HUMAN USE AND SMALL MAMMAL COMMUNITIES OF Araucaria FORESTS IN NEUQUÉN, ARGENTINA

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Abstract: Small mammals were sampled in five closed, humid, Araucaria araucana forests that differed in the degree of anthropogenic disturbance in southwestern Neuquén province. Nine species were captured in 3416 trap nights. Abrothrix longipilis and Oligoryzomys longicaudatus made up 88% of all captures. Small mammal relative abundance was 52 times higher where grazing was absent compared to a site with intense grazing pressure. Seed predation, primarily by livestock and feral exotic mammals, varied from 59.7% to 15.1% of marked seeds per day. Small mammal community productivity and composition were correlated with understory structure (Mantel test, r = 0.529, p = 0.04), and with rates of seed predation (r = -0.91, n = 4, p = 0.08). Forests with less complex understories had fewer captures and lower mammal diversity. Exotic large mammals appear to affect native small mammals by simplifying the structure of the forest understory and by competing for seeds. Four native species (Abrothrix longipilis, Oligoryzomys longicaudatus, Chelemys macronyx, and Irenomys tarsalis) ate Araucaria piñones. Anthropogenic changes in small mammal communities indicate that management of feral and domestic mammals needs to be a prominent part of the conservation of these majestic forests.


INTRODUCTION

Araucaria araucana dominates xerophytic Andean forests of northwestern Patagonia and adjacent Chile in pure stands and mixed with Nothofagus species (Roig, 1998), but exploitation in the 20th century resulted in a sharp decline in the health and distribution of these forests (Aagesen, 1998). In spite of recent protection, the future of araucaria communities is uncertain and precarious in many areas. Rechene (2000) estimated that over 60% of the remaining araucaria forests in Argentina are now in a degraded state. About one third of all Argentine araucaria forests lie within Parque Nacional Lanín (PNL) in southwestern Neuquén Province, where they are used for grazing, firewood extraction, and seed harvest. Clearly, one of the challenges for PNL is to balance this human use and the Park’s conservation mission (Martín and Chehébar, 2001). While anecdotal information abounds about the impact of people on these forests, systematic assessment is recent. For example, Sanguinetti et al. (2001a, 2001b, 2002) have initiated studies on the effects of grazing and seed harvest on forest regeneration. Despite the efforts to understand the impacts on regeneration, little
is known of the effects of human disturbance on forest elements other than *Araucaria* itself. Since *Araucaria* is dominant in these forests, it will influence many other species in the community. *Araucaria*’s influence may be heightened because it has a prominent masting cycle in which seed production varies more than twentyfold between mast and inter-mast years (Sanguinetti et al., 2001a, 2001b, 2002). *Araucaria* cycles have greater amplitude and higher seed production than those of northern temperate forests, where masting contributes to population fluctuations among small mammals that have far-reaching consequences (Ostfeld et al., 1996). In pure stands of *Araucaria* or in *Araucaria-Nothofagus* mixed forests, such effects are likely amplified by the dominance of this single species with large nutritious seeds. Human seed gathering and the use of the seed crop as forage for livestock remove a potentially important food resource for native animals. Since small mammals may act as seed dispersers as well as seed predators, they represent a key link in forest food webs. Community structure may track changes in natural masting cycles and anthropogenic changes in seed availability and forest structure.

Pearson and Pearson (1982) found that the Patagonian forest small mammal fauna consisted of six “forest endemic” and three “wider-ranging” species also found in the steppe, with more semi-fossorial, terrestrial, and scansorial small mammal species than Panamanian forests. The small mammal faunas of the western (Distrito Occidental) and sub-Andean districts (Distrito Subandino) of the Patagonian Phytogeographic Province appeared as a uniform and very distinct cluster in the analysis of Pardiñas et al. (2003). These same species (in data from Rio Negro and Chubut) formed a distinct biogeographic group that represented the Andean forest and Sub-Andean megabiozones (Monjeau et al., 1997). These forests appear to contain a rich, distinctive assemblage of small mammals.

