Allendorf 1989, Parsons 1990, Manning & Chamberlain 1994). FA is used as a cue in intersexual encounters as an indicator of individual quality, and mate selection favors those individuals that show lower FA (e.g. Møller 1992, Swaddle & Cuthill 1994, Møller & Eriksson 1995). In cases where FA mediates sexual selection, mating is not random and asymmetric individuals achieve lower fitness (Møller 1992, 1995, Watson & Thornhill 1994). Consequently, viability analyses that do not acknowledged interindividual differences in morphology assuming random mating, may overestimate reproductive size of small populations. Additionally, asymmetry can affect individual performance, reducing ability to escape form predators, or to acquire food resources. Asymmetric individuals can face reduced survival through an increment of predation or parasitism, or lower competitive success compared to more asymmetrical individuals (Rettig et al. 1997, Martín & López 2001).

Fragmentation is an environmental change that conveys the loss of habitat quantity and decrease habitat quality (Saunders et al. 1991, Murcia 1995). These negative effects are differentially addressed by species, pending on the affinity of the taxon to the original and non-fragmented habitat. The stronger the dependence with the original habitat, the higher the negative effects that fragmentation can have on remnant populations, with consequent increments in FA. Habitat specialist should address elevated levels of FA due to fragmentation compared to generalist taxa.

Morphology, asymmetry and population persistence

Small populations that survive in fragmented habitats are far to behave as ideal genetic populations, and normally do not satisfy ideal populations demands like random mating, equal sex ratio, constant population size, and an equal probability for all adults to contribute offspring to the next generation (Frankham 1995). Those species that face population reduction, along with habitat deterioration, may achieve elevated levels of FA. Asymmetry increments may affect individual's fitness via mate acquisition, or via survival reduction. In the first case, differences in mating probability could be reflected in the parental contribution to the next generation, through the increment of variance in reproduction. This would generate an unequal contribution of gametes to the next generation, with the consequent decrease in population reproductive size. Secondly, elevated FA may reduce total population size, produced by the diminished survival capacities of asymmetrical individuals. The direct consequence of these modifications involve the raising of vulnerability to extinction of small populations, which are in elevated threat due to other stochastic and deterministic factors, like environmental or demographic stochasticity (Caughley 1994). This can constitute a morphological path to the four extinction vortices proposed by Gilpin & Soulé (1986).

Explicitly including morphology in the analysis of extinction of small populations can have implications for viability population analysis. First, morphology should be explicitly incorporated to population viability models, as a regulatory parameter of population demography for example, adding realism to theoretical simulations that are used in management of endangered species (e.g. Lacy 2000). Those populations with elevated FA should be considered more vulnerable, and therefore should be at elevated extinction risk (e.g. Lens & Van Dongen 1999, Lens et al. 1999, 2002). Secondly, asymmetry might be used to assess quality of small populations. The explicit incorporation of asymmetry analysis in fragmented habitats, can become a non-expensive tool to assess population's quality in remnant habitats (e.g. Lens et al. 2002). These analyses should be directed to a suite of species, mostly represented by habitat specialists. Also, temporal analysis of asymmetry patterns would allow the assessment of long term effects of population declining. The analysis of archaeozoological or museum specimens, can help to establish original levels of population quality, and this information can be useful for managing and restoration programs.

Morphology constitutes pivotal feature in biology that has served as foundation substrate for the most significant biological and ecological theories, like natural selection (e.g. Brown & Wilson 1959), or competition theory (e.g. MacArthur & Levins 1967). Morphology is also related to other phenotypic components like behaviour, and can constitute a convergent point to address small population's extinction studies. I propose that morphology can represent a significant connection for components of population's phenotype that can be explored from a theoretical perspective, as well as an empirical avenue in the analysis of small populations from a conservation standpoint of view.

Extinction is a process that affects global patterns of species distribution, whose changes are triggered by diverse factors that occur at different spatial as well as temporal scales. Consequently, a complete investigation of this process should combine information regarding long-term population's characteristics, as well as short-term ecological analysis. This would permits the elucidation of diverse factors, and their interactions, that could have participated in the extinction process.

The case of *Octodon bridgesi*

The reduction of geographic range is a form of the extinction that involves the disappearance of populations (Soulé 1983). *Octodon bridgesi*, an acknowledged dense cover specialist, suffered a reduction of 100 km in their northern range during Late Holocene (Chapter 2), due to the extinction of their northernmost populations. Currently, *O. bridgesi* lives in a highly altered habitat, dominated by exotic *Pinus radiata* plantations, where small remnants of native forest are scattered (Chapter 3). Based on these peculiarities, *O. bridgesi* has been considered a vulnerable species, that should face extinction, unless causal factors that modified their habitat and reduce their population size are eliminated (Glade 1988).

Historical reduction in population size of this species (Chapter 2), along with its present existence in a particularly modified habitat (Chapter 3), should be observed as increments in FA pattern of extant population of *O. bridgesi*, compared to ancient taphocenosis of this taxon (Chapter 4). This historical reduction in geographic range should also be observed through the historical analysis of population demography of extant populations, that should acknowledge reductions in population size in their genealogical relationships (Chapter 4). Finally, if FA asymmetry can pose a threat to the population survival of vulnerable populations, it should affect individual's ability to reproduce or to survive (Chapter 5). Particularly, asymmetric individuals should be avoided in mating selection, decreasing their probability to leave descendants. These aspects are all evaluated in the following chapters, and constitute the first assessment of the role FA can play in the maintenance of small and endangered populations.

CAPÍTULO 2

HOLOCENE DISTRIBUTION OF OCTODONTID RODENTS IN CENTRAL CHILE[2]

Distribución Holocénica de roedores Octodóntidos en Chile central

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[2] Para ser publicado como: Saavedra B & JA Simonetti. Holocene distribution of Octodontid rodens in central Chile.

RESUMEN

Describimos la distribución Holocénica de Octodóntidos (*Aconaemys fuscus, Octodon bridgesi, O. degus, O. lunatus, O. pacificus* and *S. cyanus*) en Chile central, comparándola con la distribución actual. El patrón de distribución Holocénico se infirió de registros zooarqueológicos. *Octodon degus, Octodon lunatus, Octodon bridgesi*, and *Aconaemys fuscus* muestran una reducción en su rango geográfico. A pesar de que los mecanismos específicos que explican este patrón permanecen sin ser resueltos, la perturbación humana parece ser el factor distal que explicaría la reducción en el rango de distribución para algunas de estas especies.

ABSTRACT

We describe Holocene distribution of Octodontids (*Aconaemys fuscus, Octodon bridgesi, O. degus, O. lunatus, O. pacificus* and *S. cyanus)* in Central Chile, comparing Holocene with present day distribution. Holocene pattern was inferred from zooarchaeological records. *Octodon degus, Octodon lunatus, Octodon bridgesi*, and *Aconaemys fuscus* showed a reduction in their geographic range. Although specific mechanisms remains to be tested, human disturbance to the habitat seems to be the distal factor that explains reduction in range for some of these taxa.

INTRODUCTION

Octodontids represent a conspicuous group among Chilean rodents (Contreras et al. 1987, Gallardo & Kirsch 2001). As a result of a long evolutionary history in southern South America, this taxon gathers 11 endemic species, six of which occupy central Chile: *Aconaemys fuscus, Octodon bridgesi, O. degus, O. lunatus, O. pacificus* and *Spalacopus cyanus*. These taxa are currently distributed from 27°S to 38°S, mostly in the region of Mediterranean climate of Chile (Contreras et al. 1987). Octodontids use different habitats, like *O. lunatus* and *O. bridgesi* that preferentially inhabit dense vegetation, or *O. degus* that prefer more open shrublands (Contreras et al. 1987, Simonetti 1989a, Muñoz-Pedreros 2000). Despite being a comparatively well known group, several aspects of their ecology and distribution remain unresolved, a fact reflected in the wealth of new distributional records of these taxa (e.g. Hutterer 1994, Podestá et al. 2000, Díaz et al. 2002). The state of knowledge is even worse for the paleoecology of these taxa, since scarce knowledge of past distribution and abundance of Octodontids exists (Simonetti 2000).

Human activities might have affected population's persistence of several Octodontid species, determining local extinction in late Holocene and historical times. *Octodon bridgesi* for example, disappeared from the Andean range in central Chile due to habitat clearance for horticultural development (Simonetti 1989a, 1994). It also went extinct in the coastal range due to local intensification of agriculture in areas previously unused by local farmers (Simonetti & Saavedra 1998). The current absence of *O. bridgesi* in north-central Chile was then achieved only recently, as a result of local extinction driven by human activities.

Changes in geographic distribution have been also reported for other Octodontids. *Aconaemys fuscus* for instance, currently confined to the southern Andes, ca. 1,000 years ago inhabited areas close to Santiago, more than 100 km north of its current distribution (Simonetti & Saavedra 1994). On the same vein, *O. lunatus* and *O. degus*, currently restricted to central Chile, were found at least 50 km south of their current distribution in archaeological sites dated 1,000 years old (Saavedra et al. 1991).

These evidences suggest that present-day distribution for Octodontids was achieved recently. As wealth of new information is available, here we describe the Holocene distribution of Octodontid in central Chile, based on published and new zooarchaeological records, aiming to illustrate their geographic range dynamics, in order to sustain the claim that present-day Octodontid assemblages are a recent phenomenon.

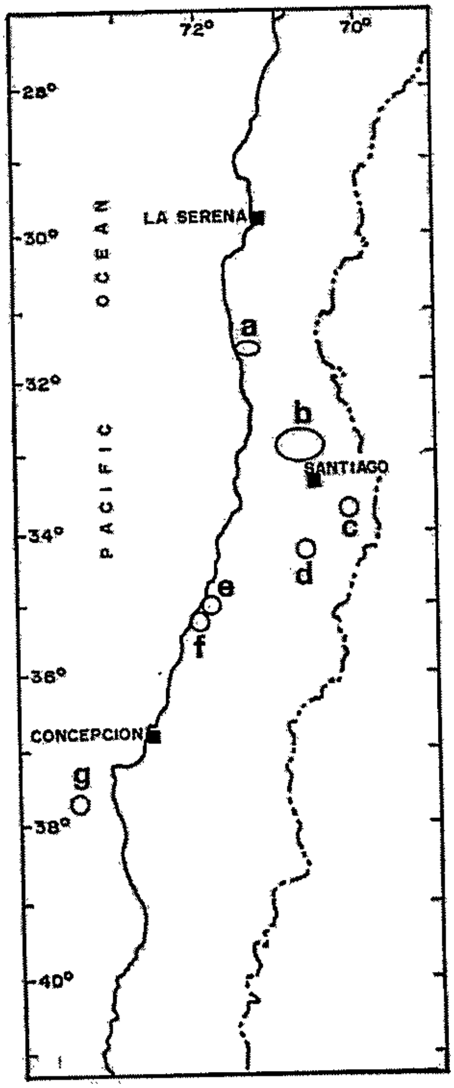
METHODS

Holocene distribution was inferred for the six Octodontids that currently inhabit central Chile: *Octodon degus, O. lunatus, O. bridgesi, O. pacificus, A. fuscus* and *S. cyanus*. Their distribution was inferred based on zooarchaeological composition of 12 new recorded archaeological sites, and seven published archaeological sites (Saavedra et al. 1991, 2002, Simonetti 1994, Simonetti & Saavedra 1994, 1998). All sites were excavated using regular archaeological methods, and rodent analysis was made based on usual identification keys (e.g. Reise 1973, Pearson 1995), as well as comparison with reference material. For descriptive purposes, we present archaeological sites arranged in seven areas that are distributed longitudinally, from Huentelauquén in the north, to Isla Mocha in the south (Fig. 1). For each site, we recorded Octodontid composition. Due to the scarcity of zooarchaeological records in Chile, we also include information regarding other Caviomorphs found in new sites, although this data is not analyzed here.

New zooarchaeological information was recovered from: 1) Huentelauquén (31°38' S-71°33' W, Fig. 1), located in the northernmost portion of central Chile. Here we report the zooarchaeological content of site "04. Mi. Hue. 2". This is an Early Holocene site dated 9,110 - 8,800 years BP (Weissner et al. 2000), where 2,962 bone specimens were retrieved. From these, 752 (25.4%) were small mammals, and *O. lunatus, O. degus*, and *S. cyanus* were found. *Abrocoma bennetti* and *Lagidium viscacia* were the other caviomorphs found in the site. 2) La Granja (34°24' S-71°11' W), located 100 km south of Santiago (Fig. 1). Bone material was recovered from three archaeological sites: "La Granja 1", "La Granja 2", and "La Granja 3", excavated during 1993-1995 (Planella & Tagle 1998). These sites dated in 1,400 – 975 years BP. A total of 5,249 bone specimens were recovered, comprising 1,928 rodent (36.7%). Octodontids detected were *A. fuscus, O. degus, and S. cyanus.* Other Caviomorphs were *A. bennetti* and *Myocastor coypus*. 3) Chanco (35°43' S - 72°29' W) is a coastal area in the southern margin of the Mediterranean zone (Fig. 1). Three sites were analyzed: "Punta La Gaviota", "Cerro Las Conchas", and "Conchal Valenzuela", dated in 5,685 - 500 years BP (Gaete et al. 1992, Gaete & Sánchez 1993, Sánchez & Gaete 1993). A total of 474 bone specimens contained 128 (27%) rodents. *Aconaemys fuscus* was the only Octodontid present in this site. Other species here were *M. coypus* and *A. bennetti.*

Among published zooarchaeological records we included: 1) Cordón de Chacabuco, located 70 km north of Santiago (32°59' S - 70°42' W, Fig. 1). Here, five archaeological sites were excavated: "Las Chilcas 1", "Las Chilcas 2", "Piedra El Indio", "El Carrizo", and "La Nogalada" (Hermosilla & Saavedra 2000), dated 2,830 to 160 years BP. Octodontids

FIGURE 1. Geographic location of archaeological areas included in this analysis. Letters are: a) Huentelauquén, b) Cordón de Chacabuco, c) El Manzano, d) La Granja, e) Quivolgo, f) Chanco and g) Isla Mocha. Size of the circles indicates differences in number of sites. Major cities are denoted by black boxes.



included *A. fuscus, O. bridgesi, O. degus, O. lunatus,* and *S. cyanus.* 2) El Manzano (33°16' S - 70°37' W), located in the Andean range close to Santiago (Fig. 1), where two archaeological sites ("La Batea 1" and "El Manzano 1") were excavated (Simonetti 1989a, 1994, Saavedra et al. 1991, Simonetti & Saavedra 1994). These sites have a chronology from 8,900 up to ca. 500 years BP. Octodontids recorded were *A. fuscus, O. bridgesi, O.*

lunatus, O. degus, and *S. cyanus.* 3) Quivolgo (35°19' S - 71°24' W), a coastal location at the mouth of Maule River, where the site "07Co24" was excavated (Saavedra et al. 1991, Simonetti 1994, Fig. 1). Here five Octodontids were recognized: *A. fuscus, O. bridgesi, O. lunatus, O. degus,* and *S. cyanus.* 7) Isla Mocha, is the single off-continental area analyzed (38°22' S - 73°3' W, Fig. 1). Four sites were excavated: "P5-1", "P22-1", "P25-1", and "P31-1". *Octodon pacificus* was the only Octodontid found in these remains (Quiroz & Sánchez 1993, Saavedra et al. 2002, see Anexo 3).

Zooarchaeological remains covered almost all the Holocene, including sites from Early Holocene (e.g. Huentelauquén: ca. 9,000-8,000 years BP), to Late Holocene (e.g. La Granja 1: ca. 1,200-500 AD), as well as recent historical times (e.g. Piedra El Indio: ca. 500 years BP). Length of human occupation varied among sites, ranging from 7,400 years (e.g. El Manzano 1), to less than 300 years (e.g. La Granja and Isla Mocha sites). To pursue our analysis, only the pattern of presence/absence of a taxon was considered, ignoring changes in the abundance of bone remains (Reitz & Wing 1999).

RESULTS

Six Octodontids were recorded during the Holocene in central Chile. Although the same species are observed today in the area, significant reductions in geographic range were detected for four of these taxa. Among *Octodon, O. degus,* currently the most abundant Chilean caviomorph, showed an extended latitudinal range during this period (Fig. 2). Until 1,000 years BP, its southern limit was found in Quivolgo, extending its current distribution ca. 50 km south. *Octodon lunatus* was also found in this site also, ca. 155 km south of its present distribution, representing a change of at least two degrees south during Holocene

(Fig. 2). *Octodon lunatus* was present in Quivolgo at least until ca. 1,000 years BP (Saavedra et al. 1991). This species is now restricted to the coastal range of central Chile from Fray Jorge (30°39' S - 71°40' W) to Quilpué (33°03' S - 71°26' W), and presumably in the Andes close to Santiago (33°46' S - 70°27' W, Fig. 2). During most of the Holocene, *O. bridgesi* reached up to 33°S, and was recorded in El Manzano, Las Chilcas and La Granja (Fig. 2). Currently, *O. bridgesi* is restricted to the southern portion of central Chile, depicting a reduction of 100 km in their northern range. Finally, the presence of *O. pacificus* in all archaeological sites analyzed in Isla Mocha, indicates its presence in the island during Holocene. This species was captured once in 1959 (Hutterer 1994), and no other record has been registered again, despite intensive trapping efforts over the last decades (Pefaur & Yáñez 1980, Saavedra et al. 2002, see Anexo 3).

Changes in distribution also modified patterns of sympatry among Octodontid species. *Octodon degus* and *O. bridgesi* overlapped during the Holocene. Co-occurrence was observed in six out of 19 archaeological sites. *O. lunatus* and *O. bridgesi* also showed co-occurrence during the Holocene, and were found together in six sites. In Quivolgo, the archaeological coexistence of the three continental *Octodon* species was acknowledged for the first time (Saavedra et al. 1991). Currently, *O. degus* and *O. bridgesi*, as well as *O. lunatus* and *O. bridgesi* are allopatric species (Contreras et al. 1987).

Aconaemys fuscus also showed a significant range reduction in their northern distribution during Holocene. During early Holocene, *A. fuscus* occupied Andean areas close to Santiago, along with coastal sectors of the Maule River (Fig. 2). This species was also found in Tagua-Tagua records (34°30' S – 71°10' W), dated ca. 10.000 years BP (Simonetti 1989b). Currently, *A. fuscus* is mostly confined to southern Andes from Curicó to Temuco (38°44' S - 72°35' W), reaching the coast near Concepción. Our findings imply

FIGURE 2. Holocene and present distribution of *Octodon degus, O. lunatus, O. bridgesi* and *O. pacificus* in central Chile, inferred from zooarchaeological and literature analysis, respectively.

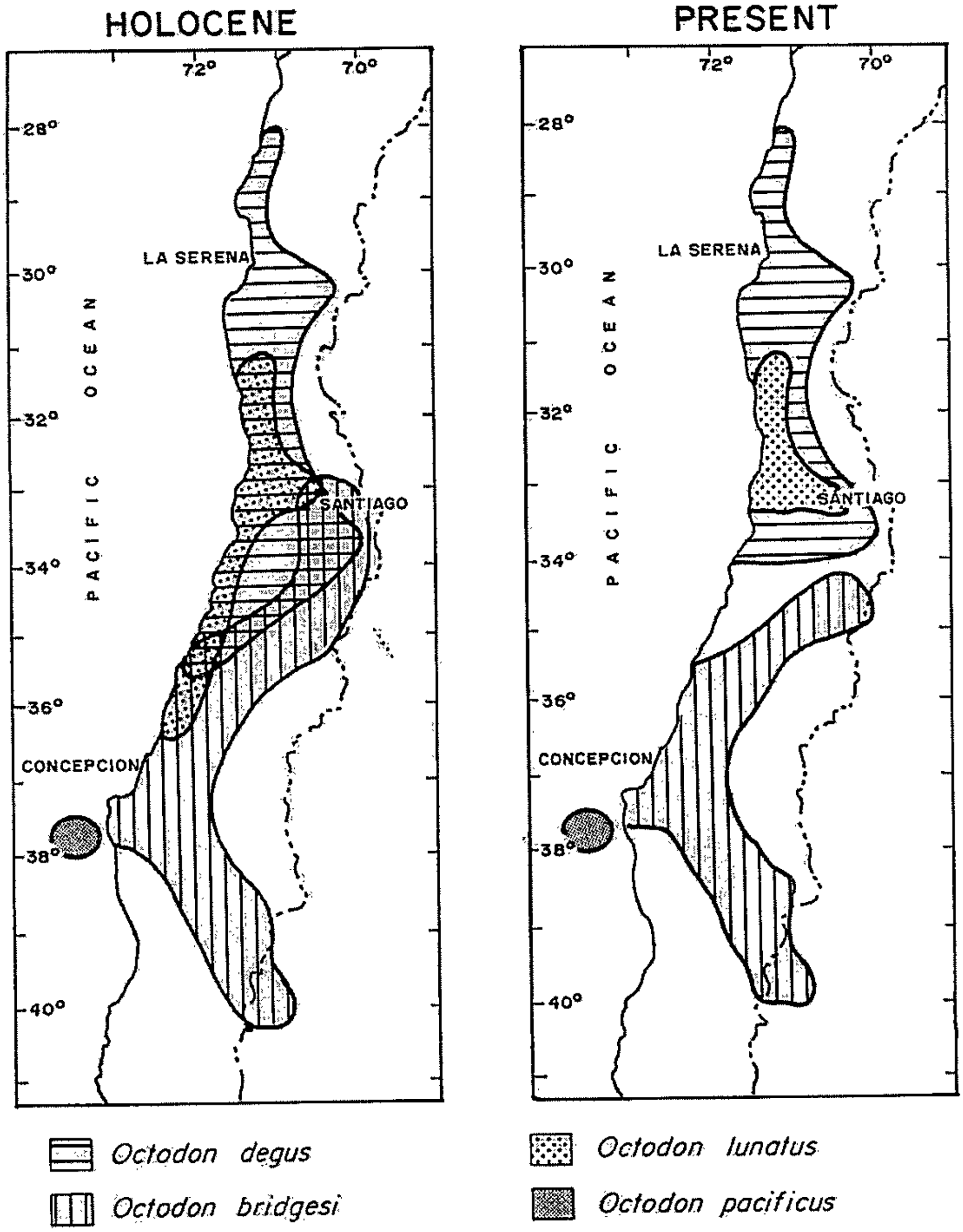
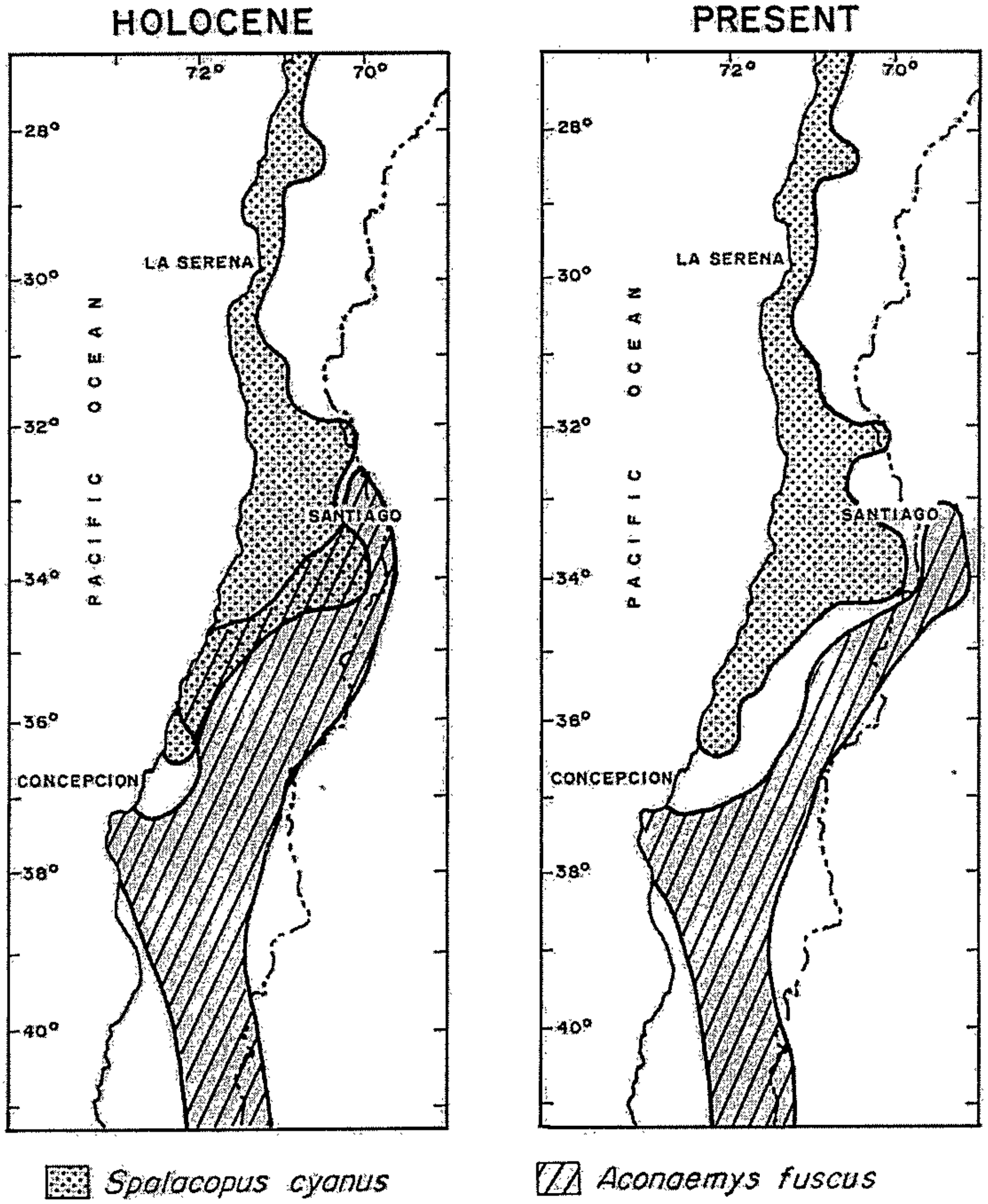


FIGURE 3. Holocene and present distribution of *Spalacopus cyanus* and *Aconaemys fuscus* in central Chile inferred from zooarchaeological and literature analysis, respectively.



a reduction of ca. 120 km in their northern limit.

