Trophic preferences in an assemblage of mammal herbivores from Andean Puna (Northern Chile)

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1. Introduction

Andean Puna ranges between 7°S and 27°S, and between 3500 and 5500 m.a.s.l. (Baied and Wheeler, 1993). This placement involves strong abiotic constraints on the vertebrate fauna inhabiting such ecosystems. Specifically, partial pressure of oxygen is reduced (Aceituno, 1997) and daily thermal oscillations are huge. Mean annual temperature at 4000 m is 8 °C, but daily thermal amplitude is 17 °C (Winterhalder and Thomas, 1978). The snow tropical precipitation (Bolivian winter), typical of the hydric regime of the monsoonal desert (Novoa and Villaseca, 1989), is concentrated between November and March. These environmental variations affect primary production, which is not only globally low but also seasonally and geographically variable (Baied and Wheeler, 1993). Plants display phenotypes adapted to such extreme conditions (Bliss, 1962), making them differentially available as food sources for herbivorous vertebrates.

Freeland and Janzen (1974) proposed that the consumption of a particular plant by an herbivorous mammal is limited by its capability for detoxifying or excreting secondary metabolites, resulting in highly variable diets (trophic niche breadth). Alternatively, Westoby (1978) established that one plant species may be insufficient for fulfilling all the nutritional requirements of the herbivorous mammal and, hence, more plant species are to be consumed to obtain an optimal diet.

The nitrogen levels are higher in the tissues of the mammal herbivores than in the plants they consume (Mattson, 1980). Most plant species eaten contain low nutrient levels and their physical and chemical properties (i.e., secondary compounds) frequently make them difficult to digest (Dearing et al., 2005; McNab, 2002). Not surprisingly, leaf eating herbivores are estimated to consume three times the dry mass eaten by insectivores or carnivores in the same conditions (McNab, 2002). Although an increase in the food intake may still keep the nutritional and energetic balance, the ability for processing plant items with high fibre contents is a constraining factor (McNab, 2002). Such pressures on diet optimisation are more evident in environments where primary production is low, such as the South American plateau. For instance, the camelid Vicugna vicugna (vicuña), which displays strong...
morphic and physiological adaptations to live in deserts (Hofmann et al., 1983), spends 89% of its time to foraging (Cassini et al., 2008). As another example, the rodent Chinchilla breviceps (short-tailed chinchilla), restricted to the least productive areas from northern Chile (Pires, 2008) partly due to the intense hunt exploitation it was subjected, displays lower levels of basal metabolism and lower thermal conductance than those expected for mammals of similar size (Messerli et al., 1993). Finally, Spotorno et al. (1998) reported that the rodent Abrocoma cinerea (ashy chinchilla rat) similarly displays very low thermal conductivity (68.6%) considering its body size (Herreid and Kessel, 1967).

Partly due to these specialisations and also to the logistic difficulties for reaching the Andean grasslands, the knowledge on the trophic ecology of mammal herbivores distributed in this habitat is still very incomplete. This is especially true for the camelid vicuña and the rodent short-tailed chinchilla, both mammals included in the Appendix I of CITES Convention whose distribution is restricted to the high Andes (Pires, 2008). In contrast, ashy chinchilla rat still lacks conservation status due to insufficient data (Muñoz-Pedreros and Yáñez, 2009).

The aims of this work are: 1) to describe and compare the diets of three sympatric Andean herbivores, the rodents ashy chinchilla rat and short-tailed chinchilla, and the camelid vicuña, during the humid season in a site of Northern Chile; 2) to assess plant preferences by comparing diet of each species with plant availability, and 3) to discuss the possible factors involved.

2. Materials and methods

2.1. Study area

The study was carried out in the Morro Negro sector (24°30’S; 69°45’W; 3,400 m.a.s.l.) within the Llullaillaco National Park, sited 275 km Southwest of Antofagasta (II Región, Chile). Annual precipitation ranges from 20 to 50 mm year⁻¹ (Messerli et al., 1993) and is concentrated in the winter and summer seasons (Arroyo et al., 1998; Di Castri and Hajek, 1976). However, being in the Eastern border of the desert of the II Región, it is under the influence of the so called Bolivian Winter, with the occasional occurrence of high precipitation in summer (Ammann et al., 1996).

