Acta Theriologica 48 (2): 229–237, 2003.
PL ISSN 0001–7051

Feeding habits of guanacos *Lama guanicoe* in the high Andes of north-central Chile

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Cortés A., Miranda E., Rau J. R. and Jiménez J. E. 2003. Feeding habits of guanacos *Lama guanicoe* in the high Andes of north-central Chile. Acta Theriologica 48: 229–237.

The guanaco *Lama guanicoe* Muller, 1776 has a wide distribution along the Andes and Patagonia. We studied the feeding behaviour of a guanaco population that lives over 4100 m altitude in the Andes of north-central Chile. By contrasting the diet of guanacos during a dry year with that of a wet year and comparing it with the plant availabilities in the field, we tested the hypothesis that the guanaco is a generalist herbivore. We predicted that under such extreme habitat conditions guanacos should consume whatever plant species are available in the environment, especially in a dry year, when vegetation is scarcer. In addition, we compared its diet at three different age classes. We estimated the diet through the microhistological analysis of plant remains found in guanaco pellets collected during January of 1997 (ie after a dry year) and 1998 (ie after a wet year; 41 vs 495 mm, respectively). Then, we computed dietary preferences, food niche-breadth, and food-niche overlap between years and among age classes. Vegetation cover and plant species richness were higher during the wet than during the dry year. The most common plants in the environment were perennial graminoids and legumes. Contrary to our prediction, the guanaco preferred a few plant species, showing a relatively narrow diet breadth that changed little between years differing in plant abundances. The diet proportions differed among the three age classes, however. Our data indicate that at least in this high-elevation population, guanacos are selective and non-opportunistic herbivores. This specialized feeding behaviour is puzzling given the energetic demands of living in a harsh environment with low availabilities of resources. The hypothesis that this is due to the lower palatability of the plants not eaten, remains to be tested.

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Key words: *Lama guanicoe*, diet food selection, herbivore, high Andes, plant cover, Chile

Introduction

Among large herbivores of South America, the guanaco *Lama guanicoe* Muller, 1776 is distributed along the Andes from the northern highlands (18°S) through Tierra del Fuego and Isla Navarino (55°S) in Chile (Redford and Eisenberg 1992). In Argentina the guanaco ranges from Jujuy (23°S) in the northeast, west to the Province of Buenos Aires (39°S) and south to Tierra del Fuego (Olrog and Lucero 1981). Although the social behaviour and dietary habits allow this camelid to occupy

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a variety of habitat types (Franklin 1982, 1983) ranging from sea level to 4200 m in elevation, the guanaco is considered a “vulnerable” species in Chile (Glade 1993).

Nonetheless the limited numbers of guanacos in the wild, they constitute an important resource for local people (Franklin and Fritz 1991). For instance, in Argentina juvenile guanacos or chulengos are legally harvested for their hides. Between 1972 and 1979, 443 655 chulengo pelts were exported, 223 610 of them between 1976–1979 were sold for 5.6 million US$. In 1979 alone, 86 000 pelts were exported, representing an income of 3.6 million US$ (Ojeda and Mares 1982). In Chile, because of their reduced numbers due to overharvesting and competition with domestic stock (Raedeke 1979), guanaco hunting was banned as early as in 1929 (Iriarte *et al.* 1997), and given its higher abundance in the southern ranges a strong conservation and management program was started in 1975 (Cunazza 1980). In addition, the guanaco protection in Torres del Paine National Park represents a landmark for the species’ recovery success, increasing in numbers from 175 in 1975 to 3000 in 1993 (Sarno and Franklin 1999). In parallel, this population, as well as some Argentinean guanaco populations, have been intensively studied, including mortality causes, feeding habits, population dynamics, social structure and organization, and competition with vicuñas *Vicugna vicugna* and livestock (Raedeke 1978, 1979, 1980, Jefferson 1980, Franklin 1982, Wilson 1984, Wilson and Franklin 1985, Ortega and Franklin 1988, 1995, Cajal 1989, Bonino and Pelliza-Sbriller 1990, 1991, Garay *et al.* 1995, Baldi *et al*. 2001).