Spalacopus cyanus is the only Octodontid that did not show significant modification in its distribution range during Holocene compared to its present day one (Fig. 3). During Holocene, *S. cyanus* was distributed from Huentelauquén to Quivolgo along the coast, and in the Andean portion near Santiago. The same distribution is observed today for the species (Fig. 3). Stratigraphical co-occurrence of *A. fuscus* and *S. cyanus* was observed in six out of 19 sites. No coexistence is observed today for these species (Contreras et al. 1987).

DISCUSSION

Four out of six Octodontid species show reductions in their geographical range in the recent past in central Chile. Human activities have been suggested as the cause of regarding local extinction of *O. bridgesi* in the Andes and in the coastal range close to Santiago (Simonetti 1989a, Simonetti 1994, Simonetti & Saavedra 1998). In the Andes of central Chile, local horticulturalist reduced vegetation cover ca. 1,500 years ago to obtain agricultural lands, determining the disappearance of *O. bridgesi*, a dense vegetation specialist, from the area (Simonetti 1989a). The same habitat reduction was drive in coastal range in central Chile ca. 200 years ago, due to the development of intense wood cutting and wheat production, triggering the local extinction of this taxon (Simonetti & Saavedra 1998). Local extinction in the Andean sites was preceded by changes in the relative abundance of the generalist *Octodon degus* and *O. bridgesi* in stratigraphical (i.e. temporal) sequences. While *O. degus* became progressively more abundant in recent times, *O. bridgesi* became scanty, coupled to the historical reduction of vegetative cover (Simonetti 1989a).

Although central Chile has been characterized by a long history of human presence (Aschmann 1991), local extinction observed for other Octodontid species can not be directly associated to human disturbance. *Octodon degus* for example, uses preferentially habitats with low vegetation cover, being regularly found in human-modified habitats (Mann 1978, Meserve et al. 1984). Based on habitat preferences, *O. degus* should have been favored by human-induced changes in habitat cover. Nevertheless, *O. degus* showed a reduction in its southern limit, where elevated human disturbance has been also recognized (Miller 1980). Interestingly, *A. fuscus* experienced range reduction during Holocene. Due to its fossorial habits, habitat destruction by domestic cattle has been advanced as a causal factor to explain its range reduction (Muñoz-Pedreros 2000). Nevertheless, *S. cyanus* is also a fossorial taxon that did not acknowledge this disturbance in their geographic range, suggesting that human activities do not have equivalent effects on the persistence of different species. Factors like climate seem not to be important in explaining Holocene rodent dynamics. Most changes in species distribution occurred in the last 1,500 years, where no significant alterations in climate are registered (Villagrán & Varela 1990, Villagrán 1994).

Geographic reduction of Octodontis occurred in all cases due to extinction of border populations: southern limit for *O. degus* and *O. lunatus*, and northern limit for *O. bridgesi* and *A. fuscus*. This may be explained based on small population size and non-optimal habitats associated to marginal populations (Brown 1984). Also, since five out of six Octodontids analyzed here are of conservation concern (Miller et al. 1983), the understanding of range reduction may help to stop future declining of these populations. Human disturbance has been an important factor in determining the persistence and extinction of local populations in central Chile throughout the Holocene, including historical times (Miller 1980). Therefore, the study of specific mechanisms associated to this range reduction may help to stop further declining in these populations.

Timber extraction, forestry, or livestock grazing has been developed in central Chile more intensively than in other area of the country (Miller 1980). Other human-induced disturbances like introduction of exotic predators and competitors like the black rat (*Rattus rattus*), rabbits (*Oryctolagus cuniculus*), or goats (*Capra hircus*), might also have negative effects on native Octodontids (Simonetti 1983, Jaksic 1998). Introduced goats for example, reduced vegetation cover by consuming native vegetation. This reduction favors the presence of *O. cuniculus*, which also feed on native vegetation, reducing overall food and habitat resources for native species like *O. degus*, and probably reducing its abundance (Simonetti 1983).

Concurrent with the total decline of geographic range, native Octodontids experience the fragmentation of their populations. Remnant populations are smaller and more isolated, jeopardizing population persistence. Considering historical changes depicted here, it is possible to predict the imminent disappearance of *O. lunatus*. Geographic range of this taxon is now entirely confined to central Chile, where the lack of protected and undisturbed areas is critical (Cofré & Marquet 1999, Simonetti 1999). Although *O. bridgesi* found refuge in southern forests, on the east side of Andes (Podestá et al. 2000), populations are small and do not assure long term persistence. If deforestation continues with the present acceleration, the species will probably disappear from the mayor portion of its west distribution.

Holocene records for Octodontids evidence the elevated dynamism of Chilean rodent assemblages. Present-day patterns of rodent distributions have been achieved very recently, differing from past arrangements. Although human presence can explain some of these changes, specific research must be directed to understand the overall pattern for Octodontid species distribution during the Holocene, as well as today. Moreover, these vicissitudes must be acknowledged every time global faunal analysis are made. Compared to other Mediterranean areas, small mammals of central Chile are regarded as poor in species richness (e.g. Glanz 1977). Acknowledging the fact that present assemblages are very recent, and have been mostly shaped by human-associated factors, intercontinental comparisons should include species recently extinct like *O. bridgesi* and *A. fuscus* (Simonetti 1994). This long-term perspective should also be applied when population surveys are developed for elaborate evolutionary, conservation, and management analysis.

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CAPÍTULO 3

SMALL MAMMALS OF MAULINO FOREST REMNANTS, A VANISHING ECOSYSTEM OF SOUTH-CENTRAL CHILE[3]

Pequeños mamíferos en remanentes de bosque Maulino, un ecosistema que desaparece del centro-sur de Chile

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[3] Para ser publicado como: Saavedra B & JA Simonetti. Small mammals of Maulino forest remnants, a vanishing ecosystem of south-central Chile.

RESUMEN

El bosque Maulino localizado en la región costera de Chile centro-sur ha sido severamente alterado por intensa actividad humana. En la actualidad, el paisaje está dominado por grandes extensiones de pino insigne, donde se encuentran inmersos remanentes de bosque nativo. Aquí evaluamos las consecuencias de la fragmentación del bosque Maulino y del reemplazo del hábitat por plantaciones exóticas sobre la fauna de pequeños mamíferos. Describimos características del hábitat, la composición y abundancia de ensambles de pequeños mamíferos en bosque continuo y fragmentado, además de plantaciones de *Pinus radiata*. Comparamos condición corporal y poblacional entre hábitats, además de evaluar movimientos entre hábitat nativo y exótico. Encontramos mayor riqueza específica en el bosque continuo, la que incluyó *Abrothrix longipilis, A. olivaceus, Oligoryzomys longicaudatus, Irenomys tarsalis, Geoxus valdivianus, Rattus rattus, Octodon bridgesi, Thylamys elegans,* y *Dromiciops gliroides*. Encontramos mayor abundancia de micromamíferos en bosque fragmentado y plantaciones de pino, donde *A. longipilis, A. olivaceus, O. longicaudatus*, y *T. elegans* dieron cuenta del 80% del total de capturas. La condición de los individuos y de la población no se afectó por la fragmentación y reemplazo de hábitat, a pesar que atributos de microhábitat variaron entre fragmentos. La fragmentación del bosque Maulino parece tener un impacto significativo en la riqueza de pequeños mamíferos, amenazando la persistencia de taxa raros. Prácticas de conservación y manejo se discuten para proteger este ecosistema altamente alterado.

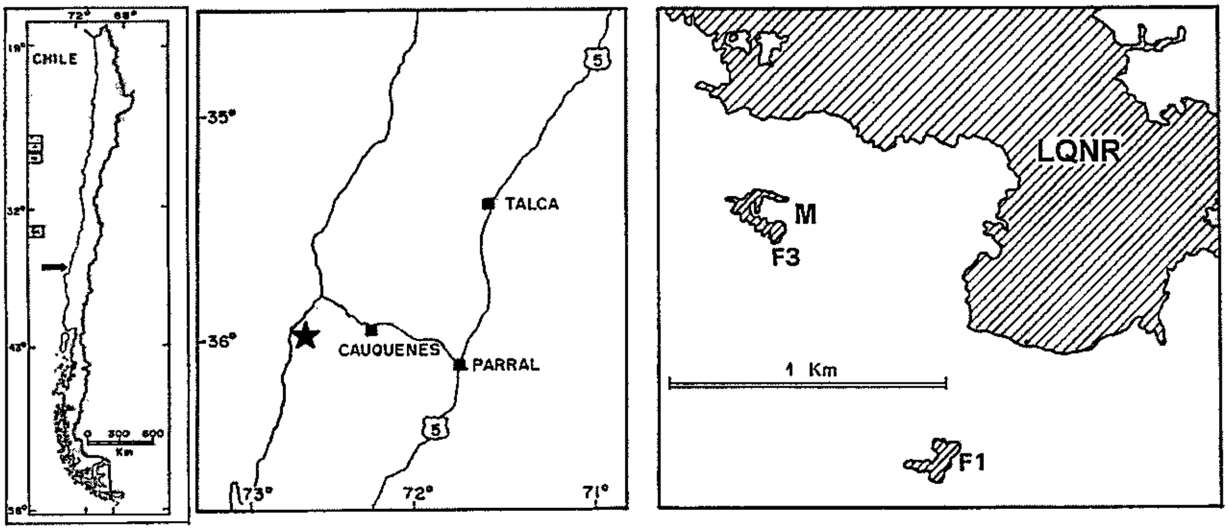
ABSTRACT

The Maulino forest is located at the coastal range of south central Chile, has been severely disrupted by intense human activities. Currently, landscape is dominated by large extensions of plantations of Monterrey pine, where remnants of native forest are immersed. Here, we assess consequences of Maulino forest fragmentation and habitat replacement upon small mammal fauna. We describe habitat characteristics, small mammal's composition and abundance in fragmented and continuos forest, but also in *Pinus* plantation. Population and body condition was compared among habitats, along with movements among native and exotic habitat. Higher species richness was found in continuos forest comprising *Abrothrix longipilis, A. olivaceus, Oligoryzomys longicaudatus, Irenomys tarsalis, Geoxus valdivianus, Rattus rattus, Octodon bridgesi, Thylamys elegans*, and *Dromiciops gliroides*. Higher abundance was observed in fragmented forest and *Pinus* plantations, where *A. longipilis, A. olivaceus, O. longicaudatus*, and *T. elegans* accounted for 80% of total captures. Population and individual condition were not affected negatively by fragmentation and habitat replacement, although habitat characteristics differed among surveyed habitats. Fragmentation of Maulino forests seems to have a significant impact on overall small mammal's richness, menacing the persistence of rare taxa of small mammals. Conservation and management practices are discussed to protect this highly endangered habitat.

INTRODUCTION

The Maulino forest is a unique deciduous forest located in the coastal range of south-central Chile (Fig. 1, 35°55'S-36°20S). This forest harbors a suite of endemic and relict taxa, such as populations of the tree *Gomortega keule*, the only living species of the monotypic family Gomortegaceae (San Martín and Donoso 1995). Among small mammals, the Maulino forest embraces populations of *Dromiciops gliroides*, the single representative of the Order Microbiotheridae*;* *Irenomys tarsalis* and *Geoxus valdivianus*, the single species of sigmodontine genera endemic to the temperate forests of southern Chile and Argentina (Redford and Eisenberg 1992), and *Octodon bridgesi*, the single *Octodon* species found in southern forests. These species are typical components of a more southern

Fig. 1.- Location (star) of fragments of Maulino forest surveyed for small mammals. Shaded area corresponds to native forest: LQNR, National Reserve Los Queules; F1, Fragment 1; F3, Fragment 3; M, *Pinus radiata* Matrix.



Valdivian fauna (Osgood 1943), revealing that they attain their northernmost populations at the more mesic Maulino forest (Saavedra and Simonetti 2000, 2001).

Forest at the coastal range have been severely disrupted by intense human activities, including forest clearing for agricultural purposes, logging and currently, replacement of natural vegetation by commercial plantations of exotic tree species. These activities have resulted in a massive reduction and fragmentation of the Maulino forest (Lara et al. 1995). Areas formerly covered by Maulino forests are currently dominated by large extensions of plantations of Monterrey pine (*Pinus radiata*). Remnants of the native forest are immersed in this exotic matrix, scattered in a highly fragmented pattern (San Martín and Donoso 1995; Bustamante and Castor 1998). Similar to the Tumut Fragmentation Experiment in Australia (Lindenmayer et al. 1999), the landscape in south-central Chile contains small islands of native vegetation in a sea of Monterrey pines. However, the consequences of forest fragmentation and replacement for the biota have been scarcely addressed (e.g. Estades and Temple 1999).

Although small mammals are able to thrive in exotic plantations, few taxa use this habitat compared to native shrublands (Muñoz and Murúa 1990; Muñoz-Pedreros et al. 1990). In fact, species richness is higher in native forest compared to *Pinus* plantations, despite the scarce existence of native remnants. Higher habitat complexity, determined primarily by the availability of refugia due to the presence of a well developed understory in native forest compared to exotic plantations, is presumed to explain this pattern (Muñoz and Murúa 1990). The effect of forest fragmentation *per se* upon the diversity and abundance of Chilean small mammals has been assessed only for Valdivian forest, where no association among species richness and abundance to fragment size is found (Kelt

2000). Frequent disturbance, and limited habitat diversity were advanced to explain this lack of relationship (Kelt 2000). Unfortunately, small mammal's presence in the surrounding matrix, or the capacity of mammals to move among fragments was not assessed in Valdivian remnants. Moreover, generality of these findings remains to be assessed.

Here, we estimate the consequences of forest fragmentation upon small mammal fauna of Maulino forest. First, we describe microhabitat characteristics of continuos and fragmented native forest, and also from *Pinus* plantations. Then, we assess whether forest fragmentation impinges upon the richness of small mammals. Based on classical biogeography theory, we expect to find richer assemblages in larger and continuous forests, and depauperate ones in small forest fragments, as well as in the pine matrix surrounding them. With this information, we describe small mammal's assemblages, as well as habitat availability in continuous, fragmented and *Pinus* matrix. At the population level, we assess potential changes in population size, and reproductive status comparing small mammals' populations among continuous forests, fragments and a *Pinus* plantation. If fragments and matrix are low quality or stressful habitats, populations ought to be comprised by individuals of diminished biological conditions, less abundant and exhibiting lower reproductive success. Furthermore, we explored whether forest fragmentation is in fact perceived as an habitat disruption by the small mammals, testing whether small mammals move from remnants of native vegetation into the surrounding matrix of pines. If this "sea of pines" is an inhospitable habitat, small mammals ought to be restricted to patches of native vegetation, suffering from encroachment at the fragments compared to those surviving in continuous forest.

MATERIAL AND METHODS

Study site. We performed our faunal survey in Los Queules National Reserve (35°59'S-72°41'W, 540-570 m.a.s.l.), and surrounding forest fragments in the Coastal range of south central Chile. A large tract of forest is 600 ha, the last piece of continuous Maulino forest, shelters Los Queules National Reserve (LQNR hereafter), a 145 ha conservation unit. Native forest is surrounded by *Pinus radiata* plantations, where several small remnants of native forest are immersed (Fig. 1). Continuous forest, along with forest remnants, are typical Maulino forest, with *Nothofagus glauca, Aextoxicum punctatum, Cryptocarya alba, Gevuina avellana* and *Persea lingue* as dominant tree species (San Martín and Donoso 1995). Diversity and abundance of the mammalian fauna was assessed at LQNR, and two nearby fragments: one 3 ha (Fragment 3, 35°59'S-72°41'W, 570 m.a.s.l.), and another of 6 ha fragment (Fragment 1, 35°58'S-72°42'W, 348 m.a.s.l.). Additionally, we surveyed small mammals in neighboring *P. radiata* plantation to Fragment 3 (Fig. 1).

Sampling. We carried out bimonthly trapping of small mammals from January 1999 to February 2000. In LQNR, we operated two grids (10 x 5 medium-sized Sherman traps, 3,600 m^2 each). In Fragment 3, we operated a smaller grid (6 x 5 medium-sized Sherman traps, 2,000 m^2) grid, which covered a significant fraction of the fragment. In the *P. radiata* matrix adjacent to Fragment 3 we installed a 10 x 5 medium-sized Sherman traps grid, covering 3,600 m^2 size. In Fragment 1, we operated a 10 x 5 medium-sized Sherman traps grid, also covering 3,600 m^2, that we used to evaluate movements between forest remnants and the pine plantation. Here, half of trapping grid was set inside the forest fragment, while the other half laid in adjacent *P. radiata* plantation. This grid was also included in microhabitat analysis. χ^2 test was used to compare observed captures as a function of the expected captures if small mammals did not show preferences among native and exotic habitat. This grid was activated one week during January 1999 and February 2000. In each grid, traps were located 10 m apart. Live trapping sessions lasted for at least five trapping nights. All traps were baited with rolled oats and checked daily at dawn, since all mammals are nocturnal.

Faunal survey. Assemblage's richness and abundance were estimated as the total number of taxa captured, and as trapping success and minimum number of animals known to be alive, respectively. Each captured specimen was individually marked, measured and released. Body condition was assessed only for non-reproductive adults of *A. longipilis* and *A. olivaceus* captured during December 1999-February 2000, comparing the ratio body mass/body size among individuals captured in native forest and *Pinus* matrix. Reproductive status was assessed for females registering if vagina was open, or if there were signs of lactation like enlarged nipples. For males, we recorded if testicles were scrotal or abdominal. We distinguished among juvenile and adult individuals. We compared the reproductive proportion and age structure among continuos forest, forest remnants and exotic matrix.

Habitat analysis. Habitat description was based on twenty-eight habitat metrics that were recorded at every trap station in October 1999. These measures followed Glanz (1970), and included variables aimed to describe habitat characteristics at ground, shrub and tree level. At each trap station, four line transects were taken, each two meters long, by pushing a board through the vegetation in 90° direction, from a distance of one meter away from the trap placement (Glanz 1970). Percentage of cover at ground, shrub and tree level was recorded. At ground level (up to 50 cm) we estimated percentage of cover for litter (GRLITTCOV), branch (GRBRACOV), stem (GRSTECOV), shrub (GRSHRUCOV), herb (GRHERCOV), pine litter (SHRPLICOV), and percentage of bare soil cover (GRSOILCOV). At shrub level (from 50 cm to 3 m) we measured percentage of cover for empty space (SHREMPCOV), juvenile trees (SHRJUVCOV), branch (SHRBRACOV), shrub (SHRSHRCOV) and herb (SHRHERCOV) cover. At tree (more than 3 m) level we estimated percentage of cover for branch (TRBRACOV), native trees (TRNATCOV), pine (TRPINCOV), and percentage without overstory cover (TRWOSCOV). The density of the shrub foliage in three different levels above ground (0-10 cm (FODEN010), 11-25 cm (FODEN1125), and at 1-2 m (FOLDEN12) was determined by placing the board vertically at a distance of one meter from the observer, and estimating the percentage of the board obscured by vegetation at each level. We also estimated the maximum herb (HERBHIGHT) and shrub high (SHRUBHIGH) within three meters of the trap. Also within this ratio we estimated fungi and fern (FFRICH), herb (HERBRICH), shrub (SHRUBRICH), and tree richness (TREERICH), by direct counting of species. Finally, we measured slope (SLOPE) in angles, along with soil hardness (SOIL) estimated as the cm a stick was able to penetrate the soil surrounding the trap. We took four measures of soil hardness within a ratio of three meters of each trap location.

To compare habitat among fragments we conducted an ANOVA among LQNR, Fragment 3, and exotic matrix. To evaluate the association of small mammals to habitat, we conducted a stepwise multiple regression among trapping success and habitat variable. A variable was allowed to enter the model when $P \leq 0.1$. Trapping success was estimated as the number of captures in each trap. Regressions were made for the most common taxa, including: *Abrothrix longipilis, Abrothrix olivaceus, Oligoryzomys longicaudatus, Octodon bridgesi,* and *Thylamys elegans.*

RESULTS

Species composition and abundance. We captured 435 individuals over a total of 8,747 trap/nights (5% overall trapping success). Six murids (*Abrothrix longipilis, Abrothrix olivaceus, Oligoryzomys longicaudatus, Irenomys tarsalis, Geoxus valdivianus*, and the introduced *Rattus rattus*), one caviomorph (*Octodon bridgesi*), one didelphid (*Thylamys elegans*), and one microbiotherid (*Dromiciops gliroides*) comprised the fauna of Maulino forest (Tab. 1). Four taxa (*A. longipilis, A. olivaceus, O. longicaudatus, T. elegans*) accounted for 80% of total captures, and were used in subsequent quantitative analyses.

The continuous forest at the LQNR supported the highest species richness, where nine species were recorded. In contrast, despite larger extensions occupied by exogenous *Pine* plantations this was the poorest habitat, embracing six species (Tab. 1). The higher richness at the continuous forest was accounted for by the simultaneous presence of *D. gliroides, I. tarsalis, G. valdivianus* and *O. bridgesi*, albeit they were scarce (Tab. 1). In fragments, combination of rare taxa only included *I. tarsalis and O. bridgesi* in Fragment 3. *Dromiciops gliroides* never was captured outside the continuous forest.

Overall abundance of small mammals was higher in fragments and the exotic matrix, where trapping success doubled the abundance attained by small mammals at the continuous forest (Tab. 1). *Abrothrix longipilis* and *A. olivaceus* were the most abundant taxa in fragments and the surrounding matrix. *Oligoryzomys longicaudatus* was abundant in continuous forests, showing an extremely seasonal pattern with 87.5% of the captures occurring during April, June and August (Fig. 2). Rare taxa like *G. valdivianus, D. gliroides*, or *I. tarsalis* were more "abundant" in continuous forest (Tab. 1). Although the introduced murid *R. rattus* was present in all surveyed habitats, it was more abundant in continuous forest (Tab. 1). *Octodon bridgesi* was significantly more abundant in Fragment 3 and the *Pinus* plantation. Only one individual was captured in the continuous forest, and no capture was recorded in Fragment 1 (Tab. 1 and 2).