Otherwise, climate is dry and mean annual temperature 2 °C (Luebert, 1998).

2.2. Study species

Ashy chinchilla rat ranges from South-western Perú to the extreme northern border of Chile, also being present in Southern Bolivia and across the Andean range in Argentina, from Salta province and probably South of Mendoza (Muñoz-Pedreros and Yáñez, 2009). This rodent has been considered a probable consumer of shrubs (Cortés et al., 2002a).

Short-tailed chinchilla is a rodent distributed in South of Perú, Western Bolivia, Northwestern Argentina and Northern Chile (Muñoz-Pedreros and Yáñez, 2009). It is characterised by a high thermoregulatory capability, low energetic requirements (low basal metabolic rate, BMR), as well as by efficient mechanisms for preventing water loss (Cortés et al., 2003b). Regarding its feeding habits, literature suggests a diet based on herbaceous plants (Cortés et al., 2002a).

The vicuña is found at the mountain and plateau levels (3000 to 4600 m.a.s.l.) of Ecuador, Perú, Bolivia, Argentina and Chile (Muñoz-Pedreros and Yáñez, 2009). Considering the blood parameters, this species is the best adapted to high altitude environments in comparison to other South American camelids (Jürgens et al., 1988). However, such advantage does not extend to water dependence since it is an obligate and frequent drinker (Wheeler, 2006). Regarding its diet and selected food, no studies are currently available for Chile, although some descriptive studies are available for other populations (Benítez et al., 2006; Borgnia et al., 2008; Cassini et al., 2009). Cajal (1989) mentions a diet based on Poaceae and short grasses, most belonging to the genus Stipa. Benítez et al. (2006) and Borgnia et al. (2008) also indicated a dominance of Poaceae in the diet.

2.3. Sampling and diet analysis

Sampling was carried out in March 2001. Samples of leaves, flowers and stems of all the plants present in the study area were collected and later determined at species level (Table 1) by comparison with the specimens in the herbarium of Universidad de

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### Table 1

<table>
<thead>
<tr>
<th>FAMILY/species</th>
<th>Plant typology</th>
<th>Plant cover (%)</th>
<th>Plant consumption (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>FAMILIES</strong></td>
<td><strong>%</strong></td>
<td><strong>%</strong></td>
<td><strong>%</strong></td>
</tr>
<tr>
<td><strong>Asteraceae</strong></td>
<td></td>
<td><strong>A. cinerea</strong></td>
<td><strong>C. breviceps</strong></td>
</tr>
<tr>
<td>Baccharis tola</td>
<td>S</td>
<td>0.05</td>
<td>0.80</td>
</tr>
<tr>
<td>Papilioniaceae</td>
<td></td>
<td><strong>Adesmia pinicipes</strong></td>
<td>0.05</td>
</tr>
<tr>
<td>Adesmia erinacea</td>
<td>S</td>
<td>0.08</td>
<td>0.80</td>
</tr>
<tr>
<td>Solanaceae</td>
<td></td>
<td><strong>Fabiana bryoides</strong></td>
<td>5.10</td>
</tr>
<tr>
<td>All shrubs</td>
<td></td>
<td>5.28</td>
<td>59.50</td>
</tr>
<tr>
<td>Poaceae</td>
<td></td>
<td><strong>Stipa chrysophylla</strong></td>
<td>3.55</td>
</tr>
<tr>
<td>Malvaceae</td>
<td></td>
<td><strong>Crisanthera amicola</strong></td>
<td>0.06</td>
</tr>
<tr>
<td>All herbaceous plants</td>
<td>3.61</td>
<td>40.50</td>
<td>17.10</td>
</tr>
<tr>
<td>Fibres</td>
<td></td>
<td>0.90</td>
<td>17.70</td>
</tr>
<tr>
<td>Undetermined materials</td>
<td></td>
<td>0.80</td>
<td>2.10</td>
</tr>
<tr>
<td>Bare ground</td>
<td></td>
<td>91.10</td>
<td></td>
</tr>
<tr>
<td><strong>Trophic niche breadth (I/F ± CI 95%)</strong></td>
<td>0.26 ± 0.06</td>
<td>0.29 ± 0.05</td>
<td>0.42 ± 0.04</td>
</tr>
</tbody>
</table>
The method of least significant differences (LSD) multiple comparisons (Sokal and Rohlf, 1995).