Small mammal communities of Araucaria forests are likely to serve as useful indicators of forest integrity and human impact for a variety of reasons. First, because small mammals consume a conspicuous food resource in the forest (*Araucaria* mast), they represent a key link in the forest food chain. Second, the community has comparatively high diversity, endemism, and productivity (Pearson, 1983; Monjeau et al., 1997; Pardiñas et al., 2003). Third, small mammals partition habitat at both the coarse and fine scale (Patterson et al., 1990; Lozada et al., 2000). Fourth, these species differ greatly in their dietary proportions of animal matter, fungi and vegetation, and seeds and fruits (Meserve et al., 1988). As a result, changes in habitat structure and food availability are likely to manifest themselves in the community. Fifth, seed harvest and grazing are likely to act like hunting (Redford, 1992), so that human impact may be discernible in the small mammal community, even though it can not be seen in forest structure. For these reasons, we studied small mammal communities in Araucaria forests that differ in the level of human activity. We also made preliminary assessment of the relationship of small mammals to the seed crop as seed predators.

**MATERIALS AND METHODS**

We chose five closed, humid *Araucaria* forests between 1200 to 1400 m in elevation in the vicinity of PNL in southwestern Neuquén. These forests all consisted of mixtures of *Araucaria araucana*, *Nothofagus pumilio* and *N. antarctica*. The level of human impact varied directly with ease of access from very intense to modest (Table 1). In some areas, people establish summer “puestos” near which they graze livestock in meadows and in araucaria forests. In the fall, herds are encouraged to forage on the araucaria seed fall. Whole communities extract firewood for winter use throughout accessible areas. Collecting of araucaria seeds, “piñones”, occurs over a broad area. The Tromen forest is protected by virtue of its location between the border with Chile and the Argentine customs and immigration post. Collecting seeds occurs sporadically.

The 2002 field season was a year of moderate to low seed productivity (Sanguinetti et al., 2002). Estimated seed production in the Tromen forest in 2002 was 228 kg/ha, only 34% as much as in 2000. Similarly at Rucachoroi, production was 24% of the peak in the East and 13% in the West.
year like 2002, there are very few seeds on the forest floor, even immediately after the seed fall. In contrast, during a peak, many seeds are on the forest floor at the end of the season and a crop of seedling trees enters the population the following spring (Sanguinetti, pers. comm.). Because of the potential importance of production for levels of predation, the results reported here should be interpreted within the context of a low-production year.

We trapped small mammals during the 2002 seed fall, between late February and early April. At each study site, Sherman live traps were placed on the ground in the vicinity of 10 to 12 Araucaria seed trees, arranged so that 2 large (model XLF15) and 3 small (model LFATDG) traps were placed within a tree’s seed shadow and a similar group of 5 traps was placed nearby off the seed fall. Traps were baited with an Araucaria seed scale and a mixture of ground peanuts, vegetable oil, oatmeal and Mantecol (a peanut candy bar). Traps were checked each morning. Captured animals were identified, weighed, and marked with a small spot of paint on the hindquarters before release. Trap success (captures per trap night) is used as an index of relative abundance (Pearson, 1995; Thompson et al., 1998). Taxonomy follows Pearson (1995).

We estimated the rates of seed predation with seed scales marked with a spot of yellow paint on the distal part of the scale away from the seed. Since seed scales were removed from the forest floor by predators, the size of each seed fall could not be estimated directly from numbers of seed scales remaining. Instead, it was estimated by counting sterile cone scales that fall from the cones at the same time as the fertile seed scales. Data from an ongoing study of pre-dispersal predation on seed scales showed that the number of sterile scales is strongly correlated with the number of seed scales (r = 0.86, n = 112, p < 0.01, Shepherd and Ditgen, unpublished data). Scales from the current year’s seed fall were distinguished from those of previous years by color and state of degradation. All scales were counted in 10 circular quadrats of 0.5 m² located every 2 m on a transect through the center of the seed fall. The density of sterile scales was multiplied by the basal area of the seed tree to create a seed fall index that was assumed to be proportional to the total fallen seeds under the tree.