Habitat description and preferences. Habitat characteristics differed among continuous and fragmented forest, as well as with the *Pinus* matrix (Tab. 3). Twenty out of 27 habitat variables differed among fragments. *Pinus* plantation differed from Fragment and LQNR in nine variables, showing lower litter cover, higher pine shrub cover, lower without overstory cover, higher pine tree cover, lower shrub and herb richness, higher foliage density at 0-10 cm and 10-25 cm, and lower herb height (Tab. 3). Fragment 3 and LQNR were more similar, with 12 out of 20 similar variables, among them were for example litter cover, shrub richness, or foliage density (Tab. 3).

Microhabitat variables explained small percentage of variance in trapping success for Maulino small mammals, although all regression models were highly significant (Tab. 4). For *A. olivaceus*, microhabitat explained 30% of trapping success, while for *O. bridgesi*, microhabitat characteristics explained only 14.8% (Tab. 4). Nevertheless, it is noteworthy that only 14 variables are important in determining trapping success (Tab. 5), and that these differ among small mammals. Analyzing relevant variables to trapping success (Tab. 5), along with habitat attributes for each fragment (Tab. 3), one can conclude that for *A. longipilis* ground branch cover is the most important variable in explaining species

Table 1.- Trapping success (TS), number of captures (NC) and minimum number of individuals known to be alive (MNKA) for each taxon of small mammal captured in Maulino forest and adjacent *Pinus radiata* plantation. Similar proportions are underlined.

	Site									
	LQNR[a]			FRAGMENT 3			*Pinus radiata* MATRIX			
Taxon	TS	NC	MNKA	TS	NC	MNKA	TS	NC	MNKA	χ^2
Rodentia										
Muridae										
Abrothrix longipilis	2.14	84	39	2.17	23	17	5.64	103	52	35.3^{**}
A. olivaceus	0.59	23	17	3.20	34	23	3.40	62	34	70.6^{**}
Oligoryzomys longicaudatus	1.92	75	62	0.66	7	7	0.93	17	12	13.7^{**}
Irenomys tarsalis	0.002	6	4	0.09	1	1	nc[b]	0	0	1.1
Geoxus valdivianus	0.15	1	1	nc	0	0	nc	0	0	
Rattus rattus	0.59	23	ne	0.09	1	ne	0.38	7	ne	11.4^{*}
Octodontidae										
Octodon bridgesi	0.03	1	1	1.32	14	12	0.88	16	7	24.0^{**}
Marsupialia										
Didelphidae										
Thylamys elegans	0.43	17	9	4.52	48	16	0.88	16	5	12.0^{**}
Microbiotheriidae										
Dromiciops gliroides	0.15	1	1	nc	0	0	nc	0	0	
Total captures	5.91	231	134	11.97	127	76	12.11	221	110	81.7^{**}
Total traps		3,909			1,061			1,825		

[a] Los Queules National Reserve; [b] not captured; [c] total number of captures. * $0.001 < P < 0.05$; ** $P < 0.001$

Table 2.- Number of total captures of small mammals in Fragment 1, and its adjacent *Pinus radiata* plantation. Minimum number know to be alive is shown in parenthesis.

Taxon	Maulino Forest	*Pinus* Matrix	Total
Rodentia			
Muridae			
Abrothrix longipilis	27 (8)	72 (46)	99 (48)
A. olivaceus	16 (5)	62 (24)	78 (25)
Oligoryzomys longicaudatus	6 (5)	10 (9)	16 (14)
Irenomys tarsalis	1 (1)		1 (1)
Geoxus valdivianus		2 (1)	2 (1)
Rattus rattus	9	2	11
Marsupialia			
Didelphidae			
Thylamys elegans	39 (11)	10 (5)	49 (14)
Total captures	89 (30)	156 (85)	245 (102)
Total species	5	5	5
Total traps	955	997	1,952

trappability, since this value is higher in *Pinus* plantation, where species abundance was higher. Also, foliage density in the first 10 cm above ground seems to be important for the trappability of this species. Elevated shrub high seems to explain capture pattern for *A. olivaceus*, that was higher in Fragment 3 and exotic matrix. For *O. longicaudatus* the presence of pines seem to negatively affect species presence. Higher abundance of this species was observed in LQNR where lower pine abundance existed. Higher abundance of *T. elegans* observed in Fragment 3 is associated to

Fig. 2.- Minimum number of individuals known to be alive (MNKA) surveyed in three fragments of Maulino forest, during January 1998-February 2000.

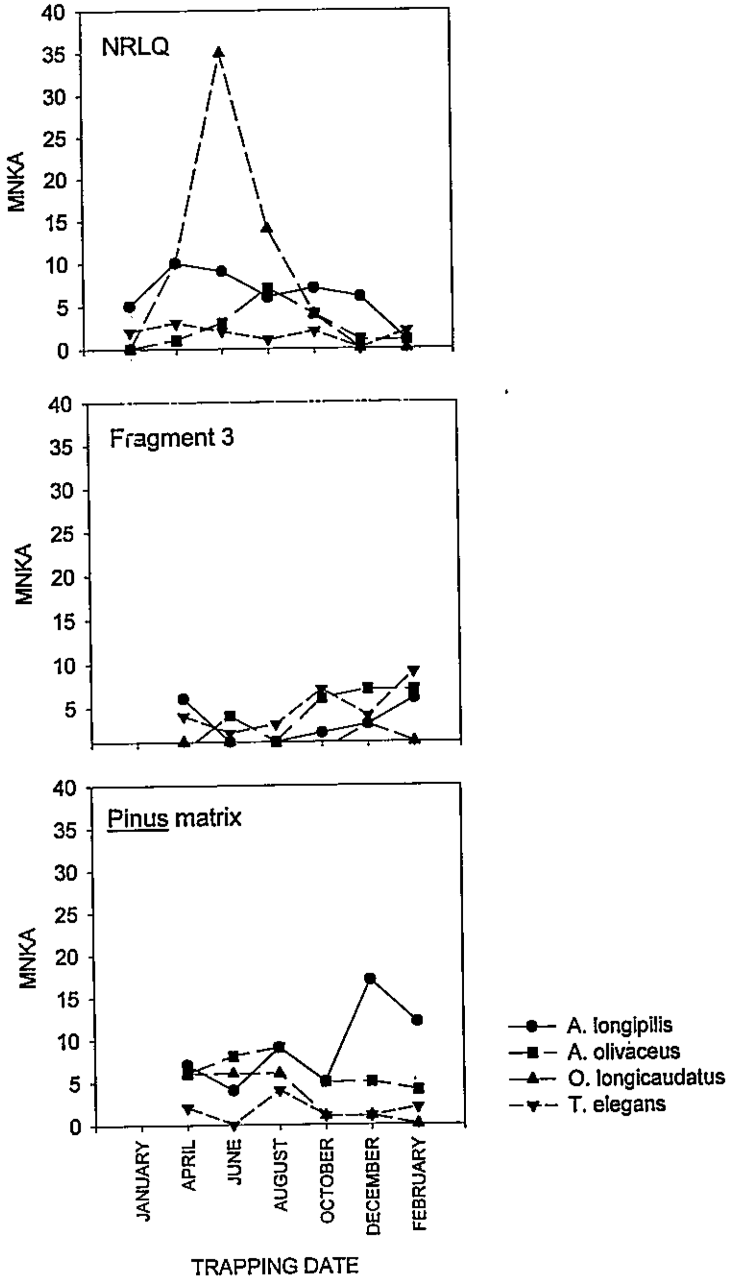


Table 3.- ANOVA for microhabitat measurements among continuous forest, forest remnants of Maulino forest (Fragment 3 and Los Queules National Reserve, LQNR) and exotic *Pinus radiata* matrix. Letters indicate differences based on Sheffé *posteriori* test. Acronisms in text.

	LQNR[a]			Fragment 3			*Pinus* Matrix				
Microhabitat variable	Average	SD	N	Average	SD	N	Average	SD	N	F	P
GRLITTCOV	70.7^{a}	9.1	97	72.8^{a}	18.1	30	54.5^{b}	24.0	50	12.1	<0.001
GRBRACOV	7.2^{b}	8.6	97	10.7^{a}	11.4	30	12.2^{a}	22.1	50	2.3	0.108
GRSTECOV	8.1^{b}	7.8	97	3.5^{a}	6.5	30	1.9^{a}	3.5	50	16.4	<0.001
GRSHRUCOV	0.9	4.6	97	0	0	30	0	0	50	1.6	0.199
GRHERCOV	8.9^{ab}	15.6	97	0.6^{a}	3.4	30	15.7^{b}	23.8	50	7.3	<0.001
GRSOILCOV	4.0^{c}	5.7	97	11.7^{a}	15.1	30	0.5^{b}	1.9	50	20.9	<0.001
SHREMPCOV	51.6^{b}	25.2	96	31.2^{ab}	24.2	30	44.2^{b}	23.6	50	8.0	<0.001
SHRJUVCOV	20.0^{c}	17.1	96	9.8^{a}	12.8	30	1.0^{b}	3.3	50	32.1	<0.001
SHRBRACOV	12.2	16.0	96	8.9	16.8	30	6.3	14.7	50	2.4	0.097
SHRSHRCOV	7.0^{c}	14.3	96	46.9^{a}	28.5	30	31.7^{b}	22.4	50	57.0	<0.001
SHRHERCOV	8.8^{b}	16.3	96	2.6^{ab}	6.6	30	0^{a}	0	50	9.1	<0.001
SHRPLICOV	0^{a}	0	100	0^{a}	0	30	3.3^{b}	11.2	50	5.8	0.003
TRWOSCOV	1.8^{a}	4.9	96	5.8^{a}	6.7	30	15.6^{b}	22.0	50	19.9	<0.001
TRBRACOV	0	0	100	0.2	1.1	30	0	0	50	2.5	0.081
TRNATCOV	23.2^{c}	4.8	100	18.7^{a}	7.3	30	0^{b}	0	50	421	0
TRPINCOV	0^{a}	0	100	0^{a}	0	30	81.4^{b}	23.5	50	782.5	<0.001
TREERICH	2.6^{c}	1.1	97	1.7^{a}	1.1	30	1.1^{b}	0.5	50	41.0	<0.001
SHRUBRICH	3.3^{a}	1.7	97	2.9^{a}	1.5	30	2.0^{b}	0.9	50	11.5	<0.001
HERBRICH	3.0^{a}	1.6	97	5.7^{a}	2.6	30	1.6^{b}	1.6	50	48.5	<0.001
FFRICH	0.3^{c}	0.5	96	1.3^{a}	0.6	30	0.3^{bc}	0.4	50	49.6	<0.001
FODEN010	28.9^{a}	27.0	96	22.2^{a}	24.0	30	49.4^{b}	24.6	50	13.8	<0.001
FODEN1125	27.5^{a}	25.4	96	19.4^{a}	24.2	30	43.1^{b}	25.1	50	9.9	<0.001
FOLDEN12	31.7	21.7	96	39.8	22.0	30	28.8	22.9	50	2.4	0.092
HERBHIGHT	58.4^{a}	58.4	97	71.3^{a}	86.1	30	21.1^{b}	20.5	50	9.9	<0.001
SHRUBHIGH	238.1^{b}	94.6	97	294.7^{a}	110.1	30	257.6^{ab}	76.1	50	4.3	0.014
SLOPE	11.8^{a}	9.8	95	31.3^{b}	11.8	30	10.7^{a}	7.9	50	52.9	<0.001
SOIL	10.2^{c}	2.8	95	7.0^{a}	2.6	30	8.8^{b}	2.8	50	15.4	<0.001

Table 4.- Models for microhabitat association obtained by stepwise multiple regression, for *Abrothrix longipilis, A. olivaceus, Oligoryzomys longicaudatus, Thylamys elegans* and *Octodon bridgesi*, captured in remnants of Maulino forest, and adjacent *Pinus radiata* matrix, in Tregualemu, VII Region, Chile.

TAXON	R	R^2	ADJUSTED R^2	S.E.	F	d.f. 1	d.f. 2	P
A. longipilis	0.477	0,228	0,195	1,930	6,921	9	211	< 0,000
A. olivaceus	0,547	0,300	0,263	1,301	8,146	11	209	< 0,000
O. longicaudatus	0,401	0,161	0,104	0,764	2,819	14	206	0,001
T. elegans	0,494	0,244	0,204	0,928	6,125	11	209	< 0,000
O. bridgesi	0,385	0,148	0,108	0,532	3,668	10	210	< 0,000

Table 5.- Standardized coefficients for stepwise multiple regression among microhabitat variables for *Abrothrix longipilis, A. olivaceus, Oligoryzomys longicaudatus, Thylamys elegans* and *Octodon bridgesi*, captured in remnants of Maulino forest, and adjacent *Pinus radiata* plantations, in Tregualemu, VII Region, Chile. Only significant variables are shown. Acronyms in text.

MICROHABITAT VARIABLE	*A. longipilis*	*A. olivaceus*	*O. longicaudatus*	*T. elegans*	*O. bridgesi*
GRLITTCOV	0.202				
GRBRACOV	0.148				0.269
GRSTECOV	-0.121				
SHRJUVCOV	-0.156				
SHRSHRCOV				0.218	
SHRBRACOV		0.135		0.162	0.165
TRNATCOV				0.181	-0.192
TRPINCOV			-0.217		
FODEN010	0.199				
FOLDEN12	0.127			-0.158	
SHRUBHIGH		0.159		0.142	
SOIL				-0.158	
FFRICH			0.264		

Table 6.- Number of females (F), juveniles (J), and reproductive (R) out of total individuals (from Table 1) captured in Maulino forest fragments, and adjacent *Pinus radiata* Matrix. χ^2 and P were non significant for each comparison and are not shown. [a] Los Queules National Reserve.

	LQNR[a]			Fragment 3			*Pinus* Matrix		
Taxon	F	J	R	F	J	R	F	J	R
Abrothrix longipilis	22	6	23	8	1	15	18	7	38
A. olivaceus	12	3	4	13	4	17	14	3	23
Oligoryzomys longicaudatus	38	22	4	1	3	0	5	1	0
Thylamys elegans	6	3	1	11	5	5	2	2	2

elevated shrub cover and higher soil hardness. Finally, the distribution of *O. bridgesi*, which was captured in Fragment 3 and the *Pinus* plantation, seems to be associated to elevated shrub cover.

Population structure and body condition. Proportion of females, and juveniles, and also proportion of reproductive individuals did not vary among fragments (Tab. 6). There were no differences in body condition (BC) among sexes for *A. longipilis* (F=0.9; 32 d.f.; P=0.35), or *A. olivaceus* (F=0.28; 13 d.f.; P=0.61). BC did not vary among native and exotic habitat for *A. longipilis* (F=0.57; 30 d.f.; P=0.64; Forest-BC 124.1 ± 7.3, N=15; *Pinus* Plantation-BC 120.5 ± 11.4, N=19). On the contrary, *A. olivaceus* achieved higher BC (F=8.6; 13 d.f.; P=0.011) in exotic matrix (BC=99.3 ± 4.6, N=7) compared to native forest (BC=87.3 ± 9.9, N=8).

Movements. A total of 102 individuals were captured in Fragment 1, and were used to test for habitat preferences among native and exotic vegetation. Here, 245 captures were achieved, comprising a total of seven species (Tab. 2). For *A. longipilis*, only six individuals (10.7% of the total) moved between native forest and *Pinus* plantations. All were adult males, except for one juvenile. For *A. olivaceus*, four (13.8%) individuals moved among native and *Pinus* matrix, all adults, three of them males. For *T. elegans*, two individuals (11.8%) moved among adjacent habitats. These were one male and one female, both adults.

DISCUSSION

Fragmentation of Maulino forest, along with habitat replacement affected small mammal's composition and abundance. As expected, species richness was higher in continuous forests, exceeding richness in fragments and *Pinus* plantations. Continuous forest shelters a particularly interesting small mammal assemblage, due to the coexistence of relict populations of Valdivian fauna like *D. gliroides, G. valdivianus, I. tarsalis*, and *O. bridgesi*, a combination not observed in any other forest type today (Reise and Venegas 1987; Saavedra and Simonetti 2000, 2001). Since central-south Chile probably acted as a forest refugee during Quaternary glaciations (Villagrán et al. 1995), mammals now inhabiting Maulino forest probably constitute the oldest representatives of the fauna currently thriving in the more southern Valdivian district. In Maulino forest rare species are concentrated in continuous forest, while fragments harbor mostly common taxa. Fragmentation of Maulino forests seems to have a significant impact on overall small mammal's richness, menacing the persistence of rare taxa of small mammals. The fact that rare species are concentrated in continuous forest indicates that this native spot has a significant value for the persistence of these populations. Despite larger extensions occupied by exotic *Pinus radiata* plantations, this was the habitat with lowest species richness, like Burca site located southern of our study site (Muñoz and Murúa 1989). Nevertheless, total abundance was higher in *Pinus* plantations where Maulino forest remnants are included, a pattern not described before for this fragmented forest.

Here, as has been observed in other forests of southern Chile (Muñoz and Murúa 1989; Kelt 2000), *A. longipilis, A. olivaceus, O. longicaudatus* and *T. elegans*, are the principal components of small mammal assemblages, becoming extremely important to define the observed abundance pattern in Maulino forest. All these taxa use and/or are more abundant in the *Pinus* plantations, indicating that this constitute a suitable habitat for them. This fact is reflected not only in abundance pattern, but also at the individual level, where body condition is even higher in *Pinus* matrix compared to native forest at least for *A. olivaceus*. Lack of population response to fragmentation might be a general pattern that has been observed at population level in species that primarily inhabit mature forests (e.g. Mahan and Yahner 1998). Increased body condition in more fragmented habitat has also been observed in other generalist taxa (Díaz et al. 1999). These findings indicate that *Pinus* plantations do fulfil at least partial habitat requirements for several small mammals that inhabit Maulino forest, mostly due to the existence of ground structures, like branches or shrubs, that are probably used as refuges by these rodents. Habitat suitability of *Pinus* plantations may be increased by the existence of significant food resources like insects that show similar abundance in *Pinus* matrix compared to forest fragments (Grez et al. 2002). *A. longipilis, A. olivaceus*, and *T. elegans*, are the most abundant taxa in *Pinus* plantations, do include insects in their diet (Muñoz-Pedreros et al. 1990).

Monterrey pine matrix is a suitable habitat for other species like the carnivores' red fox (*Pseudolapex culpaeus*) and the felid *Oncifelis guigna* (Acosta 2001). Although none of these carnivores prefer *Pinus* plantations to native forest, they are able to use this habitat as food source, or corridor among native forest fragments. Also *Pinus* plantations that surrounded Maulino forest fragments do not constitute a barrier for several bird species, including understory birds (Estades and Temple 1999, Vergara 2002). Depending on species idiosyncrasies, these taxa are able to use *Pinus* plantations developing nesting activities and achieving important abundances. All these evidence suggest that at least for these taxa, forest fragments and *Pinus* plantations are not opposite habitats for some species, and they are used as part of a continuum where forest fragments are articulated through pine plantations.

Our findings have important consequences for the conservation and management of the last remnants of Maulino forest that persist immersed in this very modified habitat. Preservation of the large tract of native forest seems to be indispensable for the maintenance of elevated species richness at the landscape level, preventing the disappearance of rare and endangered taxa. They seem to find a refuge in this last spot of Maulino forest that is not supported by smaller forest fragments. At the same time, the maintenance of forest remnants interspersed in a well developed *Pinus* plantation, seem to be an adequate management practice for ensuring persistence of common species that are able to use this foreign habitat, along with increasing the connectivity of forest remnants for uncommon taxa. This landscape approach to the conservation of this seriously modified habitat seems to be a realistic alternative to conserve native fauna that still inhabits the area.

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CAPÍTULO 4

HISTORICAL DEMOGRAPHY AND FLUCTUATING ASYMMETRY IN A MARGINAL POPULATION OF *OCTODON BRIDGESI* (RODENTIA)[4]

Demografía histórica y de asimetría fluctuante en una población marginal de *Octodon bridgesi* (Rodentia)

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[4] Para ser publicado como: Saavedra B & JA Simonetti. Historical demography and fluctuating asymmetry in a marginal population of *Octodon bridgesi* (RODENTIA)

RESUMEN

Reducción del tamaño poblacional determinado por pérdida de hábitat puede tener consecuencias genéticas y morfológicas, disminuyendo la variación genética e incrementando la asimetría fluctuante, respectivamente. Reducciones de largo plazo del tamaño poblacional producto de la actividad humana, deberían dejar rastros en las relaciones genealógicas y patrones de asimetría de poblaciones remanentes. *Octodon bridgesi* ha sufrido la reducción de larga data producto de la actividad humana, la que ha restringido su límite norte a la región costera de Chile centro-sur. Además, esta área está altamente fragmentada y *O. bridgesi* vive en un hábitat profundamente modificado. Acá evaluamos los efectos que esta historia de perturbación humana pudo tener sobre las poblaciones de esta especie, evaluando su demografía pasada, así como los patrones de asimetría fluctuante a través del tiempo.

La reducción histórica de su rango de distribución, modificaciones contemporáneas del hábitat, además de tamaños poblacionales pequeños no han producido trazas genéticas significativas en la población analizada. Estos factores además, no han determinado cambios en asimetría fluctuante en la población. Los estimadores genéticos indican que la población analizada se encuentra estable, o al menos a incrementado su tamaño poblacional. Justamente el patrón opuesto al esperado por nosotros. Asimismo, los indicadores morfológicos no evidencian reducción poblacional, o estrés ambiental. Discutimos posibles explicaciones a los patrones observados.

ABSTRACT

Reduction of population size determined by habitat loss can have genetic and morphological consequences, reducing genetic variability and increasing fluctuating asymmetry, respectively. Long-term reductions in population size, triggered by human activities, should leave signatures in genealogical relationships and asymmetry patterns of remnant populations. *Octodon bridgesi* has suffered from long term decline due to human disturbance of their natural habitats, reducing its northern limit to the coastal region in south-central Chile. Moreover, this area is now highly fragmented, and *O. bridgesi* lives in a highly modified landscape. Here we assess the effects historical human activities exerted on *O. bridgesi*, evaluating its past demography, and fluctuating asymmetry patterns though time. Historical range reduction, contemporaneous habitat modification and small population size of *O. bridgesi* did not produce significant traces in genetic composition of populations located in northern limit of the geographical range of this species. These factors also do not produce changes in asymmetry evaluated in space and time. All coalescent estimators of population genetics indicate that extant population of *O. bridgesi* behaves at least as stable populations. Some estimators even indicate an increase in population size, just the opposite expected by Late-Holocene and contemporaneous history for this species Fluctuating asymmetry parameters, do not vary among populations that differ in range distribution and are submitted to elevated habitat modifications. Evidence indicates that extant populations of this species do not acknowledge historical range reduction in their demographic history, and that habitat modification has not produced a negative effect at this morphological level. Possible explanations to this pattern are discussed.

INTRODUCTION

Historically, humans have triggered changes in natural populations, reducing their size, or distributional range (Grayson 2001), determining in numerous occasions the extinction of populations (Diamond 1984). Human activities can reduce the size of natural populations directly via hunting, or indirectly via reduction of habitat quantity and quality. Loss of habitat can have consequences on genetic and, indirectly to morphological attributes of the small remnant populations, with consequent effects on its long-term survival (Hoffman & Parsons 1997). Theoretical and empirical evidence indicate that reductions in population's size diminish genetic variability of populations due to the relative increase of genetic drift and inbreeding (Hartl 2000). Genetic loss will depend on magnitude and intensity of population size reduction (Amos & Balmford 2001). Reduction of population size, along with the loss of habitat quality, may have additional consequences on individual morphology. Organisms that suffer from genetic stress, and are subjected to elevated environmental stress can undergo increases in fluctuating asymmetry (FA) (Møller & Swaddle 1997). Deficient buffer mechanisms necessary for individual development derived from the lack of genetic variability (Mitton & Grant 1984), along with elevated developmental noise produced by the raise of environmental stress (Palmer 1996a), increase the magnitude or frequency of subtle deviations between left and right side from bilateral characters in several organisms (see Møller & Swaddle 1997). When reduction of population size and habitat quality act simultaneously, it is possible to expect a strong effect on FA. Elevated asymmetry impinges upon individual's fitness, reducing the capacity of individuals to survive and leave descendants (Møller 1997). Asymmetry can reduce ecological performance, with consequent effects on survival and reproduction (see Møller & Swaddle for a revision). These can become a particular mechanism by which a small population can face increased probability of extinction (Chapter 1).