3. Results

3.1. Trophic availability

The total plant cover of the study area was scarce: 8.9%, the remaining 91.1% being bare ground. Plants were represented by five families, five genera and six species. The most abundant ones were the shrub *Fabiana bryoides* (Solanaeae) and the perennial herbaceous species *Stipa chrysophylla* (Poaceae) with covers of 5.10% and 3.55%, respectively (Table 1).

3.2. Diet composition and selection

Ashy chinchilla rat mostly consumed shrub species (81.2%), particularly *Bacharis tola*, which represented 79.0% of its total diet. Of the two herbaceous species available only one was consumed (*S. chrysophylla* 17.1%). The diet of short-tailed chinchilla included mostly the grass *S. chrysophylla* (59.1%) and, to a lesser extent, the shrub *Adesmia erinacea* (19.1%), the remaining ones with values less than 2% (*F. bryoides* 0.3%, *Cristaria andicola* 1.7%). The vicuña mainly consumed the herbaceous species *S. chrysophylla* (59.6%) and *C. andicola* (21.6%) and, with less importance, the shrub *B. tola* (6.7%) (Table 1).

When the proportions of plant species consumed (excluding the undetermined material and the fibres) were compared to those expected from availability estimated by plant cover, significant shifts were detected for the three mammals studied ($p < 0.0001$), indicating either preference or rejection for certain plant species (Table 2). Of the five plant species eaten by ashy chinchilla rat, two, *B. tola* and *A. erinacea*, were “preferred” (consumed in higher proportion than available in the field, $p < 0.05$) whereas the other three, *S. chrysophylla*, *A. caespitosa* and *F. bryoides*, were “avoided” (consumed in less proportion than available $p < 0.05$) (Table 2).

The short-tailed chinchilla and the vicuña selected for three plant species in common, the herbaceous *S. chrysophylla* and *C. andicola*, and the shrub *A. erinacea*: The shrub *F. bryoides* was avoided by all three mammal species. The vicuña also showed preference for *B. tola* (Table 2).

3.3. Trophic diversity and overlap

When comparing the niche breadth ($H'$) between the three species studied (Table 1), two statistically significant groups were detected ($F_{2, 30} = 7.75; p < 0.0019$): the first, constituted by the two rodents, the ashy chinchilla rat ($H' = 0.26$) and the short-tailed chinchilla ($H' = 0.29$), and the second, only containing the vicuña ($H' = 0.42$).

The trophic overlap estimated through Schoener’s Index (PS) was significantly higher ($F_{2, 30} = 43.5; p < 0.00001$) between the short-tailed chinchilla and the vicuña (PS = 0.69) than between either the two rodents (PS = 0.19) or between the ashy chinchilla rat and the vicuña (PS = 0.26).

4. Discussion

The Puna vegetation has been described as xerophytic (Hofsted et al., 2003). The plant species inhabiting such ecosystems exhibit adaptations to the extreme climate which decrease their palatability (e.g., secondary metabolites, structural carbohydrates, Lambrinos et al., 2006). This adds to the general low plant availability of the study site. Herbivore mammals exploiting these resources would have strong constraints unless they display
adaptations for ensuring efficient processing of plant matter and energy (Batzli and Hume, 1994). Namely, the foraging behaviour and morpho-physiological specialisations (incisive teeth with continuous growth, highly efficient digestion) allows the vicuña to consume short grasses that are beyond the scope of other camelids (Hofmann et al., 1983). Similarly, the Puna rodents are able to cut and process plant matter with a high content in fibres (cellulose) (Owen, 1980).