Forest understory was sampled by recording cover at 200 points spaced at 2 meter intervals along a line transect. At each point, vegetation within 3 m above the point was recorded in the following categories: tree, sapling, tree seedling, cane, shrub, grass, forb and cryptogam. Only trees and cane were identified by species. The presence of logs, coarse woody debris, and rocks was noted at all points; where none of these and no vegetation was present, the point was described as bare soil or leaf litter. Understory complexity was described by counting the number of points in the following categories: bare soil and/or rocks (substrate only); substrate plus leaf litter and/or coarse woody debris including logs; the preceding plus 1 to 3 different kinds of vegetation. Differences were summarized in an index of understory complexity by assigning the above 5 categories a score of 0 to 4 and then calculating an average score per point for each stand. Correspondence analysis (Statistica 6.1) was used to describe the multidimensional

<table>
<thead>
<tr>
<th>Human Impacts</th>
<th>Grazing pressure</th>
<th>Firewood gathering</th>
<th>Seed collection</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rucachoroi East, E</td>
<td>heavy</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Rucachoroi West, W</td>
<td>moderate</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Remeco, R</td>
<td>moderate</td>
<td>light</td>
<td>present</td>
</tr>
<tr>
<td>Chiquilhuín, C</td>
<td>light to moderate</td>
<td>light</td>
<td>present</td>
</tr>
<tr>
<td>Tromen, T</td>
<td>none</td>
<td>none</td>
<td>present</td>
</tr>
</tbody>
</table>

Table 1
Human impacts at small mammal study sites.
pattern of differences among the sample area understories.

In order to examine the relationship between understory structure and small mammal communities, a Mantel test (Poptools 2.6.2, Hood, 2004) evaluated correlation between stand dissimilarity matrices based on small mammals trapped and understory structure. Total individuals captured were used rather than relativized data because community productivity as well as species composition is important.

RESULTS

Total trapping effort consisted of 3416 trapnights with 347 captures, for an overall trapping success of 10.2%. Of these, 90 were marked, recaptured, animals, so a total of 257 individual animals were captured (Table 2). Since we used traps of two different sizes, we tested for the effect of trap size on capture rate. For all sites taken together, the capture rate was higher in larger traps, but not significantly so ($X^2 = 3.754$, df = 1, $p = 0.053$).

Similarly, for those species with more than 20 total captures (Oligoryzomys longicaudatus and Abrothrix longipilis), there was no significant effect of trap size on capture rate ($X^2 = 0.937$, $p = 0.331$ and $X^2 = 3.150$, $p = 0.076$ respectively, df = 1). We ignored the effect of trap size in all analyses.

Human impact and the small mammal community

Of the nine species captured, the long-haired mouse, A. longipilis, and the long-tailed mouse, O. longicaudatus, were the most common, comprising 88% of all individuals captured (Table 2). The Norway rat, Rattus norvegicus, was the only non-native species encountered. Productivity varied greatly between sites. Only two animals were caught in over 700 trap nights at the site (Rucachoroi East) with the greatest human impact; trap success was over 50 times higher in the least impacted forest.

The range of understory structure is shown in Figure 1, which compares the understory of the two sites that differed most in structure and overall trapping success. At Rucachoroi East, heavy grazing has greatly simplified the habitat of small mammals; more than half of the understory was devoid of vegetation and woody debris. In contrast at Tromen, almost 70% of the understory was vegetation that occurred in multiple layers.

The first two dimensions of a correspondence analysis (Fig. 2) of stand understories accounted for 46% and 37% of inertia respectively. The first dimension is related to stand composition. Araucaria predominated at Tromen and Rucachoroi East, while the other stands had a greater admixture of N. antartica and N. pumilio. Rucachoroi West had the greatest mixture of different plant types, including the greatest abundance of cane (Chusquea culeou) and shrubs. The correlation between stand coordinate axis 2 and understory complexity index is very high ($r = -0.996$, $p<0.001$), so this dimension represents understory complexity. At Rucachoroi East plant litter and bare soil predominated with little vegetation surviving grazing pressure. At Tromen, herbaceous, tree seedling, and tree sapling layers created a much more complex understory.