In the absence of traditional genetic analysis, designed to estimate heterozygosity levels of individuals and populations, it is possible to analyze population genetics using a recently developed theoretical framework called the coalescent (Hudson 1990). Under this approach, it is possible to estimate historical population demography, and indirectly genetic status of the analyzed population. Demographic history leaves traces in the genes of individuals of extant populations (Emerson et al. 2001). Under a coalescent approach, it is possible to explore population history from a demographic view, through the analysis of genetic relationships that trace the lines of descent back through the ancestral population, until they find their common ancestors or coalesce (Hudson 1990). The underlying genealogy of a population sample contains all possible information about population demographic process. The coalescent approach predicts the patterns of polymorphism we expect to see under different demographic models. Under a neutral model, where demographic processes are not affected by external forces, the parameter θ, that for an haploid system like mitocondrial DNA (mtDNA) is $2Ne\mu$, with Ne as the effective population size, and μ representing the mutational rate for the analyzed molecule, can be estimated directly from the proportion of pairwise differences per nucleotide site of the population sample, that is π the nucleotide diversity (θ_π). Based on the infinite sites model, that assumes that mutations are unique and affect no more that one site, in sequences of DNA is possible to expect that a mutation in a single nucleotide yields polymorphism of the sample. If mutations are neutral, that is they are not affected by selection for example, mutations occur uniformly in time at rate μ per nucleotide per site per generation, and the expected proportion of segregating sites in the sample must equal the mutation rate per nucleotide site times the total length of the coalescent. This allows another estimator of θ, determined by the number of polymorphic sites and the number of alleles of the sample, θ_S (Hartl 2000). Under a neutral demographic model, both estimators of θ should be equal (Tajima 1989). Using this as a null model, it is possible to uncover demographic history of the population, and indirectly its present genetic status. For example, if a population deviates from the normal coalescent model indicating that the population underwent a demographic bottleneck, it is possible to expect for this population a reduction in other genetic markers, like isozymes. On the contrary, if the analyzed population does not deviates from the neutral coalescent model, indicating that the population has remained stable in number throughout several generations, it is possible to expect no reduction of genetic losses in other non-neutral markers. The same scenario is expected if the analyzed population has experienced a increment in its size.

Particularly, population growth does however, leave specific signatures in patterns of polymorphism. In a growing population, most mutations will land on the long external branches of the genealogy, generating a mutational pattern characterized by low frequency mutations, leading to relatively higher estimates of θ_S, and relatively lower estimates from pairwise differences θ_π. Growth will also tend to create a very shattered haplotype structure, in which a large proportion of all mutations creates a new haplotype. Population growth leads to negative values of Tajima D tests (Tajima 1989). On the contrary, the effect of a bottleneck is to generate a brief period of rapid coalescence. If the bottleneck is very strong, only a very few lineages survive, but each of these ancestral lineages leave many descendants in the population. Consequently, mutations that arose on these ancestral lineages will be present on multiple individuals, hence be at intermediate frequency. The rapid coalescence during the bottleneck will create sets of very closely related haplotypes that are defined by mutations in the ancestral lineages that survive the bottleneck. In terms of the summary statistics, recent bottlenecks lead to an excess of intermediate-frequency alleles and a dearth of rare mutations, leading to positive Tajima D statistics (Tajima 1989). Also, a growing population will affect the distribution of pairwise differences between sequences (Harpending et al. 1998) in a different form that should be affected by a shrinking population. Bottlenecks create almost exactly the opposite signature as population growth. This is perhaps not surprising given that the two processes are effectively the opposites of each other. In summary, it is possible to explore population demography using neutral markers under a coalescent approach, and indirectly with this analysis to infer general genetic behavior of extant populations (Hudson 1990).

Long-term human activities determined the modification of the geographic range for several species of Chilean rodents (Chapter 2). Among them, *Octodon bridgesi* was extirpated from their northernmost range due to the local extinction of populations (Simonetti & Saavedra 1998). *Octodon bridgesi* disappeared from the Andean range in central Chile due to habitat clearance for horticultural development ca. 1,500 years BP (Simonetti 1989, Simonetti & Cornejo 1990, Simonetti & Saavedra 1994). It also went extinct in the coastal range due to intensification of agriculture in areas previously unused by local farmers ca 200 years BP (Simonetti & Saavedra 1998). Human activities determined a northern range reduction of the species that restricted populations to its southern margins (Chapter 2). Currently, *O. bridgesi* inhabits a highly modified habitat characterized by extensive replacement of natural habitats by *Pinus radiata* plantations (Chapter 3). Due to logging activities, native forest has been severely disrupted resulting in a massive reduction in area, along with fragmentation of the natural Maulino forest (Lara et al. 1995).

Here we assess the effects that historical human activities exerted on populations of *O. bridgesi*, evaluating its past demography based on coalescent estimators (Emerson et al. 2001), and at the same time we evaluate the effect that these activities could have on individual morphology, analyzing fluctuating asymmetry patterns though time. If reduction in range size produced by historical human pressure, along with current habitat perturbation affected populations of *O. bridgesi*, these processes should have leave signatures in genetic as well as morphological level of extant populations of this species. Population size reductions should be observed in demographic estimators based on genetic composition of extant populations (Tajima 1989, Harpending et al. 1998). Along with demographic evidence, increased asymmetry should be observed in modern populations compared to ancient ones, that apparently had higher population size and developed in pristine habitat.

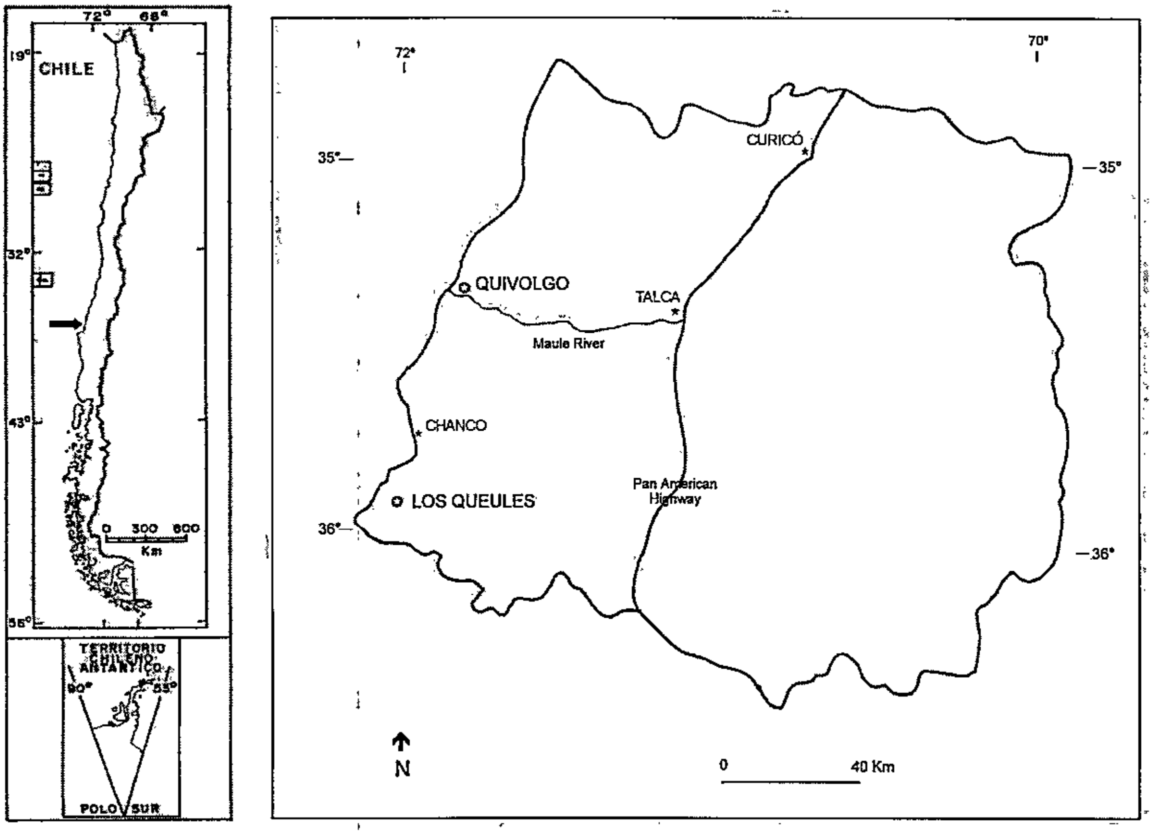
METHODS

Demographic as well as morphological analysis included populations of *O. bridgesi* either trapped or excavated from Tregualemu and Quivolgo, respectively (Fig. 1). Additionally, we used an operationally defined population conformed by specimens of *O. bridgesi* deposited in the Mammal's Collection of the Instituto de Ecología y Evolución, Universidad Austral de Chile (IEEUACH). These specimens were all captured after 1982, and come from populations located south of Quivolgo and Tregualemu, for at least 100 km. Since IEEUACH is a mixture of individuals coming from several populations, we use this group as control group. Due to its multiple origin, along with the fact that specimens from the IEEUACH come from central populations of the species, we expect demographic analysis of this group shows a stable population, indicating elevated levels of genetic variability, along with low levels of asymmetry.

Demographic analysis. Nineteen individuals of *Octodon bridgesi* were used in coalescent analysis. Nine of them were captured in Tregualemu (Chapter 2), and 10 came from IEEUACH. DNA from trapped individuals was extracted from bloodstains in FTA paper (Hansen & Blakesley 1998), using a Chelex protocol. The same method was used to extract DNA from skin samples extracted from museum specimens. Two non-overlapping fragments covering part of control region of the mtDNA were amplified using polymerase chain reaction (PCR). Newly designed primers (Obri1 5'TGAACCAAAACTCTAATCAT3'and Obri2 5'GTTTATGGGATTTTTGAATC3') amplified for a ca. 300 bp fragment, in a PCR reaction volume of 25 µL containing 2.5 µL buffer, 1.5 µL $MgCl_2$, 0.5 µL dNTPs, 0.25 µL

each primer, 10 µL template DNA and 1 U of Taq Quiagen DNA polymerase. Cycling parameters were 94 °C 1 min, 50 °C 1 min and 72 °C for 2 min. These primers successfully amplified in Tregualemu and museum specimens. Two other primers (Tuco Pro: gently borrowed by Enrique Lessa, and TDKD: Kocher et al. 1993), amplified for a ca. 450 bp fragment, and were used in the genetic analysis of the extant specimens of *O. bridgesi* captured in Tregualemu. For these primers, PCR reaction were made in a total volume of 25 µL containing 2.5 µL buffer, 0.75 µL $MgCl_2$, 0,5 µL dNTPs, 0.5 µL each primer, 12.5 µL template and 1 U Taq Quiagen DNA polymerase. Cycling parameters for this reaction were 94 °C 30 s, 45 °C 30 s, and 72 °C for 30 s. The same conditions were used to amplify a the

FIGURE 1. Location of Quivolgo and Tregualemu, sites were archaeozoological and extant specimens of *Octodon bridgesi* were recovered, respectively.



450 bp fragment in a specimen of *O. degus*. This sequence was used as an outgroup in Fu and Li neutrality tests (Fu & Li 1993). Sequences were assembled based on overlapping regions with Sequencher 4.0.5 (Gene Codes), and aligned with CLUSTALW (Thompson et al. 1994).

To evaluate demographic history of analyzed populations, we applied Tajima's D test (Tajima 1989). Under the assumption of constant population size this test evaluates the significant excess of low frequency haplotypes. Additionally, we performed the Fu & Li (1993) test of neutrality, that incorporates an outgroup. Also, we analyzed population changes in size (either expansion or shrinkage) using graphically and simulation models. First we analyzed frequency distribution of mismatched pairwise comparisons among mtDNA sequences (Harpending et al. 1998). A population that is expanding produces a unimodal mismatch distribution and exaggerates the frequency of singletons within the set of polymorphic sites. On the contrary, multimodal or right skewed mismatch distributions are generated by stable, and populations that faced a size reduction, respectively (Harpending et al. 1998). Mismatch pairwise distributions among mtDNA haplotypes were generated by program DNAsp (Rozas & Rozas 1999). Additionally, we evaluated two population expansion (or shrinking) models. In the first model, demographic parameters were estimated directly from mismatch distribution (Rogers & Harpending 1992) by a generalized, non-linear, least-squares approach, with significance tested using the sum of the squared deviations between observed and expected mismatch (Schneider & Excoffier 1999). This model is described by θ_0, θ_1 and τ, that correspond to initial population size, population size after expansion, and the time of population expansion, respectively. This model was implemented by Arlequin (Schneider et al. 2000). Finally, we estimated population changes using a maximum likelihood procedure, that permit to estimate Ne of focal population, and was implemented with the program FLUCTUATE (Kuhner et al. 1998).

Morphological Analysis. Fluctuating asymmetry was analyzed in a temporal and spatial scale. For the time comparisons, we defined three periods of increasing land use intensity: Archaic (5,500-1,500 BP), Agricultural (1,500-100 BP), and Present. Taphocenosis from

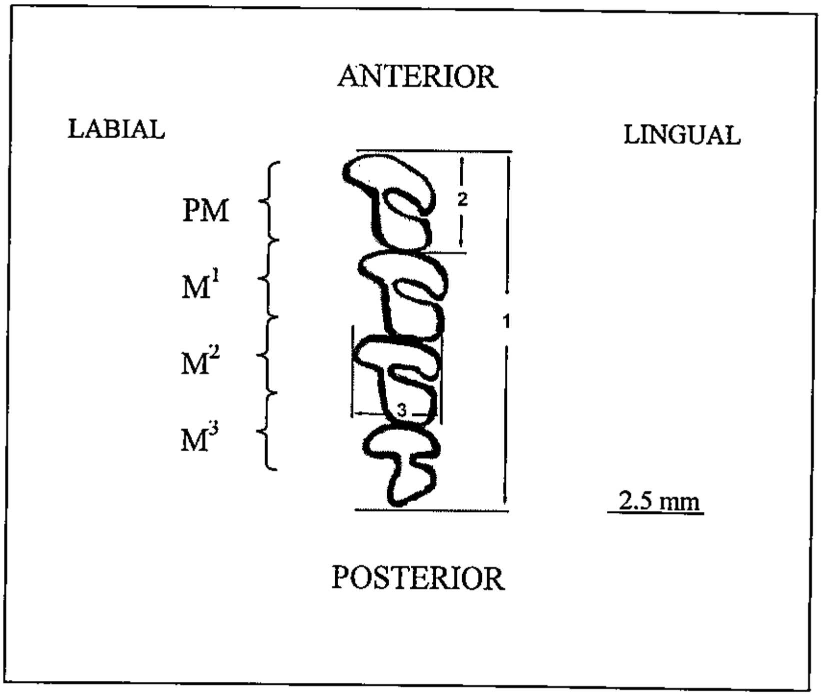
Archaic and Agricultural periods recovered from the archaeological site Quivolgo (Saavedra et al. 1991), were compared with trapped individuals from Tregualemu. We expect to find gradual increase in asymmetry from ancient to modern samples. Asymmetry should show a maximum level in extant populations captured in Tregualemu. At the spatial scale we compared populations of Tregualemu with the IEEUACH, under the expectation to find higher levels of asymmetry in Tregualemu specimens.

A total of 71 specimens of *O. bridgesi* were measured for asymmetry comparisons. Due to limitations imposed by archaeozoological material, asymmetry was estimated using maxilla and associated elements like upper molars and alveoli, where 17 measurements were made (Fig. 2, see Table 1 from Appendix). Due to conservation variability among archaeozoological and trapped individuals, number of observations varied among comparisons, and are properly indicated in each analysis.

Prior to morphological analysis, the existence of fluctuating asymmetry must be demonstrated. Also, the analysis of fluctuating asymmetry depends on the accuracy of the measurement that permits the definition of the asymmetry pattern (Palmer & Strobeck 1986, Palmer 1996b). To satisfy methodological requirements imposed by this morphological descriptor, each variable was measured twice, and both measurements were compared with t and F statistics (Palmer 1996b, Tables 2 and 3 from Appendix). Additionally, size dependence of each variable was estimated using body mass as a proxy (Appendix Tables 4 and 5). After FA is differentiated from measurement error, and size dependence is controlled, normality for the variable must be estimated. To do this, descriptive statistics of (Right-Left) estimations, along with normality estimation using Kolmogorov-Smirnov were established for each variable in archaeozoological and trapped specimens (Tables 6 and 7 from Appendix). In case of elevated measurement error, size dependency or lack of normality, the variable was eliminated from the analysis.

Three different indexes were used to estimate FA: FA1 (mean unsigned difference between right and left side of the variable), FA4 (variance of signed difference between right and left side of the variable) and FA10 (between-sides variance after removing the effects of measurement error estimated for each variable), as suggested by Palmer 1996b (Tables 8 and 9 from Appendix). Each index was compared among periods (Archaic, Agricultural and Present). Indexes FA1 and FA4 were compared using a two-way analysis of variance, with time and variable as factors. Due to low sample and unequal numbers among groups, spatial comparison was made only with FA4, using an F test. In this case, and to reduce variation among museum specimens, we compared FA among specimens trapped in Tregualemu, with a sub-sample from IEEUACH that came from one population located in Ñuble. In this case,

FIGURE 2. Right upper tooth row of *Octodon bridgesi*, indicating examples of measurement used in fluctuating asymmetry analysis. 1: Length of upper tooth row. 2: Length of upper PM. 3: Width of upper M^2.



seven additionally cranial variables were compared among populations (see Appendix for variable list). Finally, the population index FA11, that averages non-signed differences among measurements and samples (Palmer 1996b), was estimated and compared for Archaic, Agricultural and Present samples.

RESULTS

A total of 273 bp were amplified in all present day specimens from Tregualemu, and IEEUACH. Additionally, 397 bp were sequenced for Tregualemu specimens, and used in for population analysis with a total of 670 bp. Although we analyzed the mtDNA control region, the number of mutations observed in our sample was low. This fact is reflected in the presence of few polymorphic sites, especially in the IEEUACH (Table 1). Even for the largest sequence, only ten polymorphic sites were found.

TABLE 1. Genetic description of samples of *Octodon bridgesi*. Population of Tregualemu was analyzed based on all sequenced 670 BP. Additionally, and for comparative purposes only, we show genetic analysis based on 273 bp for population of Tregualemu and specimens deposited in the mammal's collection of the Instituto de Ecología, Universidad Austral de Chile (IEEUACH).

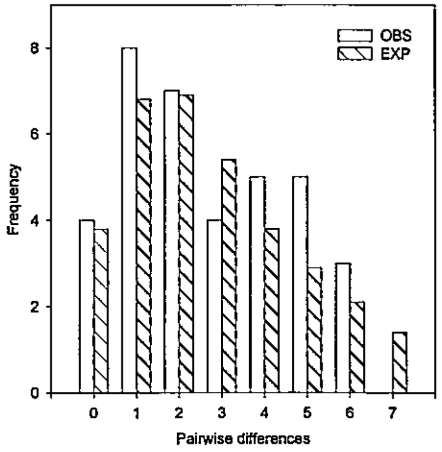
	TREGUALEMU$_{670}$	TREGUALEMU$_{273}$	IEEUACH
Number of specimens	9	9	10
Loci	670	273	273
Number of polymorphic sites	10	4	3
Mean number pairwise	1.815 ± 1.15	1.02 ± 0.7	0.955 ± 0.71
Θ_S	2.21 ± 1.23	1.47 ± 1.01	1.06 ± 0.70
$\Theta\pi$	1.82 ± 1.30	1.03 ± 0.8	0.96 ± 0.80

Contrary to our expectations, Tregualemu did not show genetic differentiation from IEEUACH (F=0.238; P>0.05), indicating similar demographic behavior in both populations. Despite a Holocene history of geographic shrinkage, the analyzed population of *O. bridgesi* does not address reduction in population size in their present day genealogical structure (Table 2). Tajima's neutral statistic were non-significant for Tregualemu (D= -0.794; P>0.1), and IEEUACH (D= -0.355; P>0.1). Although these values were non-significant, both are negative indicating an excess of low frequency haplotypes, characteristic of an expanding population (Table 2). More powerful Fu & Li's Test (1993) supports Tajima's results for Tregualemu sample (D*=0.8042; P>0.1), indicating that this population has maintained a stable population though time. Frequency of mismatched distribution of Tregualemu resembled a population that is in expansion, more than a constant size population (Fig. 2). Both models estimated positive θ, although they were not significant, probably due to low polymorphism (Table 1). Finally, θ estimated under a maximum likelihood approximation suggests that Tregualemu and IEEUACH did not experience changes in their population size. Nevertheless, when model was allowed to experience size change, it increases in time (Table 2).

TABLE 2. Demographic estimations of populations of *Octodon bridgesi* from Tregualemu, VII Región and from specimens deposited in the mammal's collection of the Instituto de Ecología, Universidad Austral de Chile (IEEUACH).

ESTIMATOR	TREGUALEMU	IEEUACH
Mismatch Observed Mean	2.694	0.956
Mismatch Observed Variance	3.533	0.862
τ	1.049	1.49
Θ_0	2.278	0
Θ_1	296.87	2.38
Sum of Squared deviation	0.0083 (ns)	0.0089 (ns)
Harpending's Raggedness index	0.0308 (ns)	0.0642 (ns)
Maximum Likelihood		
$\Theta_{\text{Constant size}}$	0.0044 (ns)	0.0074 (ns)
Θ_{Growth}	0.1169 ± 0.02	0.0056 ± 0.002

FIGURE 3. Observed and expected pairwise mismatch differences among mtDNA sequences of control region of *Octodon bridgesi* from Tregualemu, based on constant and growing population size models.



Fluctuating asymmetry. Asymmetry of maxilla from *O. bridgesi* did not change in time or space (Tables 4, 5, and 6). Although FA was present in all of the analyzed variables from archaeozoological and modern samples (Appendix Tables 5 and 6), this character did not increase towards recent time as was expected (Tables 4 and 5).

Time did not affect FA level among analyzed variables, and neither did space (Tables 5 and 6). Spatial comparison among between populations of *O. bridgesi* did not showed differences in FA level between Tregualemu and IEEUACH (Tables 6). But when FA11 population index was compared between extant populations of *O. bridgesi*, it showed elevated records in Tregualemu population, contrary to our expectations.

TABLE 3. Levene tests for fluctuating asymmetry estimates (FA10) of specimens of *Octodon bridgesi* from Archaic, Agricultural and Actual periods recovered from Quivolgo, and Tregualemu (VII Region, Chile). See Appendix for acronyms.

VARIABLE	MS Effect	MS Error	d.f. Error	F	P
UPTOROWAL	0.0012	0.0054	39	0.22	0.81
WIDUPM	0.0012	0.0028	26	0.45	0.64
WIDTHM^{1}	0.0009	0.0013	26	0.72	0.49
WIDTHM^{2}	0.0007	0.0011	22	0.66	0.53
LONGUPM	0.0007	0.0026	24	0.29	0.75
LONGM^{1}	0.0033	0.0042	25	0.78	0.47
LONGM^{2}	0.0078	0.0095	20	0.83	0.45
LONGM^{3}	0.0039	0.0038	17	1.02	0.38
WIDUPMAL	0.0136	0.0044	47	3.06	0.06
WIDM^{1}AL	0.0006	0.0039	42	0.15	0.86
WIDM^{2}AL	0.0001	0.0021	41	0.04	0.96
WIDM^{3}AL	0.0050	0.0022	23	2.30	0.12
LONGUPMAL	0.0045	0.0038	46	1.19	0.31
LONGM^{1}AL	0.0005	0.0021	43	0.23	0.79
LONGM^{2}AL	0.0008	0.0016	38	0.52	0.60
LONGM^{3}AL	0.0013	0.0016	22	0.84	0.44

TABLE 4. ANOVA for periods and fluctuating asymmetry variables estimated for specimens of *Octodon bridgesi* from Archaic, Agricultural and Actual periods, recovered from Quivolgo and Tregualemu (VII Región, Chile).