Shrubs were consumed by the three mammal species but mainly by the short-tailed chinchilla rat, whose diet mostly consisted of bakery plants, whereas these played a secondary role in the diet of the short-tailed chinchilla and the vicuña. It is worth noting that the shrub species predominantly consumed by ash chinchilla rat, B. tola, has already been reported in the diet of this species in northern Chile (Cortés et al., 2002b). Baccharis tola belongs to a genus composed of species toxic for some herbivores (Aldea et al., 2009; Stegelmeier et al., 2009). Terpenes have been isolated from this species (San Martin et al., 1983), being the main secondary compounds of its resin (Langenhorn, 2003). These substances are able to disturb the metabolism and food ingestion of many herbivores (Hume, 2005). However, they are apparently excreted in the urine of the ash chinchilla rat. The consistence of this urine is viscose acting as cement for biologic materials deposited and may be conserved for long periods being the origin of the so called paleo-burrows (Spaulding et al., 1990). In contrast to the ash chinchilla rat, the diet of the short-tailed chinchilla does not include B. tola, probably due to a lower capacity for detoxifying secondary compounds. Nevertheless, this species consumed and positively selected the shrub A. erinacea. On the other hand, the vicuña positively selected B. tola, but it only represented a minor portion of its diet.

Regarding the herbaceous plants, the Poaceae S. chrysophylla, highly consumed by the short-tailed chinchilla and the vicuña, has already been reported for the diet of other camelids and chinchillids (Benítez et al., 2006; Cajal, 1989; Cortés et al., 2002b, 2005a). Genus Stipa includes some species important as food source for herbivorous vertebrates (e.g., camelids, cattle, rodents) in the areas where they are dominant (Benítez et al., 2006; Cortés et al., 2002b). Such Poaceae provide a reduced profitability due the low nitrogen content and high concentration of fibres difficult to digest (Benítez et al., 2006; Distel et al., 2005). However, these disadvantages are less significant for camels and chinchillids given the physiological specialisations for using low quality food items already documented for both vertebrate groups (Cortés et al., 2002a, 2003b; Sponheimer et al., 2003; Tirado et al., 2007).

The Solanaceae, avoided by the three mammals belongs to the genus Fabiana, are shrubs containing secondary metabolites with diuretic effects (Álvarez et al., 2002). It is here suggested that the severe consequences on the water balance of these vertebrates in such arid environments may explain their absence from their diets.

The three mammal species also differed in the fibre content of the faeces, the ash chinchilla rat retaining the lowest values probably due to the high consumption of shrubs. In fact, shrubs hold more protein and less fibre content than Poaceae (Benítez et al., 2006). In contrast, the values of the short-tailed chinchilla and the vicuña were very high as expected from diets based on Poaceae, mainly S. chrysophylla.

5. Conclusions

In summary, the three mammal herbivores differ in the consumption of the plant species available, which seems to be due to the dissimilar abilities for responding to diverse concentrations of secondary metabolites contained by them. The plants consumed and their selection in the short-tailed chinchilla and the vicuña suggest that the palatability of the different plants is not related to their high nutritional content but rather to the low content of secondary compounds (McNab, 2002). The same would not apply to the ash chinchilla rat, which would be able to excrete such compounds, probably via urine. Although this process would involve metabolic costs, it would be compensated by the high energetic content of the plants diets rich in terpenes (Foley and McArthur, 1994).
References


Benítez, V.V., Borgnia, M., Cassini, M.H., 2006. Ecología nutricional de la vicuña, Vicugna vicugna (llallaco). The help of Gina Arancio for providing access to the herbarium of Universidad La Serena, and for identifying the plant species is appreciated. We thank Dr. Ernesto Gianoli for reviewing the manuscript. The work of MAC was supported by the projects PTDC/BIA-BDE/67678/2006 and PTDC/BIA-REC/101256/2008 funded by Fundação para a Ciência e a Tecnologia de Chile (CONICYT). The work of MCA was supported by projects FONDECYT 5960017, Programa Sectorial Biomas y Climas del Norte de Chile, Comisión Nacional de Investigación Científica y Tecnológica de Chile (CONICYT). The work of MAC was supported by the projects FONDECYT 5960017, Programa Sectorial Biomas y Climas del Norte de Chile, Comisión Nacional de Investigación Científica y Tecnológica de Chile (CONICYT).

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