A Mantel test indicated a strong influence of understory structure on the small mammal community ($r = 0.529$, $p = 0.04$). Overall capture rate (small mammal community productivity), species richness, and the Shannon index are all higher in stands with greater understory complexity.

Seedfalls, capture rates and seed predation

The number of captures per seed tree ranged from 0 (6 trees) to 13 (1 tree) with an average of 3.6 captures per tree. The number of captures was not correlated with the seed fall index ($r = 0.06$, $n = 35$, $p = 0.71$), suggesting that the density of animals was similar under all seed trees. In the aggregate, more animals were captured in trap sets off seed falls than on seed falls ($X^2 = 5.01$, df = 1, $p = 0.025$).

We made 55 daily estimates of daily predation rates on marked seed scales that were placed in paired groups on and off seed falls at three of the sites. There was no significant difference in the predation rate for seeds on
Table 2

Trapping Results. Table shows the total number of individuals captured at each site, the minimum number known alive (MNKA). Relative abundance is trap success (new captures per trap night) relativized to Rucachoroi East as a measure of relative population sizes at the sites. Recapture rate is the number of recaptures as a percentage of total captures of that species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Rucachoroi East</th>
<th>Rucachoroi West</th>
<th>Remeco</th>
<th>Chiquilihuin</th>
<th>Tromen</th>
<th>Total Captures</th>
<th>Recapture Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abrothrix longipilis</td>
<td>1</td>
<td>18</td>
<td>12</td>
<td>2</td>
<td>53</td>
<td>40</td>
<td>124</td>
</tr>
<tr>
<td>Oligoryzomys longicaudatus</td>
<td>1</td>
<td>5</td>
<td>5</td>
<td>13</td>
<td>18</td>
<td>65</td>
<td>102</td>
</tr>
<tr>
<td>Dromiciops gliroides</td>
<td>7</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td>8</td>
<td>33%</td>
</tr>
<tr>
<td>Irenomys tarsalis</td>
<td>8</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td>8</td>
<td>0%</td>
</tr>
<tr>
<td>Chelemys macronyx</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td></td>
<td></td>
<td>6</td>
<td>14%</td>
</tr>
<tr>
<td>Abrothrix olivaceus</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td>3</td>
<td>0%</td>
</tr>
<tr>
<td>Loxodontomys micropus</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
<td>2</td>
<td>0%</td>
</tr>
<tr>
<td>Geoxus valdivianus</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td>1</td>
<td>0%</td>
</tr>
<tr>
<td>Rattus norvegicus</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td>3</td>
<td>0%</td>
</tr>
</tbody>
</table>

| Total Captures:         | 2               | 38              | 32     | 76           | 109    | 257            |
| Trap Nights:            | 720             | 738             | 486    | 721          | 751    | 3416           |

| Relative Abundance:     | 1.00            | 18.5            | 23.7   | 37.9         | 52.3   |
| Species:                | 2               | 4               | 6      | 4            | 6      |
| Shannon Index:          | 0.693           | 1.186           | 1.253  | 0.714        | 0.837  |

and off seed falls ($t = 0.546$, $df = 54$, $p = 0.588$).

Eaten, or partially eaten, seed scales were found in traps with *A. longipilis*, *O. longicaudatus*, *Chelemys macronyx*, and *Irenomys tarsalis*. Seed scales were sometimes shredded and apparently used as nest material inside the trap. Anecdotal observations suggest that *Chelemys* carries off seedscales and was specifically attracted to the seed scales used as bait. Eaten seed scales were not found with trapped individuals of *Dromiciops gliroides*, *Geoxus valdivianus*, *Loxodontomys micropus*, *Abrothrix olivaceus*, and *R. norvegicus*.