SOURCE OF VARIATION	d.f. Effect	MS Effect	d.f. Error	MS Error	F	P
AGE	2	0.006	204	0.008	0.800	0.45
VARIABLE	5	0.018	204	0.008	2.369	0.04
INTERACTION	10	0.006	204	0.008	0.733	0.69

TABLE 5. F test for comparison of fluctuating asymmetry among specimens trapped in Tregualemu (VII Región, Chile) and specimens deposited in the mammal's collection of the Instituto de Ecologia y Evolución, Universidad Austral (IEEUACH), and a sub-sample of this collection captured in Ñuble. See Appendix for acronyms.

	TREGUALEMU/IEEUACH			TREGUALEMU/ÑUBLE		
VARIABLE	F	N1/N2	P	F	N1/N2	P
WIDUPINC	1.14	15/19	0.60	1.21	8/15	0.64
UPTOROW	4.41	16/18	0.99	6.62	16/7	0.99
LOTOROW	1.08	16/19	0.57	1.34	8/16	0.70
LONROS	2.56	18/16	0.97	3.44	8/16	0.98
WIDEYEFO	1.11	19/16	0.58	1.11	16/8	0.54
WIDLOPM	1.09	19/16	0.56	1.69	8/16	0.82
HIGMAND	1.66	15/16	0.83	1.76	7/16	0.83

TABLE 6. Fluctuating population asymmetry index FA11 from taphocenosis of *Octodon bridgesi* recovered from Quivolgo, and extant specimens trapped in Tregualemu and deposited in the mammal's collection of the Instituto de Ecología y Evolución, Universidad Austral de Chile (IEEUACH).

COMPARISON	FA 11
TIME	
ARCHAIC	0.5600
AGRICULTURAL	0.6500
PRESENT	0.6690
POPULATION	
TREGUALEMU	1.0071
IEEUACH	1.7808

DISCUSSION

Contrary to our expectations, historical range reduction and contemporaneous habitat modification did not trigger any significant change in demographic parameters of a population located in the northern limit of the geographical range of *O. bridgesi*. Moreover, range reduction and habitat modification did not trigger temporal or spatial changes in fluctuating asymmetry as well. All coalescent estimators of population demography suggest that analyzed population of *O. bridgesi,* behaves as a demographically stable population. Moreover, the demographic analysis gives some indication of population expansion, just the opposite we expected. In the same line, FA parameters that normally are associated with population size reductions or intense habitat modifications (Manning & Chamberlain 1994, Wauters et al. 1994), do not change in studied population, corroborating demographic analysis. The analysis of longer segments of mtDNA, containing a greater amount of polymorphic sites, or demographic inference based on other neutral markers (e.g. microsatellites) should give this pattern a stronger support.

Contrary to our expectations these results indicate that reduction of geographic range due to antropic effect did not affect population size in the analyzed extant population of *O. bridgesi*. This indicates that despite range modifications, at local level populations of *Octodon bridgesi* were able to sustain stable populations. If observed demographic parameters are true, then other non-neutral genetic markers like isozymes should elevated levels of heterozygosity. If this is observed, FA findings will have a stronger support. These tests remains to be done. Also, the lack of FA variation observed in our analysis can change if other variables like limbs are included in morphological analysis. Unfortunately, the nature of adequate zooarchaeological samples prevent this analysis, since cranial elements are the most common remains that can be recovered after a taphonomic process. Ability of *O. bridgesi* to use highly modified habitat where native forest has been replaced by exotic plantations can explain in part observed genetic and morphological pattern at the local level. Despite intense habitat modification, populations of *O. bridgesi* use exotic plantations (Capítulo 3), and survive eating exotic vegetation (leaves and phloem) (Muñoz et al. 1990). This ability probably prevented the reduction of population sizes of *O. bridgesi* at local scale, conferring resilience to the species to this perturbation, that is manifested at population level in the lack of genetic changes, and at individual level with the absence of morphological changes.

An alternative explanation to demographic and morphological pattern may be associated to the history of the forests of this region. Along with *O. pacificus* (Hutterer 1994, Apéndice 3), *O. bridgesi* are the two members of this genus that live in close association to southern forests (Greer 1968, Mann 1978, Hutterer 1994). Holocene forest distribution changed drastically during last glacial maximum, when vast areas of east and southern Chile were covered by ice (Villagrán 1994, Villagrán et al. 1995). Coastal forests from central-south Chile however, were less affected by glaciation (Armesto et al. 1995). During this period, these forests probably acted as refuges for the fauna. After the ice retreat, these populations might have acted as sources of recolonization of the newly developed forests, which can explain observed pattern of mismatch distribution. Recent findings of *O. bridgesi* on the east side of the Andean range (Verzi & Alcover 1990, Podestá et al. 2000) can be an indirect evidence of the southern direction of the expansion for populations of *O. bridgesi*. Evidence from other genetic markers, taken from analyzed and southern populations can help to clarify this hypotheses.

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APPENDIX

Table 1. List of acronyms of cranial measurements used in analysis and listed tables.

ACRONYMS	DEFINITION
UPTOROWAL	Upper tooth row at alveoli
WIDUPM	Width of upper pre-molar
WIDTHM^1	Width of upper molar 1
WIDTHM^2	Width of upper molar 2
LONGUPM	Length of upper pre-molar
LONGM^1	Length of upper molar 1
LONGM^2	Length of upper molar 2
LONGM^3	Length of upper molar 3
WIDUPMAL	Width of upper pre-molar alveoli
WIDM^{1}AL	Width of upper molar 1 alveoli
WIDM^{2}AL	Width of upper molar 2 alveoli
WIDM^{3}AL	Width of upper molar 3 alveoli
LONGUPMAL	Length of upper pre-molar alveoli
LONGM^{1}AL	Length of upper molar 1 alveoli
LONGM^{2}AL	Length of upper molar 2 alveoli
LONGM^{3}AL	Length of upper molar 3 alveoli
WIDUPINC	Width of upper incisives
UPTOROW	Length of upper tooth row
LOTOROW	Length of lower tooth row
LONROS	Length of rostrum
WIDEYEFO	Width of eyes
WIDLOPM	Width of lower pre-molar
HIGMAND	High of mandible

TABLE 2. t and F statistics between mean and variance of first and second measurement made on left and right sides of cranial variables measured from archaeozoological specimens of *Octodon bridgesi* recovered from Quivolgo, VII Región, Chile. See acronyms in Table 1 from Appendix.

VARIABLE	MEAN 1st	MEAN 2nd	N 1st	N 2nd	t	P	SD 1st	SD 2nd	F	P_F
UPTOROWA	8.30	8.29	44	44	0.05	0.96	1.34	1.34	1.00	0.99
WIDUPM	2.22	2.21	26	26	0.33	0.74	0.13	0.12	1.17	0.69
WIDTHM^1	2.08	2.05	24	24	0.53	0.60	0.17	0.16	1.15	0.75
WIDTHM^2	1.96	1.93	16	16	0.37	0.71	0.18	0.20	1.19	0.74
LONGUPM	2.27	2.25	26	26	0.39	0.70	0.20	0.16	1.62	0.24
LONGM^1	2.10	2.09	24	24	0.33	0.74	0.14	0.12	1.20	0.67
LONGM^2	2.07	1.99	14	14	1.14	0.26	0.22	0.17	1.72	0.34
LONGM^3	2.13	2.07	6	6	0.22	0.83	0.56	0.50	1.26	0.81
WIDUPMAL	2.58	2.56	66	66	0.50	0.62	0.23	0.26	1.25	0.36
WIDM^{1}AL	2.21	2.24	56	56	-0.56	0.58	0.22	0.22	1.06	0.84
WIDM^{2}AL	2.17	2.15	52	52	0.50	0.62	0.22	0.21	1.15	0.63
WIDM^{3}AL	1.88	1.94	20	20	-1.32	0.19	0.15	0.14	1.12	0.81
LONGUPMA	2.83	2.83	66	66	0.03	0.98	0.30	0.30	1.00	0.99
LONGM^{1}AL	2.32	2.34	58	58	-0.41	0.68	0.20	0.21	1.16	0.57
LONGM^{2}AL	2.18	2.19	54	54	-0.35	0.73	0.16	0.16	1.01	0.97
LONGM^{3}AL	2.14	2.09	20	20	1.42	0.16	0.10	0.12	1.29	0.58

TABLE 3. t and F statistics between mean and variance of first and second measurement made on left and right sides of cranial variables measured from specimens of *Octodon bridgesi* trapped in Tregualemu, VII Region, Chile. See acronyms in Table 1 from Appendix.

VARIABLE	MEAN 1st	MEAN 2nd	N 1st	N 2nd	t	P	SD 1st	SD 2nd	F	P_F
UPTOROWA	9.81	9.80	28	28	0.06	0.95	0.40	0.44	1.19	0.66
UPTOROWC	8.72	8.68	22	20	0.29	0.77	0.45	0.40	1.26	0.61
WIDUPM	2.11	2.13	32	32	-0.27	0.79	0.20	0.17	1.41	0.34
WIDTHM^1	2.03	2.07	34	34	-1.12	0.27	0.16	0.16	1.01	0.99
WIDTHM^2	2.03	2.00	34	34	0.87	0.39	0.14	0.14	1.11	0.77
WIDTHM^3	1.63	1.61	34	34	0.66	0.51	0.15	0.14	1.14	0.71
LONGUPM	2.16	2.14	28	28	0.40	0.69	0.19	0.21	1.20	0.64
LONGM^1	2.05	2.03	32	32	0.58	0.57	0.12	0.13	1.18	0.65
LONGM^2	1.99	1.96	32	32	0.70	0.49	0.15	0.14	1.13	0.73
LONGM^3	1.73	1.77	34	34	-0.86	0.39	0.17	0.17	1.02	0.95
WIDUPMAL	2.45	2.37	34	34	1.68	0.10	0.20	0.19	1.09	0.80
WIDM^{1}AL	2.34	2.32	34	34	0.40	0.69	0.22	0.21	1.07	0.84
WIDM^{2}AL	2.30	2.30	34	34	0.00	1.00	0.20	0.20	1.02	0.97
WIDM^{3}AL	1.98	1.99	30	30	-0.44	0.66	0.13	0.10	1.47	0.31
LONGUPMA	2.45	2.46	32	32	-0.04	0.97	0.35	0.34	1.07	0.86
LONGM^{1}AL	2.18	2.21	32	32	-0.46	0.65	0.24	0.20	1.45	0.31
LONGM^{2}AL	2.19	2.18	30	30	0.19	0.85	0.23	0.18	1.68	0.17
LONGM^{3}AL	2.06	2.04	28	28	0.27	0.79	0.19	0.20	1.12	0.77

TABLE 4. Spearman correlation between absolute value of (Right-Left) sides from cranial variables, and weight (gr.) of specimens of *Octodon bridgesi* from Tregualemu, VII Región, Chile.

VARIABLE	r_s	N	P
Width upper incisive	0.30	7	0.51
Upper tooth row	-0.05	8	0.91
Lower tooth row	0.33	7	0.47
Rostrum length	-0.41	7	0.36
Width eye foramen	0.43	7	0.34
High eye foramen	-0.21	7	0.65
High mandible	0.00	7	1.00
Width upper pre-molar	-0.79	8	0.02
Width lower pre-molar	-0.45	7	0.31

TABLE 5. Spearman correlation between absolute value of (Right-Left) sides from cranial variables, and weight (gr.) of specimens of *Octodon bridgesi* from Mammal's Collection from the Universidad Austral, VII Region, Chile.

VARIABLE	r_s	N	P
Width upper incisive	0.45	17	0.07
Upper tooth row	-0.09	16	0.74
Lower tooth row	0.22	17	0.39
Rostrum length	0.15	16	0.59
Width eye foramen	0.19	17	0.48
High mandible	-0.28	14	0.33
Width upper pre-molar	0.05	17	0.84
Width lower pre-molar	0.14	17	0.59

TABLE 6. Descriptive statistics for (Right-Left) difference from cranial variables measured from archaeozoological specimens of *Octodon bridgesi* recovered from Quivolgo, VII Región, Chile. VAR, Variance; KUR, Kurtosis; D, Kolmogorov-Smirnov statistics. All D values are non significant. See acronyms in Table 1 from Appendix.

VARIABLE	MEAN	VAR	SKEW	KUR	N	D
UPTOROWAL	-0.007	0.030	0.652	0.596	27	0.15
WIDUPM	-0.008	0.016	-1.324	1.292	13	0.29
WIDTHM^{1}	0.000	0.009	0.755	0.161	12	0.25
WIDTHM^{2}	-0.013	0.007	0.277	-1.392	8	0.22
LONGUPM	0.069	0.009	0.037	-0.818	13	0.22
LONGM^{1}	0.092	0.026	0.160	-1.710	12	0.21
LONGM^{2}	0.029	0.029	-0.618	-1.396	7	0.23
LONGM^{3}	-0.067	0.003	1.732		3	0.38
WIDUPMAL	0.030	0.022	-0.317	1.853	33	0.19
WIDM^{1}AL	-0.007	0.024	0.194	-0.130	28	0.19
WIDM^{2}AL	0.037	0.014	0.108	-0.315	27	0.18
WIDM^{3}AL	0.060	0.014	0.989	0.751	10	0.29
LONGUPMAL	0.003	0.019	0.626	-0.368	33	0.20
LONGM^{1}AL	0.021	0.012	0.103	-0.676	29	0.19
LONGM^{2}AL	-0.033	0.012	0.183	-0.778	27	0.20
LONGM^{3}AL	0.010	0.008	-0.223	-1.734	10	0.24

TABLE 7. Descriptive statistics for (Right-Left) difference from cranial variables measured from specimens of *Octodon bridgesi* trapped in Tregualemu, VII Región, Chile. VAR, Variance; KUR, Kurtosis; D, Kolmogorov-Smirnov statistics. All D values are non significant. See acronyms in Table 1 from Appendix.

VARIABLE	MEAN	VAR	SKEW	KUR	N	D
UPTOROWAL	0.14	0.02	0.01	-0.36	14	0.21
UPTOROWCR	0.10	0.03	-0.35	-1.53	11	0.25
WIDUPM	0.06	0.02	-0.21	-0.17	16	0.18
WIDTHM^1	0.00	0.01	0.71	-0.63	17	0.24
WIDTHM^2	-0.06	0.01	-0.15	-0.56	17	0.24
WIDTHM^3	-0.02	0.01	0.02	-0.82	17	0.17
LONGUPM	0.01	0.02	0.69	0.80	14	0.26
LONGM^1	-0.06	0.01	0.19	-0.95	16	0.23
LONGM^2	0.00	0.00	0.00	0.03	16	0.31
LONGM^3	0.04	0.02	0.20	0.15	17	0.21
WIDUPMAL	0.00	0.02	0.00	-1.10	17	0.20
WIDM^{1}AL	0.02	0.02	-0.61	0.58	17	0.24
WIDM^{2}AL	0.07	0.01	-0.31	-1.49	17	0.21
WIDM^{3}AL	0.07	0.01	-0.28	-0.65	15	0.23
LONGUPMAL	0.07	0.02	1.08	1.39	16	0.26
LONGM^{1}AL	-0.01	0.02	0.12	-0.91	17	0.19
LONGM^{2}AL	0.05	0.01	-0.15	-0.84	15	0.24
LONGM^{3}AL	0.03	0.02	-0.10	-0.88	14	0.16

TABLE 8. Fluctuating asymmetry (FA) indexes 1 and 4 estimated for archaeozoological specimens of *Octodon bridgesi* recovered from Quivolgo (VII Región, Chile), for Archaic and Agricultural periods (see text for description and dates of each period). See acronyms in Table 1 from Appendix.

	ARCHAIC			AGRICULTURAL		
VARIABLE	FA1	FA4	N	FA1	FA4	N
UPTOROWAL	0.1083	0.0136	12	0.1313	0.0143	16
WIDUPM	0.0500	0.0030	6	0.1143	0.0114	7
WIDTHM^1	0.0667	0.0027	6	0.0667	0.0067	6
WIDTHM^2	0.0667	0.0033	3	0.0600	0.0030	5
LONGUPM	0.0833	0.0057	6	0.0857	0.0081	7
LONGM^1	0.2167	0.0097	6	0.0667	0.0067	6
LONGM^2	0.1667	0.0033	3	0.1250	0.0092	4
WIDUPMAL	0.1000	0.0057	15	0.1167	0.0156	18
WIDM^{1}AL	0.1167	0.0106	12	0.1250	0.0073	16
WIDM^{2}AL	0.0727	0.0042	11	0.1125	0.0065	16
WIDM^{3}AL	0.0500	0.0033	4	0.1000	0.0160	6
LONGUPMAL	0.0933	0.0064	15	0.1167	0.0085	18
LONGM^{1}AL	0.0923	0.0058	13	0.0750	0.0047	16
LONGM^{2}AL	0.1167	0.0052	12	0.0733	0.0035	15
LONGM^{3}AL	0.0750	0.0025	4	0.0667	0.0027	6

TABLE 9. Fluctuating asymmetry (FA) indexes 1, 4 and 10 estimated for specimens of *Octodon bridgesi* trapped in Tregualemu (VII Región, Chile).

VARIABLE	FA1	N	FA4	N	FA10	d.f.$_{num}$/d.f.$_{den}$
UPTOROWAL	0.1714	14	0.0242	14	0.0045	13/28
UPTOROWCR	0.1727	11	0.0340	11	0.0043	9/20
WIDUPM	0.1125	16	0.0172	16	0.0028	15/32
WIDTHM^1	0.0824	17	0.0113	17	0.0004	16/34
WIDTHM^2	0.0765	17	0.0074	17	-0.0010	16/34
WIDTHM^3	0.0941	17	0.0144	17	-0.0009	16/34
LONGUPM	0.1000	12	0.0167	14	0.0096	13/28
LONGM^1	0.0938	16	0.0106	16	0.0011	15/32
LONGM^2	0.0375	16	0.0040	16	0.0004	15/32
LONGM^3	0.1000	17	0.0201	17	0.0046	16/34
WIDUPMAL	0.1059	17	0.0163	17	-0.0060	16/34
WIDM^{1}AL	0.1118	17	0.0215	17	-0.0028	16/34
WIDM^{2}AL	0.1176	17	0.0147	17	-0.0040	16/34
WIDM^{3}AL	0.0824	17	0.0095	15	-0.0021	14/30
LONGUPMAL	0.1000	15	0.0170	16	-0.0062	15/32
LONGM^{1}AL	0.1000	17	0.0156	17	0.0003	16/34
LONGM^{2}AL	0.0867	15	0.0098	15	-0.0019	14/30
LONGM^{3}AL	0.1000	14	0.0160	14	0.0008	13/28

CAPÍTULO 5

BILATERAL ASYMMETRY AND MATE PREFERENCE BY DIURNAL AND NOCTURNAL RODENTS BETWEEN REPRODUCTIVE AND NON-REPRODUCTIVE PERIODS[5]

Asimetría bilateral y preferencia de pareja por roedores diurno y nocturno en período reproductivo y no-reproductivo

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[5] Para ser publicado como: Saavedra B, RA Vásquez & JA Simonetti. Bilateral asymmetry and mate preference by diurnal and nocturnal rodents between reproductive and non-reproductive periods.

RESUMEN

La asimetría fluctuante está presente en numerosos caracteres y refleja calidad del individuo. En selección de pareja, congéneres simétricos deberían ser preferidos respecto de aquellos asimétricos. Las habilidades sensoriales varían entre períodos reproductivos y no-reproductivos, pudiendo afectar las preferencias de pareja. Acá evaluamos selección de pareja entre individuos con asimetría contrastante en el roedor diurno *Octodon degus*, y el nocturno *O. bridgesi*, tanto en época reproductiva como no-reproductiva. Nuestros resultados indican que especímenes del género pueden discriminar entre potenciales parejas con asimetría contrastante, y que el período reproductivo parece jugar un rol significativo para modelar estas preferencias. No se observó una preferencia consistente por parejas simétricas, contradiciendo lo esperado. La asimetría fluctuante jugaría un rol variable en la selección de pareja, por lo que debe ser comprobada y no asumida. Es interesante destacar que ambas especies usaron claves visuales para determinar sus preferencias, a pesar de tener hábitos circadianos contrastantes.

ABSTRACT

Fluctuating asymmetry is present in many characters, and reflects overall individual's quality. In mate selection symmetric congeners should be preferred over asymmetric ones. Sensorial abilities vary among reproductive and non-reproductive periods, and may affect mate preferences. Here, we test mate choice among individuals with contrasting asymmetry in diurnal *Octodon degus*, and nocturnal *O. bridgesi* rodents, in reproductive and non-reproductive periods. Our results indicate that specimens of *Octodon* can discriminate among potential partners with opposite asymmetry levels, and that reproductive period seems to play a significant role in modeling these preferences, since they change among periods in all analyzed cases. A consistence preference for symmetrical mates was not observed, contradicting expectations advanced by sexual selection and asymmetry. Our results support the contention that fluctuating asymmetry plays a variable role in the definition of mate choice, and therefore it should not be assumed. It is interesting to notice that species use visual cues to make decision, despite their contrasting diurnal and nocturnal life styles.

INTRODUCTION

Fluctuating asymmetry (FA) refers to small random deviations among left and right sides of characters of an individual, that are determined by genetic and environmental stress (Palmer & Strobeck 1986). FA is a morphological signal present in many characters that reflects overall individual's quality (Nilsson 1994). Since FA is the consequence of individual developmental stability, it can be used as a cue to address organism quality in decision making in intrasexual and intersexual interactions (Møller & Pomiankowski 1993). Particularly during intersexual encounters, like mate selection, symmetric congeners should be preferred over asymmetric ones, increasing the probability of transferring good genes to descendants (Møller & Swaddle 1997). The role that FA plays in mammalian intersexual encounters has been largely evaluated in species with well developed secondary sexual characters (e.g. Gomendio et al. 2000; Møller et al. 1996), while species with reduced or non-dimorphic characters have remained less explored.

Sensorial capacities vary among reproductive and non-reproductive periods, associated to different neuronal development produced by hormonal changes (Nelson 1995). Hormones and other neuroendocrine factors influence not only signals used in mammalian communication, but also the sensory systems involved in detecting such materials and extracting information from them (Doty 1986). Changes in mate preferences among reproductive periods have been largely described in humans (e.g. Gangestad & Thornhill 1998; Penton-Voak et al. 1999), while the exploration of mate preferences among different reproductive periods has remained less explored in other groups. Also for humans, the role that visual cues play in mate selection behavior has received significant attention (Thornhill & Grammer 1999; Johnston et al. 2001), on the contrary for other mammals the role that visual abilities have on mate selection behavior has remained less explored compared to other mechanisms like the olfactory systems (see Nelson 1995). Particularly if mate choice is made by diurnal and nocturnal species, it is interesting to evaluate the role visual cues may have in organisms that have contrasting circadian rhythms. It is possible to expect that diurnal species that presumably rely more on visual evidence to make decisions, find in symmetry a useful clue to mate choice. The contrary may be expected for nocturnal taxa.

Octodon, a native South American rodent genus embraces diurnal and nocturnal species. *O. degus* is a diurnal rodent that lives in colonies associated to shrubland habitats. Its reproductive period spans from May to September (Redford & Eisenberg 1992).

Testosterone level of this species increases during reproductive period, although they achieve lower level compared to other rodents (Kenagy et al. 1999), indicating that sensory changes may be expected during the year for this species. *O. bridgesi* is a nocturnal species that thrives in more dense vegetation, whose reproductive period spans form June to October-November (Muñoz-Pedreros 2000).

Here, we experimentally test mate choice among individuals with contrasting asymmetry in diurnal *O. degus*, and nocturnal *O. bridgesi* in reproductive and non-reproductive periods. We evaluate preference for mate partners with contrasting natural fluctuating asymmetry differences, and also by induced artificial asymmetry. Since artificial asymmetry is a stronger signal compared to FA, we expect to find intense preferences in these experiments. Due to hormonal-driven changes during reproductive period, we expect that preference for symmetric congeners increase during this time of the year. Also, since preference tests were based on visual indications, we expect to find a pronounced ability to choose in *O. degus*, the diurnal species.