In contrast, the sparser northern guanaco populations, exposed to a limited food base and scarce water availability, have been almost completely neglected and to date we know little about the species in its northern range. Only Raedeke and Simonetti (1988) and Cajal (1989) studied northern populations, but at lower elevations than in this study. To fill this gap partially, we examined the diet of guanacos in the high Andes of north-central Chile. In this harsh environment, given the year-round scarcity of food resources (Raedeke and Simonetti 1988), we hypothesize that guanacos should behave as a generalist herbivore, consuming whatever plant is available, especially during years with little rain. To test this hypothesis we: (1) studied the feeding habits of adult guanacos comparing contrasting years of food availabilities resulting from different rainfall amounts, and (2) compared the diet among the three guanaco age classes as recognized by Franklin and Fritz (1991) during a dry year.

Material and methods

Study site

Our study site was located at 4200 m altitude in the Cordillera de Doña Ana (29°50’03"S, 69°55’44"W), 180 km north-east of La Serena, in north-central Chile. The vegetation is made up of species of the lower Andean belt, characterized mainly by scrubby plants with cushion life forms (*Adesmia subterranea*, *Azorella cryptantha*) and few grasses (*Stipa chrysophylla*, *Deyeusia velutina*) (Squeo *et al.* 1994). Climatic conditions in the area present wet and cold winters (May to October) and dry and cold summers (December to March). Mean annual temperature is 2.6°C, with a low of –17.3°C in July and high of 24.2°C in January (data from 1981 through 1997, provided by El Indio Mining Company). Mean annual rainfall is 242.3 mm, 96% of which falls during winter. The amount of precipitation is highly unpredictable, with contrasting dry and wet years (range 27–740 mm, Squeo *et al.* 1994). We collected feces during January 1997 and January 1998. Annual precipitation for 1996 and 1997 was 41 and 495 mm, respectively.

Vegetation cover

Ground cover of plant species was obtained though the point-intercept technique (Mueller--Dombois and Ellenberg 1974). Cover of herbs and shrubby species was estimated during January of 1997 and 1998 in sixteen 16 3-m transects, randomly located on slopes and wetlands, where we frequently saw guanacos foraging. Each transect had 60 sampling points separated by 5 cm.

Reference collection

We collected leaves, stems, and flowers of every plant species found in the area (Table 1). Plants were determined to the species level. To compare with the remains found in the feces, we mounted a reference collection of epidermal tissue of all species/parts found following the technique first described by Baumgartner and Martin (1939) and refined by Dusi (1949). Black and white pictures of all material were taken under a magnification of 36 .

Collection of feces and processing of the samples

During both summers we collected samples that corresponded to one guanaco family group (see Ortega and Franklin 1995 for a definition of family group), made up of adults (2 y), juveniles (< 2 and > 1 y), and chulengos (recently born to 1 y; Franklin and Fritz 1991). Individuals of these age classes are readily recognized in the field. To obtain samples representing each age class we observed males and females with binoculars and collected the pellets just after the guanacos defecated. Both the plant and the feces samples were taken to the lab, where they were dried at 60°C for 24 h (Hansson 1970). Among the 110 fecal pellets for each age class collected, we randomly chose 20 pellets to apply the technique refined by Dusi (1949).

Diet estimation

For each age class, we analyzed 10 random fields of each of 10 preparations using a Leitz microscope with a grid of 20 by 20 squares at 36 magnification. Fields with less than 50% of the area covered by epidermal structures were discarded (Stewart 1967, Meserve 1981). With the help of the voucher collection prepared ad-hoc (see above), plant remains found in the feces were identified at the species level. The frequency of occurrence of plant species found in the feces were estimated by their relative cover on the fields (Williams 1962, Hansson 1970, Meserve 1981). We assumed that the relative abundance of plants in the feces was the same as that ingested and that all plants were digested equally.