Seed predation rates varied greatly between sites ([Fig. 3](#)). Daily rates of removal of marked seeds varied from 59.7% at the most heavily grazed site to 15.1% at Chiquilihuín. At all sites, most of the seeds would be eaten within a week of falling from the tree. This predation was primarily the work of medium and large mammals. At Rucachoroi East, the rate of seed removal depended on the presence of sheep ($F_{3,46} = 35.2$, $p<0.0001$). No seed predation occurred at night or when no sheep were present. When ‘few’ or ‘many’ sheep were present, the predation rates on marked seeds were 27% and 73% per day respectively. Livestock (sheep, goats, and cattle) grazed all sites except Tromen. At three sites (Remeco, Tromen, Chiquilihuín), wild hogs (*Sus scrofa*) rooted up vegetation, damaged small mammal traps and left scat and prints. Scat of European red deer (*Cervus elaphus*) was seen at
Understory structure at Rucachoroi East and Tromen. Substrate: points with only bare soil and/or rock; Debris: points with substrate plus leaf litter and/or coarse woody debris including logs; Veg 1-3: points with the preceding plus 1 to 3 different kinds of vegetation. Number of transect sample points sums to 200 for each stand. Structural complexity indices: Tromen (T), 1.97; Rucachoroi West (W), 1.8; Remeco (R), 1.78; Chiquilihuín (C), 1.19; Rucachoroi East (E), 0.85. See methods for index calculation.

Correspondence analysis of understory structure from five trapping sites. Tree, sapling and seedling refer only to *Araucaria*; cwd is coarse woody debris. Site symbol abbreviations: Tromen (T), Rucachoroi West (W), Remeco (R), Chiquilihuín (C), Rucachoroi East (E).
Tromen. Since both feral exotic and native mammals foraged nocturnally, we could not measure their predation separately. Field sign suggested that the primary seed predators were hogs at Tromen and hogs and lagomorphs at Chiquilihuín. The overall capture rate and seed predation rate were strongly correlated ($r = -0.91$, $n = 4$, $p = 0.081$).

**DISCUSSION**

While mammal species richness and aggregate diversity varied between our sample areas, the most dramatic impact was on relative abundance. The site without grazing pressure (Tromen) had small mammal relative abundance over 50 times higher than the heavily grazed site; sites with moderate grazing had relative abundance about 20 times higher (Table 2). Clearly, small mammal communities are affected by grazing livestock. In the extreme case of Rucachoroi East, more than 50% of the forest understory had been reduced to bare soil and capture rates were exceedingly low.

We anticipated that human impact could affect small mammal communities either directly or indirectly. Seed predation rates indicate that grazing can remove almost the entire seed crop in a year of moderate seed production. In fact, livestock seed predation is so high in intensely-used areas that even in peak seed production years it would have a profound impact on seed availability for native small mammals. The correlation of seed predation rates and small mammal captures suggests that competition for seeds may limit small mammal populations in areas with exotic mammals. Domestic livestock also appear to simplify the structure of the forest understory, thereby removing the microhabitats needed to support native biodiversity. Small mammal community structure was strongly related to understory structure. Thus, livestock can play a dual detrimental role: acting directly as competitors for food and indirectly by altering habitat structure.

Understory complexity and small mammal density are also correlated in northern temperate forests (Dueser and Shugart, 1978; Smit et
al., 2001; Schnurr et al., 2004). Smit et al. (2001) concluded that alteration of vegetation structure was the primary means by which large herbivores affected small mammals. Through its effect on the small mammal community, forest understory structure influenced seed and seedling survival and tree recruitment patterns (Schnurr et al., 2004).