METHODS

Individuals of *Octodon degus* and *O. bridgesi* were used in mate choice experiments with conspecifics of the opposite sex with contrasting asymmetry. These experiments were made during reproductive and non-reproductive periods, using natural fluctuating asymmetry and artificial asymmetry. Individuals were captured in the field and maintained in laboratory conditions in individual cages, with water and food *ad lib*, under a 12:12 photoperiod. Experiments lasted three hours, and were completely taped. The first hour was discarded from analysis, since it was considered an acclimatization period. Experiments with *O. degus* were made during the day, under natural illumination, while experiments with *O. bridgesi* were performed at night under red light. In each experiment, a test individual (male or female) was faced to two individuals of the opposite sex with contrasting asymmetry (either fluctuating asymmetry or experimental) in an experimental arena (80x80x30 cm). The test individual was able to completely see the stimulus pair, and to freely move in arena. Stimulus pair was randomly assigned to separated compartments, not able so see each other, and acoustically not-isolated.

Natural fluctuating asymmetry. Five external measurements (eye size, ear size, rostrum size, and width of incisive and nostrils) were taken to assess a general asymmetry pattern for each individual. All individuals were measured by a digital caliper (0.01 mm precision) twice by the same person, while animal was motionless. FA was established after comparing two measurements, and assessing normal distribution (Palmer & Strobeck 1986; Merilä & Björklund 1995, data not shown). FA was estimated for each variable as the absolute difference among left and right side. We averaged FA values for each individual, and arranged them in a FA axis. Individuals located at the extremes of this distribution, with low and high FA levels were used as stimulus pair. FA experiments were made during non-reproductive period for males and females of both species.

Experimental asymmetry. Asymmetry was artificially generated by the non-injurious cutting of two thirds of vibrissa in two randomly chosen males and females from *O. degus*. For *O. bridgesi* four males were randomly assigned as asymmetric. Experiments were made in reproductive and non-reproductive periods for males and females of *O. degus*, and for females of *O. bridgesi*.

In each experiment, we registered the time test individual spent in four positions in the arena: near or far to the stimulus pair, and in front of symmetric or asymmetric congener. First we compared observed time spent by test individuals near or far from stimulus pair, with time expected if they used arena randomly. We considered time spent in front of symmetrical or asymmetrical congener as an indication of mate preference. We compared observed time spent by test individuals in front of symmetric or asymmetric congeners, with time expected if they showed no preference and use arena at random. All comparisons were made with χ^2 test.

RESULTS

Natural Fluctuating asymmetry. In all experiments (Table 1), individuals made a non-randomly use of the arena. For *O. degus*, females spent significantly more time than expected in quadrants located near the stimulus pair (χ^2=32.0; g.l.=1; P<<0,001). The same was observed for males of this species (χ^2=32.5; d.f.=1; P<0.00001). For *O. bridgesi*, females spent significantly more time than expected in quadrants located near the stimulus pair (χ^2= 792.9; d.f. = 1; P<< 0.0001), and the same was observed for males of *O. bridgesi* (χ^2= 713.3; d.f. = 1; P<0.0001). These results indicate that individuals preferred to stay near the stimulus pair, spending most of the time in the portion of the arena close to them. Due to this, subsequent analyses were made using only the time individuals spent close to stimulus pair.

TABLE 1. Total experimental time used in analysis of mate preference made for *Octodon degus* and *O. bridgesi* under contrasting natural fluctuating asymmetry. In parenthesis number of individuals.

	NON-REPRODUCTIVE
Octodon degus	
Females	991 (8)
Males	932 (9)
O. bridgesi	
Females	1,821 (15)
Males	1,067 (9)

Females of *O. degus* did not show preference among males with contrasting asymmetry, while males preferred asymmetric females over symmetric ones (Fig. 1). On the contrary, females of *O. bridgesi* preferred symmetric males, a pattern not observed in experimental asymmetry experiments (Fig. 1). Males of *O. bridgesi* did not show preferences for symmetric or asymmetric females (Fig. 1).

Experimental asymmetry. In all experiments (Table 2), females and males of *O. degus* and *O. bridgesi* used the arena non-randomly, spending more time close to stimulus pair, compared to the time spent far from stimulus pair (Fig 2). Due to this, subsequent analyses were made only with time spent by test individuals near the stimulus pair.

Females of *O. degus* spent more that expected time near asymmetric males during in non-reproductive period. The opposite was observed during reproductive period (Fig. 3). Males from *O. degus* spent more time than expected near asymmetric females during non-reproductive period, and during reproductive epoch they spent longer periods in front of symmetric females (Fig. 3). Finally, females from *O. bridgesi* spent more time than expected in front of asymmetric males (Fig. 3).

FIGURE 1. Observed and expected time spent by males and females of *Octodon degus* and *O. bridgesi* near or far stimulus pair with contrasting artificial asymmetry in experimental arena, during reproductive and non-reproductive period.

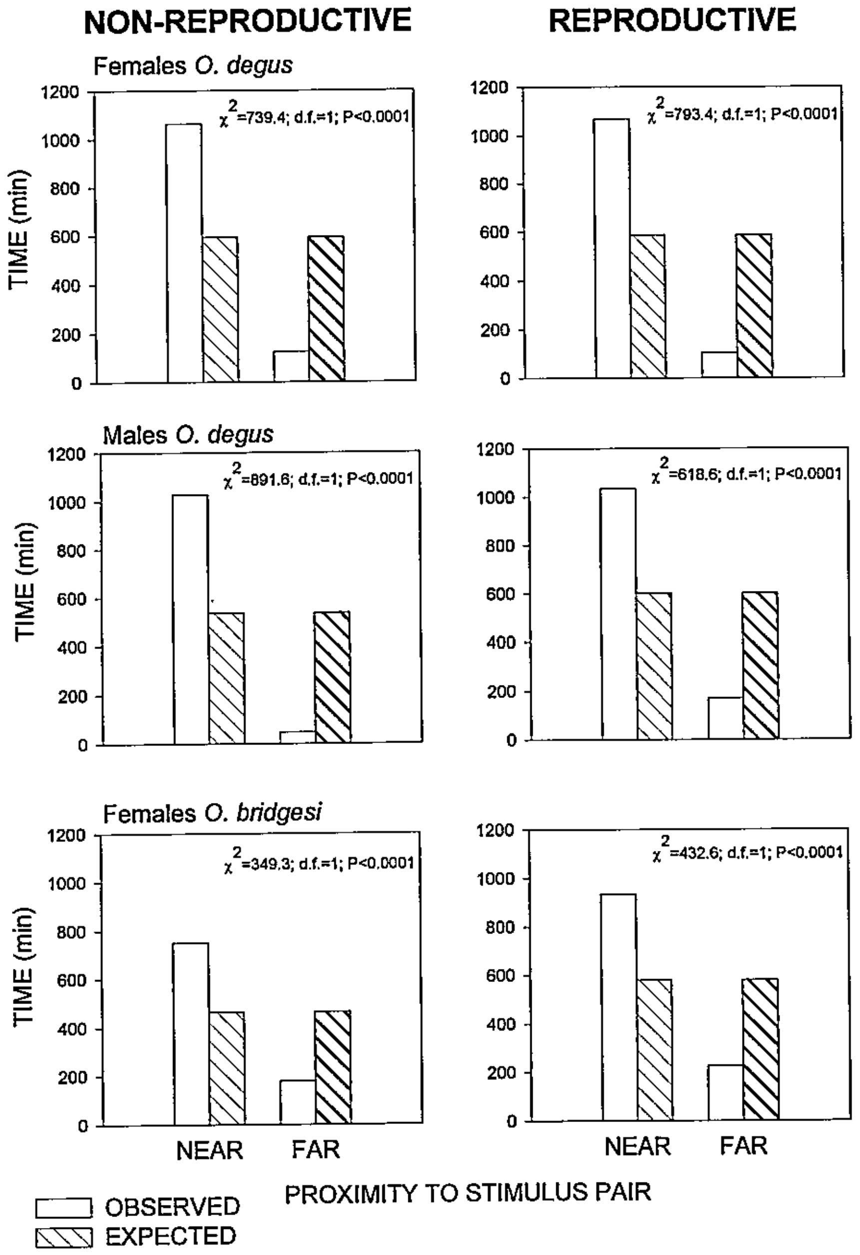


FIGURE 2. Observed and expected time spent by males and females of *Octodon degus*, and females of *O. bridgesi* near symmetrical (SYMM) and asymmetrical (ASYMM) conspecifics of the opposite sex with contrasting fluctuating asymmetry, during non-reproductive period.

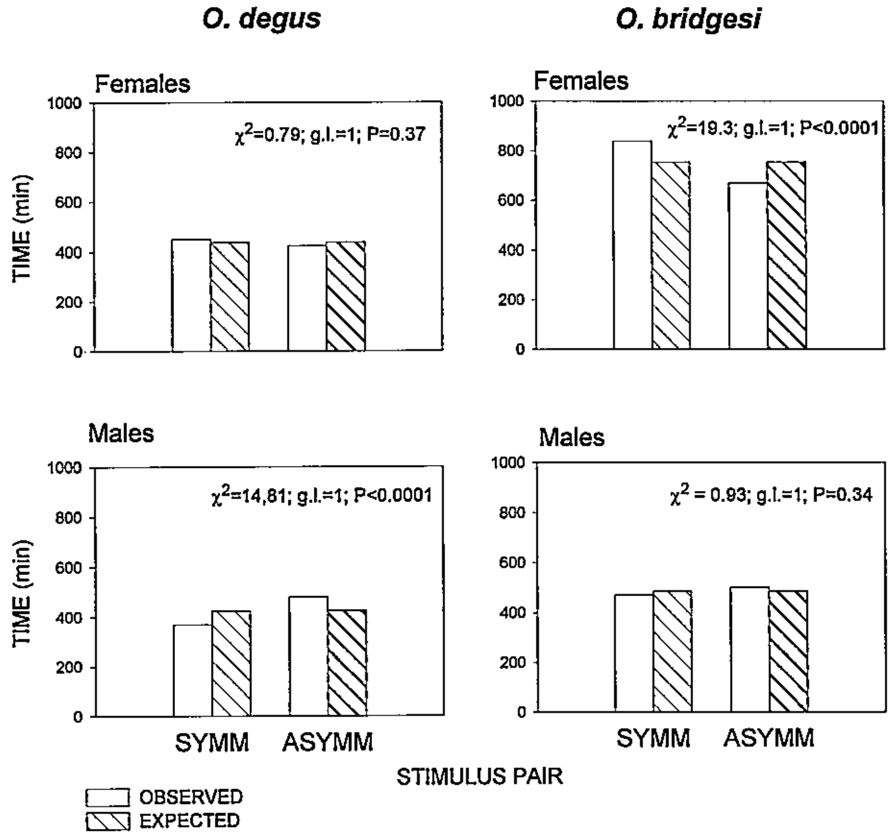
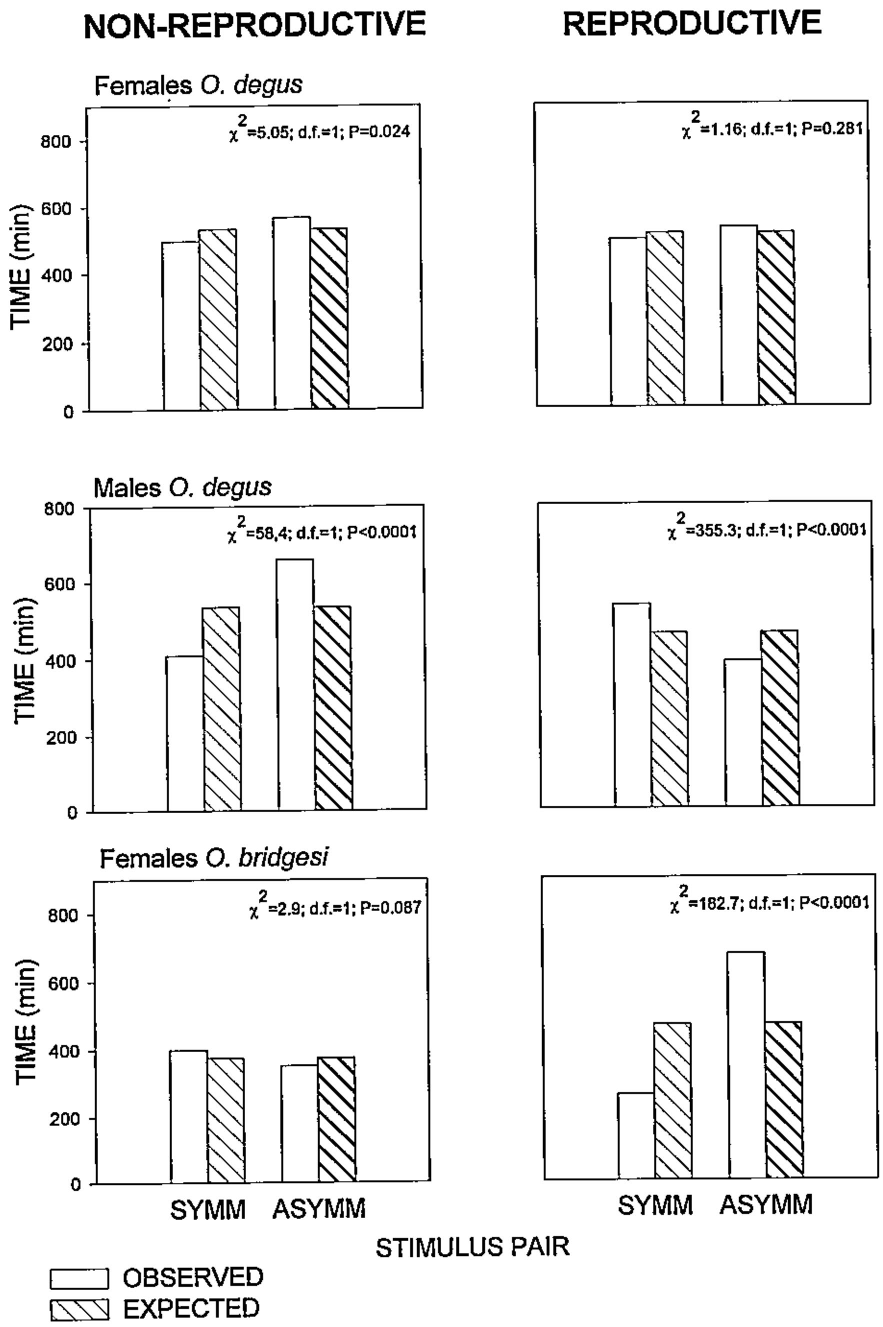


TABLE 2. Total experimental time used in analysis of mate preference made for *Octodon degus* and *O. bridgesi* under contrasting artificial asymmetry. In parenthesis number of individuals.

	NON-REPRODUCTIVE	REPRODUCTIVE
Octodon degus		
Females	1,189 (10)	1,172 (10)
Males	1,074 (9)	1,204 (10)
O. bridgesi		
Females	928 (8)	1,157 (10)

FIGURE 3. Observed and expected time spent by males and females of *Octodon degus* and *O. bridgesi* near symmetrical (SYMM) and asymmetrical (ASYMM) conspecifics of the opposite sex with contrasting artificial asymmetry, during reproductive and non-reproductive period.



DISCUSSION

Individuals of *O. degus* and *O. bridgesi* do discriminate among conspecifics with different levels of asymmetry, and their preference varied pending on reproductive period, sex and also on intensity of asymmetry. Males from *O. degus* prefer asymmetric females during non-reproductive periods, but change this preference during reproductive epoch, choosing symmetric females. *O. bridgesi* showed a different pattern of preferences. When females are faced to experimentally asymmetric males, they choose asymmetric males only during reproductive epoch. In non-reproductive period, females preferred symmetric males, based on FA differences.

Reproductive status plays a significant role in modeling these preferences, since they change among periods in all analyzed cases. Hormonal changes may be responsible of these changes. As occurs with several species, testosterone increments have been observed for *O. degus* in reproductive period (Kenagy et al. 1999). These increments explain increase copulatory behaviors in males of *O. degus* (Farfán et al. ms), and also female reproductive estrous. Although no information exists regarding hormonal changes for *O. bridgesi*, our experiments suggest that they should occur, and participate in mate recognition as well.

It is interesting to note that *O. degus* and *O. bridgesi* show preferences based on visual clues, despite their contrasting diurnal and nocturnal life styles. Usually, rodents are though to rely more on olfactory abilities, particularly if they are nocturnal. Nevertheless, this belief may be not true for all species, as has been demonstrated in visually or olfactory deprived individuals of *Apodemus sylvaticus* that are able to orientates in a familiar place, irrespective of the deprived organ (Benhamou 2001). Particularly, the urine of *O. degus* has strong UV reflectance, and as has been observed for voles, it can constitute visual as well as olfactory cues to this species (Chávez et al. 2002). Moreover, visual signs can be used only during reproductive period, as has been observed in human males, that increase their visual capabilities due to hormonal changes (Lacreuse et al. 1999). Our results indicate that visual signs may have significant role in determining mating behavior for *Octodon*, being used as decision tool even for the nocturnal *O. bridgesi.*

Although mating systems for these species are not completely established, it is possible to expect that *O. degus*, as a semi-fossorial species, that lives in burrows shared by several females and one male (Muñoz-Pedreros 2000), behaves as a promiscuous species. Although less social, *O. bridgesi* probably have a similar mating behavior. It is possible to expect then, that symmetry plays a different role in mate preferences pending on sex, with males opting more than females, and showing preference for symmetric females during reproductive periods. On the contrary, females may not rely on this attribute when choosing a mate, and their preferences can be associated to other characters.

Sex differences in mate choice observed in *O. bridgesi* can favor the reduction of effective size in a small population of this species. Previously, we indicated that asymmetry differences would reduce effective size through the increase of reproductive variance produced by the unequal access to mates (Chapter 1). Here, we discovered that mating preferences are variable for this species pending on sex, and that this can functionally modify sex ration of a small population, with the consequent effect of population effective size. Intrapopulation morphology is one of the components of individual phenotype that can affect persistence of small populations, and along with associated behavior (Reed 1999) must be included in the vulnerability analysis of endangered populations.

ACKNOWLEDGEMENTS

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DISCUSIÓN GENERAL

Poblaciones de taxa especialistas que vean reducido su tamaño, y enfrenten el deterioro de su hábitat podrían ver incrementada su asimetría fluctuante. Este incremento en asimetría podría afectar la adecuación individual vía la adquisición de pareja, o reproducción (Capítulo 1). Diferencias en la probabilidad de reproducirse y de sobrevivir afectarían la contribución parental a la siguiente generación. Una contribución desigual a la reproducción de la población, podría determinar reducción en el tamaño reproductivo de la misma, incrementando su vulnerabilidad a la extinción (Capítulo 1). Además, incrementos en AF podrían determinar reducción en el tamaño reproductivo de la población debido a la reducción en sobrevivencia de individuos asimétricos. Reducciones históricas en el tamaño poblacional podrían reflejarse asimismo en las relaciones genealógicas entre los individuos que componen poblaciones actuales (Capítulo 4). Ésta podría constituir una vía morfológica que participara en la extinción de poblaciones pequeñas, complementando así las vías para la extinción descritas en los vórtices de extinción propuestos Gilpin & Soulé (1986).

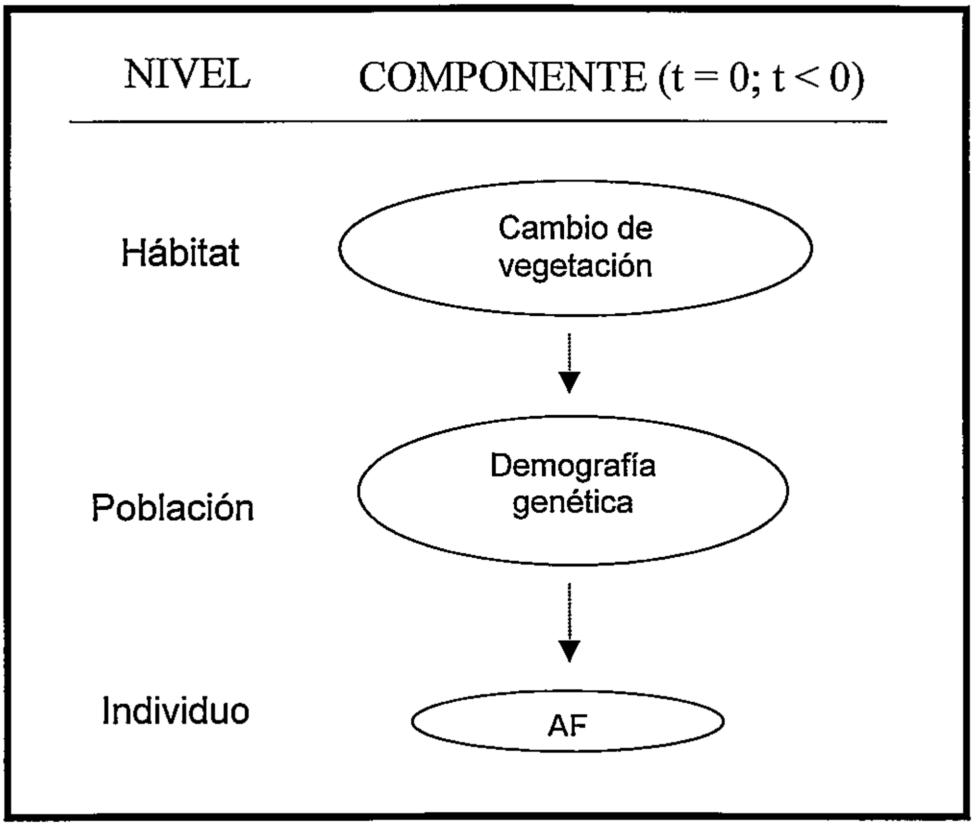
En esta tesis analizamos el patrón de extinción de *Octodon bridgesi,* una especie especialista de hábitat de alta cobertura, desde una perspectiva morfológica. Ello debido a que *O. bridgesi* presenta reducción histórica en su rango de distribución (Capítulo 2), la cual ha sido explicada por la reducción de la cobertura arbustiva producto de la destrucción de hábitat dentro de la porción septentrional de su rango geográfico (Simonetti & Saavedra 1998). En la actualidad, *O. bridgesi* vive en áreas altamente modificadas, en las que predomina el reemplazo de hábitat de bosque nativo por plantaciones de la especie exótica

Pinus radiata. La reducción histórica de rango geográfico observado para *O. bridgesi* (Capítulo 2), así como la presencia actual de la especie en hábitats profundamente modificados (Capítulo 3), sugiere que los tamaños poblacionales de *O. bridgesi* se habrían visto alterados, y seguramente han diminuido a través del tiempo. Esperamos que esta reducción en tamaño poblacional y modificación de hábitat se reflejara en el patrón de asimetría fluctuante de poblaciones actuales de *O. bridgesi*, así como en tafocenosis de la misma las cuales deberían mostrar incrementos en AF hacía períodos más recientes (Capítulo 1 y 4). Asimismo, si incrementos en AF modifican la habilidad de los individuos de participar en el procesos reproductivo de la población, ello se debiera reflejar en incrementos de la probabilidad de extinción de poblaciones de pequeño tamaño. En particular, individuos asimétricos deberían ser evitados en la selección de pareja, disminuyendo la probabilidad que ellos dejen descendencia.

Contrario a nuestras expectativas, *Octodon bridgesi* no mostró cambios en el patrón de AF en el tiempo (Capítulo 4). A una escala local, y a pesar de que en la actualidad poblaciones marginales de *O. bridgesi* viven en hábitats profundamente modificados (Capítulo 3), ellas no registran alteraciones en su morfología ni en su demografía, que revelen condiciones de estrés ambiental o genético, respectivamente (Capítulo 4). Es así por ejemplo que no se observan incrementos en AF en poblaciones contemporáneas de *O. bridgesi* que viven en hábitats que han sufrido profunda alteración. Asimismo, las relaciones genealógicas observadas en el ADN mitocondrial de *O. bridgesi*, indican que estas poblaciones se han mantenido al menos estables en el tiempo, justamente lo contrario de lo esperado basados en la historia de reducción de rango geográfico y de extinción local de las poblaciones (Capítulo 4). Además, análisis específicos destinados a establecer la relación entre AF y preferencia de pareja en *O. bridgesi*, indicaron que AF podría jugar un papel en el tamaño reproductivo de la población, pero que éste no sería tan directo como fue propuesto inicialmente (Capítulo 1). Ello debido a que existen diferencias de sexo en las preferencias de pareja, por lo que el fenómeno de reducción de la población sería menos fuerte de lo que se esperaría si machos y hembras hubiesen evitado aquellos individuos asimétricos dentro de la población al momento de reproducirse (Capítulo 5).