Dietary preference

We assessed diet preference by comparing the proportions in the diet with what was available in the field as estimated above using Ivlev's original E_i index (Krebs 1989) to determine preference as:

$$E_i = (d_i - e_i) / (d_i + e_i),$$

where d_i is the percentage of species i in the diet and e_i is the percentage of species i in the environment. The index ranges from –1 (ie complete avoidance) to 1 (complete preference), whereas an E_i around zero indicates consumption as it is available (no preference).

Food-niche breadth

Food-niche breadth or dietary amplitude was used to estimate diet specialization. It was computed by using *J'*, the standardized *H'* diversity index of Shannon-Weaner (Krebs 1989) as:

$$J' = -(\quad p_i \log p_i) / \log m,$$

where p_i, the proportion of items of species i, is computed from n_i/N. n_i is the number of items of species i and N corresponds to the number of all items recorded, and m is the total number of species detected. Food-niche breadth ranges from 0 (narrow or specialized diet) to 1 (broad or generalized diet).

Diet similarity or overlap

We used this metric to compare the diet of adult guanacos between years and for the same dry year among age classes. We used Horn's R_o (Horn 1966) index to compute diet similarity between group j and k as:

$$R_o = [\quad (p_{ij} + p_{ik}) \log (p_{ij} + p_{ik}) - \quad p_{ij} \log p_{ij} - \quad p_{ik} \log p_{ik}] / (2 \log 2),$$

where p_{ij} is the proportion of the resource i out of all resources used by group j, and p_{ik} is the proportion of the resource i out of all resources used by group k. R_o ranges from 0 (ie the two groups consume different items) to 1 (the groups consume similar items).

Results

Plant availability

During the dry year, vegetation covered 50.9% of the ground and was represented by 7 families, 13 genera, and 15 species. The perennial graminoids represented 28.6% of the total ground cover (Table 1). The relative abundance of graminoid species in decreasing order was: *Deyeuxia velutina, Stipa chrysophylla, Deschampsia caespitosa*, and *Hordeum comosum*. The legumes (Papilionaceae) made up 11.8% of the cover and were represented by *Adesmia subterranea, A. echinus*, and *A. capitellata*. The third most abundant plants were the rushes (Juncaceae) with 8.4% of ground cover (Table 1).

In contrast, during the wet year, plants covered 72.3% of the ground, and were represented by 5 families, 10 genera, and 12 species. The most abundant plants were the graminoids, increasing their relative abundance to 31.4% of the cover. The abundance order by species was the same as during the dry year. Other families, such as Papilionaceae and Juncaceae showed similar patterns, which only increased their cover slightly (Table 1). Although the median cover for all species showed no significant changes between years (Mann-Whitney U-test: $U = 114$, $p > 0.05$, $n = 15$), the annual herbaceous

Table 1. Vegetation coverage during the summers of a dry (January 1997) and a wet year (January 1998) in guanaco habitats in the highlands of north central Chile.

Species	Ground cover (%)	
	Dry	Wet
Gramineae		
Deyeuxia velutina	12.9	13.7
Stipa chrysophylla	10.9	10.0
Deschampsia caespitosa	3.6	5.3
Hordeum comosum	1.2	2.4
Papilionaceae		
Adesmia subterranea	7.2	4.5
Adesmia echinus	4.1	8.3
Adesmia capitellata	0.5	0.5
Compositae		
Chaetanthera acerosa	0.2	2.1
Senecio aff. volckmanii	0.1	–
Erigeron leptopetalus	0.2	0.3
Juncaceae		
Juncus aff. depauperatus	6.2	8.0
Patosia clandestina	2.2	3.3
Onagraceae		
Gayophytum micranthum	0.7	13.9
Portulacaceae		
Montiopsis copiapina	0.1	–
Umbelliferae		
Azorella cryptantha	0.8	–
Bare soil	49.1	27.9

Gayophythum micranthum (Onagraceae) increased in cover from 0.7 to 13.9% from the dry to the wet year (Table 1).