The problem of feral exotic species is an issue of longstanding, widespread concern in Argentina (Daciuk, 1978; Jackson, 1988; Bonino, 1999). These species are not just seed predators. Veblen et al. (1989) showed that red deer (C. elaphus) have eliminated some understory species altogether and retarded regeneration of forest dominants in Nothofagus forests. Elsewhere, feral hogs reduce native plant species diversity, facilitate invasion by exotic weeds, and prey on the young of medium-sized mammals (Bratton, 1974; Kotanen, 1995). In our study area, park personnel suggest hogs migrate into the Araucaria in the autumn where they forage on fallen seeds and root up the soil for other foods. Their impact on Araucaria forest vegetation and its mammal biodiversity is not known. We can say that even in less accessible areas, feral exotic medium and large mammals have an impact on seed fall that is similar to that of moderate domestic livestock grazing.

The two habitat generalists, A. longipilis and O. longicaudatus, that predominated among the small mammals captured are the most common species in studies of small mammals in Nothofagus forests farther south and west in Chile and are habitat generalists (Greer, 1965; Pearson and Pearson, 1982; Pearson, 1983, 1995). Their high capture rate is also a manifestation of our trapping regime, with traps placed in a variety of microhabitats on the forest floor. Arboreal (D. gliroides and I. tarsalis) and semi-fossorial (C. macronyx and G. valdivianus) species may be under-represented because of trap placement. L. micropus and A. olivaceus are reportedly more common in other habitat types (Mann, 1978; Pearson, 1983, 1995). Our captures included nine of the ten species reported for Nothofagus forests in Lanín and Nahuel Huapi National Parks immediately south of our study area (Pearson and Pearson, 1982; Pearson, 1995). The small mammal diversity of Araucaria forests appears similar to that of botanically more diverse forest types in the region.

The species that make up the small mammal community may also be a reflection of the degree to which human impact has altered understory structure. Increasing diversity of understory vegetation, like the cane and shrubs common at Rucachoroi West, adds habitat for species that are less habitat generalists and require specific features of the forest for their success. Patterson et al. (1990) found that habitat selectivity was inversely correlated with abundance and that less common species were found in more distinctive habitats. They trapped D. gliroides in places with high shrub and herbaceous cover, but earlier work (Greer, 1965; Mann, 1978; Redford and Eisenberg, 1992) associates this species with cane thickets. These studies clearly suggest a necessity for dense understory for this species. I. tarsalis is also reported to be associated with thickets of cane (Greer, 1965; Mann, 1978; Redford and Eisenberg, 1992). Whatever their particular microhabitat requirements, understory simplification is likely to eliminate such species.

Four species, including the two most common native small mammals (A. longipilis and O. longicaudatus) eat Araucaria piñones, confirming the key position of small mammals in the food chain of these forests. As a result, we expect the Araucaria masting cycle to be reflected in the level of seed predation and rodent population biology (Ostfeld et al., 1996). We have begun a long term study to assess the relationship between small mammal population dynamics and the Araucaria seed production. C. macronyx did appear to carry off groups of seed scales. More recently (May, 2004), we used automatic cameras to record C. macronyx carrying off a pile of 20 seeds within two hours. We are pursuing further studies to evaluate its interaction with “piñones” as a potential seed dispersal agent.

Because of this interaction of rodents and seeds, we expected higher capture rates on the seed fall as a result of their attraction for ro-
Human use can clearly alter the small mammal fauna of Araucaria forests. The aggregate impact of intense grazing and firewood collection can greatly simplify the forest understory and essentially eliminate these native animals. The recent conservation literature (e.g., Brandon et al., 1998; Christensen, 2004) suggests that successful implementation of sustainable human use requires on-going monitoring and active adaptive management. Clearly, management of the impact of feral and domestic mammals needs to be a prominent part of the conservation of these majestic forests.

ACKNOWLEDGEMENTS

This work was supported in part by a grant from the College of Liberal Arts of Mercer University, Macon Georgia. The Corporación Interstatal Pul mari allowed access to the Remeco site and provided housing and logistical support. Help was provided at all stages by personnel of Parque Nacional Lanín, especially by Javier Sanguinetti. Two reviewers made helpful comments that resulted in improvements in the manuscript.

LITERATURE CITED