A escala local, resulta interesante destacar cómo modificaciones significativas de hábitat, como lo es el reemplazo de la vegetación nativa por plantaciones de una especie exótica, no resultan necesariamente en alteraciones en otros componentes del sistema, como es la demografía a largo plazo de *O. bridgesi*, o diferencias intrapoblacional de su morfología (Figura 1). En este trabajo hemos observado que la significativa perturbación (sensu Pickett et al. 1989) que afecta el bosque Maulino, hábitat original de *O. bridgesi*, no se transmitiría directamente a las poblaciones de este roedor nativo. A pesar que la perturbación antrópica modifica profundamente la estructura y organización del bosque, ella no afecta directamente a otros niveles del sistema, como son las poblaciones asociadas de este roedor. Estas diferencias podrían explicarse debido a la estructuración jerárquica de los sistemas naturales, los cuales están compuestos por niveles los que a su vez contienen diferentes componentes. Por ello, frente a un evento de perturbación el cual ha sido definido a un nivel, en nuestro caso el reemplazo de bosque por plantación, no necesariamente es transferido a otros niveles o componentes del sistema. En este sentido, la falta de cambios en el patrón de AF en poblaciones actuales de *O. bridgesi*, las cuales viven asociadas a

FIGURA 1. Esquema que indica las relaciones entre los diferentes niveles y componentes analizados para establecer el efecto de la perturbación de hábitat sobre las poblaciones e individuos de *Octodon bridgesi*. En esta tesis los componentes se analizaron en dos períodos de tiempo: actual (t = 0) y pasado (t < 0), en poblaciones vivas y arqueozoológicas de la especies, respectivamente. La flecha punteada indica que el reemplazo de hábitat no se transfiere a los otros niveles analizados.



hábitats altamente modificados, indica el alto grado de resiliencia (sensu Pimm 1991) que estas poblaciones animales tendrían a la perturbación antrópica de su hábitat. En particular, es posible proponer que la dependencia que tiene este roedor con hábitats que presenten alta cobertura arbustiva (Muñoz & Murúa 1989, Muñoz-Pedreros 2000), no depende de la composición del mismo. Entonces si se cambia la vegetación, por ejemplo bosque nativo por plantación de especies exóticas, pero se mantiene cobertura arbustiva, como sucede bajo ciertas condiciones de manejo en plantaciones de *Pinus radiata* (Vita 1996), la persistencia de *O. bridgesi* se ve favorecida en el sistema. Así, es posible proponer que las poblaciones de *O. bridgesi* se alternarían localmente durante el proceso de reemplazo de hábitat, permitiendo la persistencia de poblaciones bien desarrolladas de la especie en el área. En primer lugar, una vez que se corta el dosel y se instalan renovales de *Pinus radiata*, estos serían utilizados activamente por los individuos que resisten la tala, los cuales sobreviven en parte consumiendo la savia presente en los individuos recién plantados (Muñoz-Pedreros et al. 1990). Ello explicaría que esta especie sea considerada plaga dentro del ámbito forestal (Rodríguez 1993), puesto que esta conducta determina la muerte de parte de los árboles recién plantados, afectando la productividad local. Cuando el manejo de la plantación considera la mantención de un estrato arbustivo compuesto tanto por especies nativas como introducidas (Capítulo 3), se favorecería la permanencia de *O. bridgesi.* Debido al adecuado desarrollo de dosel arbustivo, individuos de esta especie satisfacerían sus requerimientos específicos de cobertura arbustiva, encontrando asociado una buena base de recursos tróficos, además de escasa presencia de depredadores aéreos (Muñoz & Murúa 1990, Muñoz-Pedreros et al. 1990). En resumen, bajo determinadas condiciones de manejo, las plantaciones no constituirían un estrés determinante que afecte negativamente el desarrollo local de poblaciones de *O. bridgesi*. Este tipo de manejo forestal asimismo permite la mantención de fragmentos de bosque nativo de diferente tamaño, lo que favorecería la persistencia en el área no sólo de *O. bridgesi*, sino además de carnívoros y cánidos nativos, aves rinocríptidas, e insectos epígeos, los cuales son capaces de mantenerse en este sistema (Acosta 2001, Vergara 2002, Grez et al. 2002), haciendo uso favorable de las nuevas condiciones ecológicas establecidas por las plantaciones.

A una escala regional de larga data, la persistencia de poblaciones de *O. bridgesi* podría ser explicado por aspectos de la historia Holocénica de los bosques templados del sur de Chile, donde en la actualidad se encuentra presente *O. bridgesi*. La distribución Holocénica de estos bosques sufrió un importante cambio durante el último máximo glacial, momento en el cual vastas áreas del sureste chileno fueron cubiertas por hielo (Villagrán 1994, Villagrán et al. 1995). En este período los bosques costeros del centro-sur de Chile, donde se encuentran actualmente las poblaciones de *O. bridgesi*, no habrían sido afectados por este proceso de glaciación (Armesto et al. 1995), pudiendo constituir para refugio para la flora y fauna austral (Saavedra & Simonetti 2000, 2001). Luego del retiro de los hielos, estas poblaciones podrían haber servido de fuente para la recolonización de los bosques recién formados. Esta historia demográfica sería la que daría cuenta de los patrones morfológicos y genéticos observados en *O. bridgesi* en la actualidad.

Evidencia reciente sustenta la hipótesis que la zona costera habitada actualmente por *O. bridgesi*, habría constituido refugio para la fauna durante el último período glacial. Ello debido a que este sistema alberga las poblaciones más nortinas de diversa fauna sureña, representantes típicos del bosque valdiviano como el pudú (*Pupu puda*), la lauchita arbórea (*Irenomys tarsalis*), el ratón topo pardo (*Geoxus valdivianus*), y el monito del monte (*Dromiciops gliroides*), todos ellos recientemente descritos para esta zona (Saavedra & Simonetti 2000, 2001). Asimismo, en esta área se han encontrado las poblaciones más nortinas registradas para la culebra de cola corta (*Tachymenis chilensis*, Simonetti 2001), y de 24 especies de coleópteros epígeos (Grez et al. 2002), todos característicos de los bosques sureños. El elevado aislamiento que habría producido el avance glacial, se refleja además en la presencia de una especie de insecto y otra anfibio, las que serían endémicas para esta zona (Grez et al. 2002, A. Veloso com. per.), las que probablemente especiaron *in situ* producto del aislamiento.

Las poblaciones de *O. bridgesi* que habitan la región costera del centro-sur de Chile probablemente actuaron como fuente para la colonización del valle y faldeos cordilleranos más australes, dando origen a las poblaciones de la especie que se encuentran presentes hacia el sur de la distribución en la actualidad (e.g. Verzi & Alcover 1990, Podestá et al. 2000, Capítulo 2). Ello explicaría el patrón demográfico inferido del análisis molecular de una población borde de *O. bridgesi*, el que la muestra como una población estable demográficamente, con algún indicio de expansión poblacional (Capítulo 4). Las poblaciones costeras de *O. bridgesi* localizadas en la zona centro-sur de Chile, constituirían los reservorios más antiguos para esta y otras especies, agregando un valor de conservación genético a esta zona, la cual concentra la mayor proporción de endemismos de mamíferos y de otros taxa en nuestro país (Simonetti 1999). Esta hipótesis puede ser contrastada ampliando el muestreo genealógico a marcadores nucleares por una parte, a la vez que estableciendo las relaciones filogeográficas entre la población aquí estudiada, y poblaciones más australes de la especie. Asimismo, patrones similares deberían observarse en otras especies presentes en esta área y que tengan asociación estrecha con bosques sureños.

La historia poblacional de larga data es desconocida para la gran mayoría de las especies, a pesar que ella puede ser la causa de patrones ecológicos y evolutivos de las poblaciones actuales. El análisis de las relaciones genealógicas entre individuos de una población, así como de los cambios en morfología a través del tiempo, puede aportar elementos importantes para el conocimiento de la demografía de larga data una población. Esta información puede servir para establecer una reconstrucción de la historia poblacional, así como para proyectar el desarrollo de la población en el futuro.

Finalmente, la alta diversidad de factores que participan en el proceso de desaparición de especies se conjuga de manera diferente dependiendo tanto de los atributos específicos que presenta las especies vulnerables, como de las condiciones ambientales que amenacen su persistencia. Ello indica que análisis fructíferos destinados a evaluar el riesgo de extinción de poblaciones en el futuro, debe centrarse en la interacción de ambos factores, más que de la descripción aislada de cada uno de los componentes. En este sentido, el uso de AF para evaluar el estado de deterioro de poblaciones pequeñas, puede ser de gran utilidad, por cuanto combina información relativa a dos de los aspectos más significativos que participan en el proceso de extinción. Asimismo, el análisis del proceso a diferentes escalas, tanto globales como locales, así como el estudio de fenómenos de orden individual y poblacional, favorece el entendimiento del proceso de extinción que afecta a poblaciones en peligro, con la consecuente utilidad para la conservación de dichas especies.

ANEXO 1

A NORTHERN AND THREATENED POPULATION OF *IRENOMYS TARSALIS* (MAMMALIA: RODENTIA) FROM CENTRAL CHILE[6]

Una población nortina y en peligro de *Irenomys tarsalis* (Mammalia: Rodentia) en Chile central

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[6] Saavedra B and Javier A. Simonetti (2000) A northern and threatened population of *Irenomys tarsalis* (Mammalia: Rodentia) from central Chile. Zeitschrift für Säugetierkunde 65:243-245.

Irenomys tarsalis (Philippi, 1900), the Chilean tree mouse or "laucha arbórea", is the single species of a sigmodontine genus endemic to the temperate forests of southern Chile and Argentina (Redford and Eisenberg 1992). The geographic distribution of this rare rodent is poorly known. Along the mountain range of Chile, *I. tarsalis* is known to occur from Chillán (36° 54'S, 71° 25'W) to Puerto Ibáñez (46° 04'S, 72° 02'W). Along the coastal range, *I. tarsalis* reportedly extends from Nahuelbuta (37°58'S) down to Chiloé (42° S) and Guaitecas Islands (46° S; Reise and Venegas 1974, 1987; Pine et al. 1979). The distribution along the Chilean coastal range however, is very poorly known, and northern limits are regarded as tentative (Kelt 1993). Here we report on a population of *I. tarsalis* 210 km north of its currently known limit, associated to remnants of the endangered temperate Maulino forest, along the coastal range of central Chile (Fig. 1).

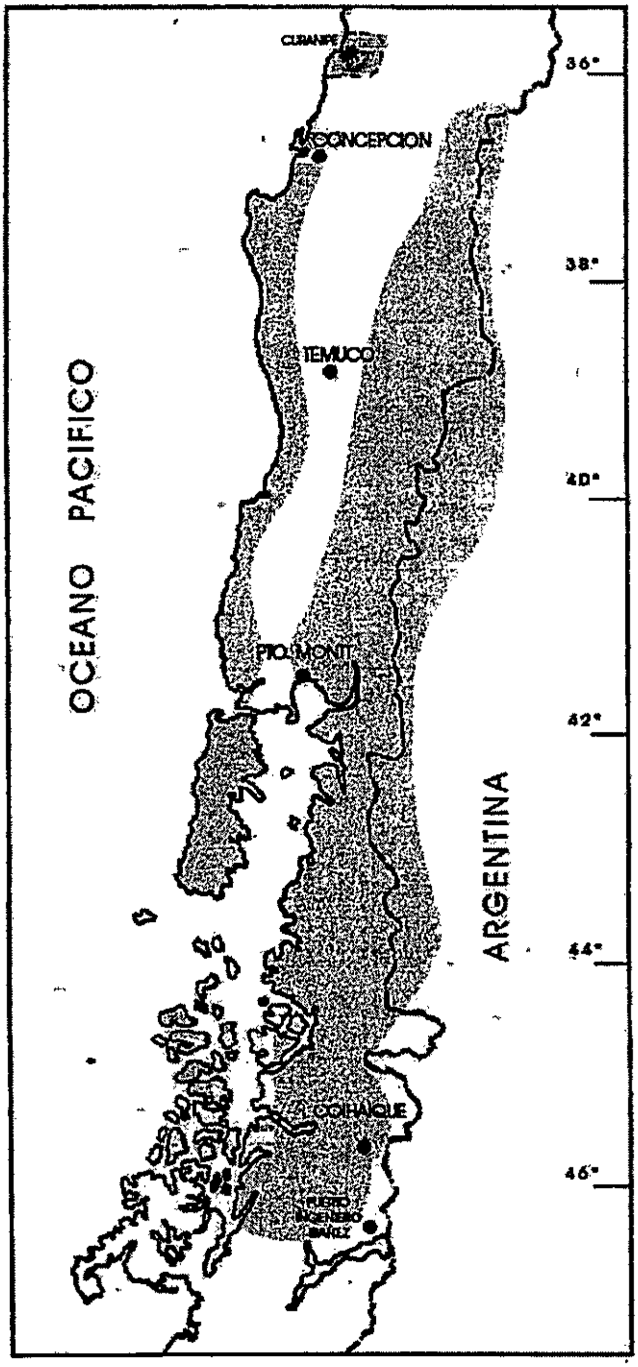
Ongoing monitoring of small mammals at a large remnant (approximately 600 ha) of temperate forest, at which National Reserve Los Queules (35°59'S-72°41'W, 540-570 m asl) is located, and neighboring forest fragments (Fragment 1: 35°58'S-72°42'W, 3 ha, 348 m asl and Fragment 3: 35°59'S-72°41'W, 6 ha, 570 m asl) surrounded by pine plantations (*Pinus radiata*), have revealed a small population of *I. tarsalis* at both, the Reserve as well as a forest fragment. This is a typical Maulino forest, with *Nothofagus glauca, Aetoxicum punctatum, Cryptocarya alba, Gevuina avellana* and *Persea lingue* as the dominant tree species (San Martín and Donoso 1995).

Sampling consists of bimonthly livetrapping sessions for at least five trapping nights each time. Since January 1999, at Los Queules National Reserve we are operating two grids of 10 x 5 (3,600 m^2) medium-sized Shermann traps, each trap located 10 m apart. At Fragment 1, we operate a 10 x 5 (3,600 m^2) grid, half of which is set inside the native forest, while the other half lies into the *P. radiata* plantation. At Fragment 3, we operate a 6 x 5 (2,000 m^2) traps grid inside the fragment. Additionally, we run a 10 x 5 (3,600 m^2) grid in the adjacent *P. radiata* plantation. Traps are baited with rolled oats and checked daily at dawn, as all small mammals are nocturnal.

To date, we have captured, marked and released five adult individuals of *I. tarsalis*. Recaptures have been low, as only three of them were recaptured just once. Four individuals (two males and two females) were captured in Los Queules National Reserve, while one female was found in Fragment 3. No specimen has been captured or recaptured in Fragment 1 or the in *P. radiata* plantation. Captures took place in January, April, and June. Body measurements are: body length 8.9 - 11 cm, tail length 14.6 - 15 cm, and hind foot 2.8 cm. All individuals escaped climbing trees after they were released, corroborating the arboreal habits of the species (Pearson 1983). Besides *Irenomys*, we also found three other murid species (*Abrothrix longipilis* (Waterhouse, 1837), *A. olivaceus* (Waterhouse, 1837), *Oligoryzomys longicaudatus* (Bennett, 1832), one caviomorph (*Octodon bridgesi* Waterhouse, 1845), and one marsupial (*Thylamys elegans* (Waterhouse, 1839)). We also captured the introduced black rat, *Rattus rattus* (Linnaeus, 1758) in all forest remnants and pine plantations surveyed (Simonetti 1983)

Irenomys tarsalis is regarded as a rare or uncommon species (Greer 1966; Patterson et al. 1989, 1990; Meserve et al. 1991). Its rarity is depicted by the fact that *I. tarsalis* represents only three out of nearly 1,700 capture records from 63 localities in Chile and neighboring Argentina (Reise and Venegas 1987). In fact, our trapping success is only 0.16% (out of 4.907 trap/nights), compared to 3.3% of *Abrothrix longipilis*, 2.4% of *A. olivaceus*, and 2.2% of *Oligoryzomys longicaudatus*.

Fig. 1. New distribution of *Irenomys tarsalis* with the new record (asterisk) in the coastal range, extending northern limit approximately 210 km. The southern limit remains unknown (modified form Kelt 1993).



We also found remains of *I. tarsalis* among scats of *Pseudalopex griseus* (Gray, 1837). This fox inhabits the Reserve and uses service roads along the *P. radiata* plantations (Acosta and Simonetti 2000, Muñoz and Murúa 1990). One out of 22 feces (4.5%) collected in September 1998 and January 1999, contained molars depicting "partial transverse lamination", clearly attributable to *I. tarsalis* (Hershkovitz 1962). The remains belonged to a single adult individual, found among remains of other 25 rodent specimens of four different taxa, including *Abrothrix* sp., *Phyllotis* sp., and *Octodon bridgesi.*

The presence of *I. tarsalis* over 200 km north of the northern known limit supports the contention that this elusive rodent may have ranged into central Chile, but deforestation could have excluded it except from forest remnants (Kelt 1993). Coastal forests form central-south Chile, remained less affected by Pleistocene glaciation processes (Armesto et al. 1995), probably acting as refuges for *I. tarsalis.* The northernmost population that we discovered, becomes then extremely valuable to test phylogeographic hypothesis and to reconstruct the biogeographic history of small mammal fauna during Pleistocene and Holocene in south-central Chile (e.g., Meserve and Kelt 1990). Unfortunately, this northern *I. tarsalis* population might vanish from their northern grounds at the same pace native forests are being eliminated or replaced, due to the scarce representation of Maulino forests in Chilean's Protected Areas System (Simonetti and Armesto 1991).

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ANEXO 2

NEW RECORDS OF *DROMICIOPS GLIROIDES* (MICROBIOTHERIA: MICROBIOTHERIIDAE) AND *GEOXUS VALDIVIANUS* (RODENTIA: MURIDAE) IN CENTRAL CHILE: THEIR IMPLICATIONS FOR BIOGEOGRAPHY AND CONSERVATION[7]

Nuevos registros de *Dromiciops gliroides* (Microbiotheria: Microbiotheriidae) y *Geoxus valdivianus* (Rodentia: Muridae) en Chile central: sus implicancias para la biogeografía y la conservación

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[7] Saavedra B & JA Simonetti (2001) New records of *Dromiciops gliroides* (Microbiotheria: Microbiotheriidae) and *Geoxus valdivianus* (Rodentia: Muridae) in central Chile: their implications for biogeography and conservation. Mammalia 65: 96-100.

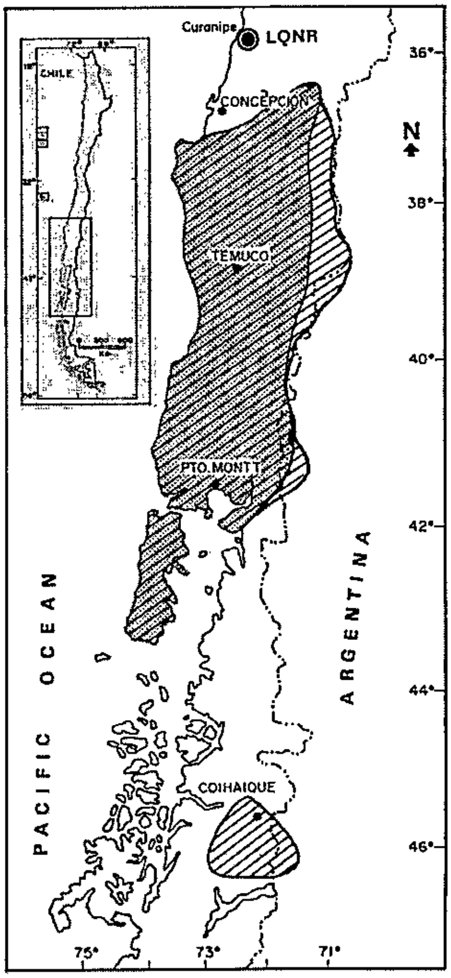
The mammalian fauna of Chile is among the best known in the Neotropics (Pine, 1982). However, new taxa and new distribution records are frequently described suggesting the diversity and distribution of Chilean mammals are yet to be fully assessed (e.g., Patterson, 1992; Palma, 1995). Herein, we describe a new locality for two small mammals, the microbioteriid marsupial *Dromiciops gliroides* ("monito del monte") and the murid rodent *Geoxus valdivianus* ("ratón topo pardo") in central Chile. Usually regarded as typical components of a southern fauna, these two species, along others like the cricetine *Irenomys tarsalis*, and the dwarf deer *Pudu puda,* are considered wholly or virtually restricted to the Valdivian faunal district (*sensu* Osgood 1943). This district extends from Nahuelbuta Cordillera (app. 38°S) southward to 47°S, overlapping with the humid southern forests (Osgood, 1943). However, while assessing the diversity and abundance of mammals in *Nothofagus* forest remnants in central Chile (36° S, Fig. 1), we have captured two of these "southern" species, *D. gliroides* and *G. valdivianus.*

Dromiciops gliroides is regarded as restricted to the rain forest of central Chile and adjacent parts of Argentina from about 36° to 43° (Hershkovitz, 1999; Fig 1). In the Andean range, its northern limit has been set in Talca Province (35°30'), while in the coast their northern limit is located south to Concepción (37°58', Hershkovitz, 1999). *Geoxus valdivianus* occurs also in southern Chile (Fig. 1). In the Andean range, its northern limit is found in Ñuble Province (36° 54' S), while in the coast it has been captured close to Concepción (Reise and Venegas, 1987). To the south, *G. valdivianus* reaches Magallanes and Río Negro Province in Argentina (Reise and Venegas, 1987; Redford and Eisenberg, 1992).

In 1999, we captured *D. gliroides* and *G. valdivianus* during sampling of small mammals in a *Nothofagus* forest and surrounding forest fragments at Los Queules National Reserve (LQNR, 35°59' S-72°41' W; 540-750 m a.s.l.), ca. 200 km north of their known distribution near Concepción (Fig. 1). Fragments of native forests are surrounded by an exotic matrix of *Pinus radiata* plantations. The vegetation of native forest is dominated by *Nothofagus glauca, Aetoxicum punctatum, Cryptocarya alba, Gevuina avellana* and *Persea lingue*, typical components of Maulino forest (San Martín and Donoso, 1995). A forest tract at the LQNR (app. 600 ha) and two nearby fragments (35°59' S-72°42' W, 3 ha; 35°58' S-72° 41' W, 6 ha), have been sampled to record small mammal diversity from January 1999-February 2000. Sampling consisted of bimonthly trapping sessions of at least five nights. We used medium-sized Sherman traps baited with rolled oats, arranged in 10 x 5 grids, traps located 10 m apart. Grids were placed inside the native forest in the LQNR, while at the fragments, half of the grid was located inside the forest remnant and the remaining traps were placed in the adjacent matrix of pine plantations.