Plant consumption by adult guanacos

During the dry year guanacos consumed only 4 out of the 15 plant species available (Table 2). By far the most grazed species was *S. chrysophylla* (54.7%), followed by *A. subterranea, D. caespitosa*, and *H. comosum*. The general diet changed somewhat, but not significantly during the wet year (Mann-Whitney U-test: $U = 14, p > 0.05, n = 5$). Consumption of *S. chrysophylla* and *D. caespitosa* increased compared to the previous year (60.0 and 10.4%) and *H. comosum* was not eaten. Consumption of *A. subterranea* decreased from 13.6 to 2.5%. The amount of fibers (ie unrecognized plant material) eaten by guanacos was high and similar during the two years (Table 2).

During the dry year guanacos preferred 3 plant species (*S. chrysophylla*, *H. comosum*, and *A. subterranea*), whereas *D. caespitosa* was neutral for them (Table 2). During the wet year *S. chrysophylla* was the most preferred plant in the diet ($E_i = 0.71$). Compared to the dry year, the preference by guanacos in the wet year for *D. caespitosa* and *A. subterranea* reversed (E_i = 0.32 and –0.29, respectively) (Table 2).

Diet diversity in guanacos was low during both years (J' = 0.32 and 0.22) and diet similarity was high between years (R_o = 0.97). This indicates that guanacos have a diet based on a few plant species regardless of food availability and diversity.

Diet of different age classes

The diet differed among the three age classes examined (Kruskall-Wallis test: $H = 13.033$, $p = 0.011$). The graminoids made the staple of the guanaco diet:

Table 2. Food items eaten, food preference (Ivlev's E_i), food diversity (standardized Shannon-Weaver's J'), and diet similarity (Horn's R_o) in adult guanacos during a dry (January 1997) and a wet year (January 1998) in the highlands of north-central Chile.

Plant species	Food items eaten (%)		E_i	
	Dry	Wet	Dry	Wet
Gramineae				
Stipa chrysophylla	54.7	60.0	0.54	0.71
Deschampsia caespitosa	5.3	10.4	−0.01	0.32
Hordeum comosum	3.6	–	0.32	–
Papilionaceae				
Adesmia subterranea	13.6	2.5	0.11	−0.29
Fibers	22.7	27.1	–	–
J'	0.32	0.22		
R_o	0.97			

Table 3. Food items eaten, food preference (Ivlev's E_i), food diversity (standardized Shannon-Weaver's J'), and diet similarity (Horn's R_o, compared groups are shown by horizontal lines) of guanaco age classes during a dry year (January 1997) in the highlands of north-central Chile.

Plant species	Food items eaten (%)			E_i		
	Adult	Juvenile	Chulengo	Adult	Juvenile	Chulengo
Gramineae						
Stipa chrysophylla	54.7	51.3	40.9	0.54	0.50	0.48
Deschampsia caespitosa	5.3	16.1	4.7	– 0.01	0.48	– 0.01
Hordeum comosum	3.6	2.2	2.3	0.32	0.07	0.17
Papilionaceae						
Adesmia subterranea	13.6	10.6	19.4	0.11	– 0.03	0.34
Fibers	22.7	19.8	32.8	–	–	–
J'	0.32	0.36	0.36			
R_o	0.97 (Adult–Juvenile)	0.95 (Juvenile–Chulengo)	0.99 (Adult–Chulengo)			

graminoid consumption increased from chulengos to juveniles (47.9 to 69.6%) and then decreased in adults (to 63.6%). These differences were apparently due to the differential consumption of *D. caespitosa* (Table 3). Most differences were due to: (a) a low consumption of fibers and *S. chrysophylla,* and a high consumption of *D. caespitosa* by juveniles; (b) a high consumption of *A. subterranea* and fibers by chulengos (Table 3).

All age classes had high and similar preferences for *S. chrysophylla*. Plant preference in the juvenile' diet was somewhat different from the other two classes in that juveniles preferred *D. caespitosa* and tended to avoid *A. subterranea* and the other classes displayed the opposite tendencies. In turn, chulengos differed from the other two groups in preferring *A. subterranea* (Table 3). In terms of diet diversity, all three age classes consumed a limited number of plants, showing a narrow trophic niche. In addition, all age classes of guanacos fed on similar species, but in different proportions, rendering high diet similarities among all pairwise comparisons (Table 3).

Discussion

The guanaco population of the high Andes of central Chile feeds on a reduced number of plant species both during dry and wet years. It appears that guanacos are highly selective in choosing their food items, grazing only on a small portion of the potential food spectra. Further, although the abundance and diversity of food in the field changed, due to increased amount of rainfall, guanacos did not show a parallel change in their diets. Thus, guanacos in highlands appear to have little diet flexibility when faced with changing conditions such as food supply and availability.

In sum, our data indicate that at least at high elevations guanacos are selective and non-opportunistic feeders.

These findings contrast with those of Cajal (1989), who studied guanacos at a similar latitude, but lower elevations. Cajal (1989) found local guanacos to be generalists, but nonetheless consumed preferentially grasses of the genus *Stipa*. Unfortunately he did not determine preferences and did not indicate the amount of rain when sampling, and thus limited our comparisons.

The most important plants consumed by adults, juveniles, and chulengos were graminoids such as *S. chrysophylla* and *D. caespitosa*, and to a lesser extent the cushion shrub *A. subterranea.* The latter species comprised an important part of the chulengo diet. We believe that this difference is explained by the foraging tactics of chulengos. We observed that chulengos rely on their mothers for access to *A. subterranea.* The females excavate the cushion plants and make them available to chulengos as these plants may be more nutritious for chulengos. *S. chrysophylla* was the most consumed and also the most preferred species, perhaps because this plant grows in both slopes and wetlands. We observed that *S. chrysophylla* was highly grazed in the two habitat types most frequented by guanacos.

As for the adults, chulengos and juveniles also fed on a limited number of plant species, exploiting mainly those resources that are relatively abundant, but showing a high degree of preference for *S. chrysophylla*. The few plants fed upon during a dry year by all age classes is consistent with the low equitability indices and the high similarities in the diet among guanacos of different ages.

Our findings indicate that highland guanacos behave as selective herbivores. This contrasts with previous reports indicating that the southern and northern guanaco populations, that inhabit lowlands, behave as generalist herbivores (Raedeke 1979, Jefferson 1980, Ortega and Franklin 1988). Being a selective herbivore and having little dietary flexibility is puzzling for highland guanacos. These two conditions might impose constraints to highland guanacos that live in environments with limited food availability and extreme climatic conditions, especially low temperatures. Low temperatures are associated with high energetic demands for thermoregulation. If this is true, we predict that highland populations should differ in their migratory behaviour and social structure from the lowland populations, which face milder habitat conditions (Cajal 1989, Ortega and Franklin 1995). This implies that severe climatic conditions would break down the known social structure in guanacos. Observations by Cajal (1989) and Cajal and Ojeda (1994) indicate that during intense blizzards guanacos move to more sheltered feeding habitats, partially supporting our prediction. However, the role of palatability and the effects of secondary compounds on feeding behaviour may help to explain the apparently counterintuitive pattern observed in highland guanacos.

Acknowledgements: G. Arancio, curator of the University of La Serena Herbarium, graciously helped with the identification of plants. The text was improved with the comments of J. Gutiérrez, J. F. Merritt, and of two anonymous reviewers. This study was funded by Barrick International Company and Universidad de La Serena.

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Received 15 March 2001, accepted 26 November 2002.

Associate Editor was Joseph F. Merritt.