In both NRLQ and Fragment 3, we recently discovered populations of *Irenomys tarsalis* (Saavedra and Simonetti, 2000). This record increased its northern limits about 200 km. Since then, further sampling of the same forests also revealed the presence of *D. gliroides and G. valdivianus*. A single adult male of *D. gliroides* (27 gr) was captured on October 1999 in the National Reserve Los Queules. This individual has not been recaptured since then. The capture of *D. gliroides* probably could increase with the use of museum special snap traps, due to high trap bias against Sherman traps shown by individuals of this species (Patterson et al. 1989). *Dromiciops gliroides* is usually associated to *Chusquea* (Chilean bamboo, Hershkovitz 1999), but this plant was absent from the trap site. *Gevuina* *avellana* and *Aetoxicum punctatum* dominated habitat around the trap. Regarding *G. valdivianus*, one adult female (35 gr, body size 98 mm, tail size 41 mm) was captured on October 1999 in LQNR. A second specimen was captured on December 1999 in Fragment 1. This was an adult male (50 gr., body size 115 mm, tail size 40 mm), with scrotal testicles. Only the male of Fragment 1 has been recaptured once. Habitat around the trap in Fragment 1 was

FIGURE 1. New record at Los Queules National Reserve (LQNR, large circle) for *Dromiciops gliroides* and *Geoxus valdivianus* in south-central Chile. Past known distribution of *D. gliroides* (lines) and *G. valdivianus* (lines and dots) is shown for South America (taken from Hershkovitz 1999, and Redford and Eisenberg 1992).



strongly modified, corresponding on a pine plantation stand, where *Aristotelia chilensis* was the dominant native tree.

In the same trapping grids, we have also captured the didephid *Thylamys elegans*, the murids *Abrothrix longipilis*, *A. olivaceus*, *Irenomys tarsalis*, *Oligoryzomys longicaudatus* and the introduced murid *Rattus rattus*, as well as the caviomorph *Octodon bridgesi*. Compared to these species, relative abundance of *D. gliroides* was low (0.96% of the known individuals to be alive in NRLQ; one of 140 individuals). Similarly, *G. valdivianus* was also scarce, comprising 0.96% of the known individuals to be alive in LQNR (one out of 140 individuals), and 0.5% of the known individuals in the forest fragments (one out of 210 individuals). These abundance were small despite sampling efforts of 3.909 and 3.012 trap/nights at the forest reserve and fragments, respectively.

The occurrence of *D. gliroides*, *G. valdivianus* and *I. tarsalis* (Saavedra and Simonetti, 2000) and also the cervid *P. puda* (unpublished data), all typical Valdivian representatives at LQNR, strongly suggest that Osgood's (1943) Valdivian fauna district may have extended further north in the recent past. The small size of these northern populations could be explained by their border status (sensu Brown 1984), compared to southern populations that probably are located close to the center of their geographical range. Southern forest distribution changed drastically during last glacial maximum, when vast areas of east and southern Chile were covered by ice (Villagrán, 1994; Villagrán *et al.*, 1995). Coastal forests from central-south Chile however, were less affected by glaciation processes (Armesto *et al.*, 1995). During this period, these forests probably acted as refuges for the fauna. *Dromiciops gliroides* along with *I. tarsalis* are the only two arboreal species of small mammals from temperate forests of southern Chile (Murúa, 1995). Small populations of these species, in addition to others like *G. valdivianus* probably remained associated to forest remnants during Pleistocene glaciation, acting as source populations for the subsequent recolonization of the valley and Andean foothills. Therefore, it is probable that populations of these taxa associated to northern coastal forests represent the oldest populations of the Valdivian district in this area, while adjacent southern and eastern populations represent younger descendants. These northernmost populations of Valdivian fauna we discovered, becomes then extremely important to test phylogeographic hypothesis and to reconstruct biogeographic history of small mammal fauna during Pleistocene and Holocene in central-south Chile.

Despite its phylogeographic relevance, these northern populations might be severely threatened by human encroachment and modification of its habitat. Deforestation and forest replacement by *Pinus* plantations are intense in the region, where substitution rate of native forests reaches over 30% (Armesto *et al.,* 1995; Lara *et al.,* 1995; San Martín and Donoso, 1995). Also the presence of *R. rattus* represents a threat to these native small mammals at the forest remnants (cf. Glanz 1970). Unfortunately, the Maulino forest is scarcely represented in Chilean's Protected Areas System, where only LQNR (150 ha size from a tract of 600 ha), along with Los Ruiles National Reserve (45 ha size, Bustamante and Castor, 1998) constitute the only Maulino forest fragments currently protected. The temperate forest of the region have high species richness, and is also rich in endemic tree species like *Gomortega keule*, *Pitavia punctata*, *Nothofagus glauca,* and *N. alessandrii* (Villagrán, 1994; San Martín and Donoso, 1995; Grez *et al.,* 1997; Bustamante and Castor, 1998). The presence of *D. gliroides* and *G. valdivianus*, along with *I. tarsalis* and *P. puda* adds another element for the urgent need to ensure the long term conservation of these forests remnants.

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ANEXO 3

PAST AND PRESENT SMALL MAMMALS FROM ISLA MOCHA (CHILE)[8]

Micromamíferos pasados y presentes de la Isla Mocha (Chile)

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[8] Saavedra B, D Quiroz & J Iriarte (2003) Past and present small mammals from Isla Mocha (Chile). Mammalian Biology 68: 1-7.

Abstract

We describe archaeozoological and extant small mammals from Isla Mocha, an island located in south-central Chile. Species composition was compared among past and present assemblages. Also composition, as well as individual and population parameters were compared among island habitats. Specimens from archaeological sites included *Oligoryzomys longicaudatus, Abrothrix* sp., and *Octodon pacificus*, whereas *Abrothrix longipilis, A. olivaceus, Oligoryzomys longicaudatus* and *Geoxus valdivianus* were captured. Higher species richness was observed in intermediate-disturbed habitat. Body size and tail length, and body mass did not vary among island habitats for *A. longipilis* or *A. olivaceus*. Higher abundance was associated with less perturbed habitat.

Key words: *Octodon pacificus*, archaeozoology, Isla Mocha, Chile

Introduction

Islands comprise an important part of the Chilean territory. Despite this, little ecological research has been done in these ecosystems. One exception is Isla Mocha, one of the few islands that have been surveyed for its fauna, vegetation, and archaeology. One remarkable mammal is *Octodon pacificus* Hutterer, 1994, the only insular endemic Octodontid (Rodentia: Hystricognathi) (Hutterer 1994). Unfortunately, it has only been captured once, in 1959 when two adult females and two juveniles were collected (now in the Museum Alexander Koenig , Bonn).

Isla Mocha has also been interesting for botanists, since it supports dense vegetation that is biogeographically related to mainland Valdivian forest (Lequesne et al. 1999). The forest on Isla Mocha is dominated by *Aextoxicon* and members of the Myrtaceae. Botanical, geological, and geographical descriptions suggest that the island has had similar vegetation conditions as at present since at least 1,760 years BP (Lequesne et al. 1999). Anthropologists have found a long history of human occupation starting ca. 3,300 years BP when hunter-gatherers occasionally occupied the island (Quiroz and Sánchez 1993; Quiroz and Vásquez 1996).

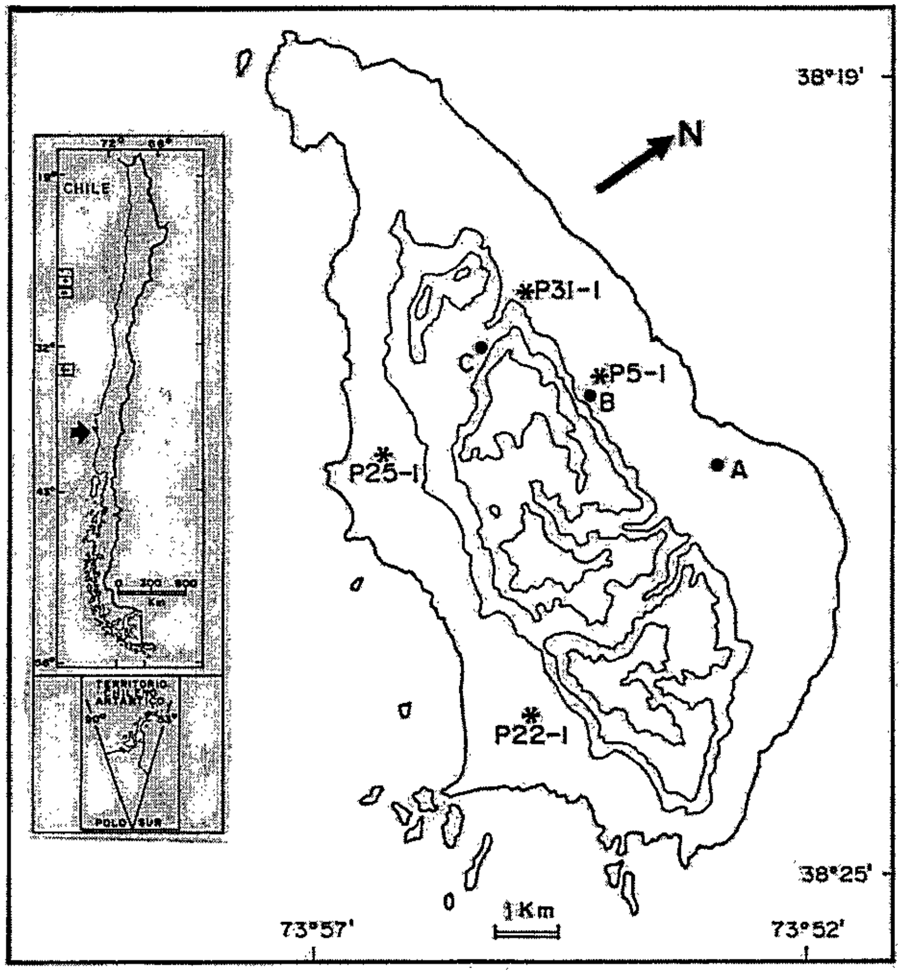
Islanders have always relied on island vegetation for their subsistence, and this has led to degradation of natural habitats. Human activity has resulted in the almost total deforestation of lowlands, which are now dominated by grasslands composed by introduced and cultivated species in which sparse and very small fragments of forest remain. In intermediate elevations, tree-cutting and subsequent erosion have given raise to an ecotone matorral that separates Valdivian forest from disturbed grasslands (Pefaur and Yáñez 1980). The Valdivian forest, now restricted to higher elevations, has suffered increased opening, and modification of species composition, primarily due to timber extraction (Lequesne et al. 1999).

To contribute to the knowledge of Chilean insular habitats, and the elucidation of the distribution of the genus *Octodon*, we investigated the small mammals of Isla Mocha. A further aim was to describe the faunal composition in time and space, analyzing archaeozoological remains along with present-day small mammals that inhabit the different habitats of the island.

Material and Methods

Isla Mocha is located 30 km W off coast in front of the Arauco Province, in south-central Chile (Fig. 1). Its maximum extension is 13 km N-S and 5-7 km E-W. Valdivian forest is restricted to highland areas above 300 m.a.s.l. (Lequesne et al. 1999). Pefaur and Yáñez (1980) found 4 native rodents *Abrothrix longipilis* (Waterhouse, 1837), *A. olivaceus* (Waterhouse, 1837), *Oligoryzomys longicaudatus* (Bennet, 1832) and *Geoxus valdivianus* (Philippi, 1858). Two introduced murids (*Rattus rattus* Linnaeus, 1758 and *R. norvegicus* Berkenhout, 1769) were also part of the rodent assemblage. Ancient human occupation was

FIGURE 1. Diagram of Isla Mocha, VIII Región, Chile. Archaeological sites P25-1, P31-1, P5-1 and P22-1 are shown by an asterisk. Small mammals trapping sites are: A, Coastal forest; B, Ecotone matorral and C, Valdivian forest.



restricted to the periphery of the island. This has left numerous archaeological sites, which are still being studied (Quiroz and Sánchez 1997). Archaeozoological material that was analyzed came from some of these sites (Fig. 1).

Archaeozoological small mammals: We analyzed small mammal remains from 4 archaeological sites (P5-1, P22-1, P25-1, P31-1) excavated during 1993-1998 (Fig. 1). Archaeological material was extracted from each 10 cm of artificial levels, with a variable number of levels for each quadrant. All these levels date pre-Columbian occupation, having an aboriginal origin. Maximum excavation depth was achieved in site P25-1, where 15 levels were extracted. Excavation plots ranged between 1-8 m^2, with a total 18,600 l of sediment recovered (for excavation descriptions and details see Quiroz and Sánchez 1993). *Octodon bridgesi* Waterhouse, 1845 was previously mentioned as a component of the archaeozoological sample of site P31-1 (Sánchez et al. 1994). Here we inspected archaeozoological assemblage of this site to confirm this description.

Each bone was identified to the most specific taxonomic and anatomical level possible. We discriminated to species, family, order or class level, using available identification keys (e.g. Reise 1973; Pearson 1995). Due to the lack of keys for *Octodon pacificus*, and to the ambiguous presence of this species in the archaeozoological record, we compared *Octodon* specimens with those described by Hutterer (1994). To infer depositional process, at the anatomical level we discriminated between cranial and post-cranial elements (Gilbert 1980). Also we established whether each bone was fragmented or showed evidence of human use such as fire or cuts, as well as its age (i.e., juvenile or adult).

Present day rodents: In January 2000, we trapped small mammals in Isla Mocha with lines of medium and large size Sherman-type traps, located each 10 m apart in the three main habitats of the island (Fig. 1). Trapping effort included coastal forest (500 trap-nights), ecotone matorral (450 trap-nights) and Valdivian forest (495 trap-nights), for a total of 1,445 trap-nights. Traps were baited with oat, and kept open for five consecutive nights. Traps were checked each morning, and captured specimens were marked, measured and released. Species composition was compared among island habitats, along with individual and population parameters. Individual condition was assessed through body weight, body size and tail length. At population level, we described population size using trapping success as an estimator of abundance. Also, reproductive and juvenile's proportion were used to describe population structure.

Results

Archaeozoological small mammals: We recovered 462 specimens in all excavated sites. 76.4% of specimens were collected from site P31-1 (Tab. 1). Sigmodontines were the most important group in the archaeozoological record, comprising 89.9% of small mammals. All specimens were adults, with only one of them showing fire marks. Bone fragmentation varied among groups, with caviomorphs showing 40.4% of the recovered material fragmented, whereas only 25% of the sigmodontines were fragmented. Post-cranial portions of animals were over-represented compared to cranial remains, comprising 79.7% (N=368), of the total sample. As for fragmentation, cranial representation varied among taxa. For caviomorphs 57.4% of recovered remains corresponded to post-cranial elements, whereas for sigmodontines this proportion increased to 82.2%.

Table 1. Number of identified rodent specimens in archaeozoological samples from Mocha Island, VIII Región, Chile. Dates are chronological intervals (i.e. BP before present) from radiocarbon dates. Number of radiocarbon dates per site is shown in parenthesis.

		Taxon		
Site	Date (years B.P.)	Caviomorphs	Sigmodontines	Total (%)
P5-1	1,200-700 (2)	2	39	41 (8.9)
P22-1	1,200-1,000 (1)	1	13	14 (3.0)
P25-1	900-700 (4)	5	49	54 (11.7)
P31-1	800-450 (12)	39	314	353 (76.4)
Total	1,200-450	47	415	462

Oligoryzomys longicaudatus, Abrothrix sp., and *Octodon pacificus* made up the archaeozoological record. These species represented 60% of the native taxa described for the island today. *O. longicaudatus*, was represented by 35 specimens of 25 individuals. Eight specimens of *Octodon* were of ≥ 6 individuals. These specimens were clearly larger than other species of the genus. Due to high fragmentation, we could only establish molar width of some of these specimens (Tab. 2). These values were similar to those of Hutterer (1994) for *O. pacificus* (Tab. 2). Therefore we assigned the archaeozoological specimens to this taxon.

Present day rodents: We captured 104 individuals in 197 captures (13.6% trapping success) on Isla Mocha in January 2000. These captures consisted of 4 species: *Abrothrix longipilis* (N=87), *A. olivaceus* (N=15), *Oligoryzomys longicaudatus* (N=1) and *Geoxus valdivianus*

Table 2. Maximum width (mm) of *Octodon pacificus'* molars recovered in archaeozoological samples from Isla Mocha, VIII Región, Chile.

	Molar		
Localization	PM	M_1	M_2
Site P-31, Quadrant 2C, Level 3, depth 80-90 cm	2.7	2.9	2.7
Site P31-1, Quadrant 2C, Level 2, depth 70-80 cm	2.8	2.9	3.0
Site P25-1, Quadrant C4, Level 2	2.1	3.0	2.7

(N=1). The ecotone matorral showed the highest species richness, with all 4 species (*A. longipilis*: N =37; *A. olivaceus*: N = 13) captured. *A. longipilis* (N=31) and *A. olivaceus* (N=2) were the only taxa present in Valdivian forest. The coastal forest was the poorest habitat, with only *A. longipilis* (N=19).

Females and males of *A. longipilis* did not differ in body size (F=1.6; P=0.2) or body weight (F=0.04; P=0.8). The same pattern appeared for body size (F=0.2; P=0.7) and body weight (F=1.3; P=0.3) of *A. olivaceus*, and therefore, individual condition was compared combining sexes. Body length, tail length and body mass did not vary among island habitats (Tab. 3) for *A. longipilis* (body length F =3.0; 84 d.f.; P=0.41; tail length F =2.3; 84 d.f.; P=0.10; weight F=0.75; 84 d.f.; P=0.47), or *A. olivaceus* (body length F =0.18; 13 d.f.; P=0.68; tail length F =0.02; 13 d.f.; P=0.88; weight F =1.29; 13 d.f.; P=0.28). Measurements of *O. longicaudatus* (body size=106.4; tail length=89.6), and *G. valdivianus* (body length=101 cm; tail length=38.4 cm; weight=13) were estimated for each specimen captured.

Population abundance varied among habitats ($\chi^2 = 27.5$, 2 d.f., P<<0.05), with coastal forest showing the lower trapping success (7.0%), followed by ecotone matorral (15.3%), and

Valdivian forest with a trapping success of 18.9%. Trapping success of the coastal forest was significantly lower compared to Valdivian forest (Z=4.9; P<<<0.001) and to ecotone matorral (Z=-4.7; P<<<0,001), but ecotone matorral and Valdivian forest did not differ in trapping success (Z=0.11; P=0.45). 79.3% of the captured *A. longipilis* were non-reproductive (Tab. 4).

Discussion

Differences in the composition of past and present small mammal assemblages from Isla Mocha raise several questions regarding insular effects. The presence of *O. pacificus* in archaeozoological samples confirms the long-term existence of this species on the island. Previously, Sánchez et al. (1994), described *Oligoryzomys longicaudatus* and *Octodon bridgesi* in the Isla Mocha archaeozoological record. Here, we add *Abrothrix* sp. to the record, and suggest the misidentification of *Octodon* in Sánchez et al. (1994). Since Hutterer (1994) described *O. pacificus* after Sanchez et al. (1994), most probably the latter assumed the presence of *O. bridgesi* due to high similarity among mandibular characters of these taxa. *Octodon pacificus* is similar to *O. bridgesi*, a taxon that lives in association with dense matorral (Muñoz-Pedreros 2000), and probably this insular representant lived associated to dense Valdivian forest that formerly covered most part of the island. Probably this explains the presence of this taxon in archaeozoological assemblages from sites located at lower elevations of the island, where forest no longer exists. Once lowlands were cleared for agricultural purposes (Quiroz and Sánchez 1993; Sánchez et al. 1994; Quiroz 1997), *O. pacificus* probably became restricted to highlands, where the forest has remained uncut. Despite our trapping

Table 3. Morphological attributes of *Abrothrix longipilis* and *A. olivaceus* captured in three habitats of Isla Mocha, VIII Región, Chile.

	Habitat type								
	Coastal forest			Ecotone matorral			Valdivian forest		
	Media	SD	n	Media	SD	n	Media	SD	n
Abrothrix longipilis									
Body length (mm)	111.9	13.3	19	113.9	18.9	37	121.9	14.4	31
Tail length (mm)	82.2	7.7	19	76.1	13.9	37	81	10.3	31
Weight (g.)	56.7	20.5	19	60.4	21.8	37	63.8	17.4	31
Abrothrix olivaceus									
Body length (mm)	-	-	-	94	11.9	13	90.3	0.14	2
Tail length (mm)	-	-	-	63.9	5.7	13	63.8	3.9	2
Weight (g.)	-	-	-	34.3	11.2	13	25	5.6	2

Table 4. Sex, reproductive, and juvenile proportion of *Abrothrix longipilis* and *A. olivaceus* individuals captured in Isla Mocha, VIII Región, Chile.

	Abrothrix longipilis	*Abrothrix olivaceus*
Females	30	7
Males	57	8
Adult	69	14
Juvenile	18	1
Reproductive	18	14
Non-Reproductive	69	1

efforts, we were not able to capture specimens of *O. pacificus* in any of the major habitats of the island. *O. pacificus* has never been captured since Hutterer (1994) despite trapping efforts made by Pefaur and Yáñez (1980), or ourselves. Island populations are now probably extremely small, and additional trapping effort should be directed especially to mountaintops, which are lesser disturbed parts of the island.

Faunal composition of the extant and archaeozoological remains varied within the island. *G. valdivianus* were not present in the archaeozoological material, although it was captured in live-trapping on the island. This discrepancy is probably explained by the small population size of the species, as it shows low abundance in its overall distributional range (Redford and Eisenberg 1992). Higher species richness was observed in the ecotone matorral, as predicted by the intermediate disturbance hypothesis. Species richness pattern is not paralleled by species abundance which shows elevated values in less perturbed Valdivian forest.

At the present, lower species richness is associated with Isla Mocha, compared to mainland assemblages. Other species that are part of mainland's small mammal assemblage, but were not captured during summer trapping period, included *D. gliroides* (Philippi, 1893) and *I. tarsalis* (Philippi, 1900) (Pefaur and Yáñez 1980). These species, absent on Isla Mocha are rare , and show low abundances overall their distribution (Redford and Eisenberg 1992; Saavedra and Simonetti 2000, 2001). Among exotic mammals, Pefaur and Yáñez (1980) captured two introduced rats (*R. rattus* and *R. norvegicus*) on Isla Mocha. These taxa were associated with the coastal areas, where human settlement is concentrated. Despite our trapping efforts, we were not able to trap any of these introduced species. They seem to live in close association with houses (islanders recognized their existence in their roofs!), not invading vegetational areas.

Population abundance for *Abrothrix longipilis* and *A. olivaceus* differed among island habitats, as well as with mainland assemblages. Higher abundance is associated to Valdivian forest on the island. Interestingly, on Isla Mocha greater abundance is associated to native forest, whereas in the mainland the same taxa achieve elevated abundances in non-native exotic plantations (Saavedra unpubl. data). A significantly habitat alteration has been observed on the mainland, where native forest has been replaced by exotic *Pinus* plantations (Lara et al. 1995; San Martín and Donoso 1995). At the organismal level insular specimens of *A. longipilis* are smaller (tail length 79.2 cm ± 11.7 cm v/s 88.9 ± 10.0 cm, ANOVA $F_{86, 48\ d.f.}=2.7$; $P<0.001$) and lighter (weight 60.8 ± 20 gr. v/s 64.2 ± 15.9 gr., ANOVA $F_{86, 48\ d.f.}=11.7$; $P<0.001$) on Isla Mocha compared to mainland specimens captured for the same time period (Saavedra unpubl. data). *A. olivaceus*, on the contrary does not show body (tail length 63.8 cm ± 5.4 cm v/s 63.1 ± 11.0 cm, ANOVA $F_{14, 20\ d.f.}=0.04$; $P=0.82$) or weight (33.1 ± 11 gr. v/s 32 ± 7.6 gr., ANOVA $F_{14, 20\ d.f.}=0.11$; $P=0.74$) differences among island and mainland populations (Saavedra unpubl. data). Generalist habits of these taxa may help to understand this pattern.

Isla Mocha rodents, both extinct and extant, constitute a significant reservoir of biological information. Genetic, morphological, as well as stratigraphic studies may yield information useful for testing phylogenetic and phylogeographic hypothesis. The fact that Isla Mocha remained unglaciated during the last glacial maximum (Lequesne et al. 1999), makes it useful for contrasts of animal responses to isolation and glaciation, along with associated phenomena like founder effects or local adaptations. Also, the long and intimate association of humans and the native biota in this island gives to these populations additional value, since anthropogenic fragmentation of natural habitats is generating island-type environment in many mainland areas (e.g. Bustamante and Castor 1998). Understanding the population responses to isolation on real islands, where significant habitat changes did take place may represent an important starting point for developing conservation policies in non-natural fragmented landscapes.

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