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**GUANACO (*LAMA GUANICOE*) BROWSING ON
LENGA (*NOTHOFAGUS PUMILIO*)
REGENERATION IN TIERRA DEL FUEGO**

Tesis

Entregada a la Universidad de Chile en cumplimiento parcial de los
requisitos para optar al Grado de

**Magíster en Ciencias Biológicas,
con mención en Ecología y Biología Evolutiva**

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FACULTAD DE CIENCIAS

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Se informa a la Escuela de Postgrado de la Facultad de Ciencias que la Tesis de Magíster presentada por la candidata.

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Ha sido aprobada por la comisión de Evaluación de la tesis como requisito para optar al grado de Magíster en Ciencias Biológicas con mención en Ecología y Biología Evolutiva, en el examen de defensa rendido el 10 de Marzo de 2008

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The image shows three handwritten signatures in blue ink, each placed over a horizontal line. The top signature is the most legible, appearing to be 'J. Simonetti'. The middle signature is more stylized and less legible. The bottom signature is also stylized and appears to be 'pp. Gallaberré'. To the right of the signatures is a circular stamp with the text 'FACULTAD DE CIENCIAS' at the top, 'CENTRO' in the middle, and 'U. DE CHILE' at the bottom.

*A Osvaldo Muñoz Ruiz-Tagle,
un gran hombre y el mejor de los padres*





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ABSTRACT

Regeneration of lenga (the main timber resource of south of Chile and Argentina) is presumed to be hampered by browsing by guanacos. Thus, in order to elucidate the factors that affect herbivory on lenga, in this work we evaluate guanaco browsing of lenga in Tierra del Fuego, in a) forests with and without previous forestry managements, b) with presence and absence of beavers (*Castor canadensis*) and c) in distinct locations at a landscape level (i.e. edge, gap and core area) in un-logged forests. Guanaco diet was also evaluated through microhistological analysis of faeces. This study was conducted in Karukinka, Tierra del Fuego from November 2006 through July 2007.

Browsing on lenga was higher in logged forests than non managed forests and in forests with beaver respect to absence of it. In harvested forests, and canopy gaps and borders of un-logged forests, where the greater penetration of light at soil level is expected to induce regeneration growth, regeneration is effectively constituted by taller and thicker seedlings (saplings). We believed that the attraction of guanaco to intervened forests is consequence of the higher development of lenga regeneration and consequently more lenga foliage availability. Gaps and borders of un-logged forests would not reflect this pattern because in the study area represents a comparative minor area than logged forests, therefore having less probability of being met by guanacos. Results from microhistological analysis show that guanaco behave as a generalist herbivorous with higher consumption of woody plants than reported in previous studies in areas dominated by steppe. These discrepancies could be explained by environmental availability since in the study area landscape is dominated by forest formations, reaffirming its character of generalist herbivore.

Keywords: lenga (*Nothofagus pumilio*), regeneration, browsing, guanaco (*Lama guanicoe*), Tierra del Fuego.

RESUMEN

La regeneración de la lenga (principal recurso forestal del sur de Chile y Argentina) se presume es obstaculizada por el ramoneo de guanacos. Con el fin de dilucidar los factores que afectan la herbivoría de lenga, se evaluó el ramoneo de guanacos sobre la regeneración de lenga en Tierra del Fuego en a) bosques con y sin manejo silvícola, b) con presencia y ausencia de castor (*Castor canadensis*) y c) en distintas ubicaciones en bosques no manejados (bordes, claros y áreas interiores). La dieta del guanaco también fue estudiada a través de análisis microhistológico de fecas. Este estudio se realizó en Karukinka, Tierra del Fuego entre noviembre de 2006 y julio de 2007.

El ramoneo de lenga fue mayor en bosques cosechados y en bosques con castor. En bosques cosechados y en claros y bordes de bosques sin manejo, donde el mayor ingreso de luz a nivel del suelo se espera induzca un crecimiento, la regeneración está efectivamente constituida por plántulas más grandes (brinzales). La atracción del guanaco hacia los bosques intervenidos sería consecuencia de una mayor disponibilidad de follaje. Claros y bordes de bosques no manejados no reflejarían este patrón porque en el área de estudio representan una superficie ostensiblemente menor respecto a los bosques manejados, luego teniendo menor probabilidad de encuentro por guanacos. Los resultados del análisis microhistológico muestran que el guanaco se comporta como un herbívoro generalista, con un mayor consumo de plantas leñosas respecto a lo reportado por estudios previos en zonas dominadas por estepa. Estas discrepancias podrían explicarse por oferta ambiental, ya que en el área de estudio el paisaje está dominado por bosques, lo cual reafirma su carácter de herbívoro generalista.

Palabras claves: lenga (*Nothofagus pumilio*), regeneración, ramoneo, guanaco (*Lama guanicoe*), Tierra del Fuego.

INTRODUCTION

Lenga (*Nothofagus pumilio*), a tree species endemic to sub-antarctic forests (Pisano, 1997), is the most important timber species from southern Chile and Argentina (Gea-Izquierdo et al. 2004). Despite its timber relevance, a great part of lenga forests, particularly in southernmost tip of South America, has not been intervened, being one of the most pristine regions in the world. Therefore, lenga forests are of great conservation value (Silander, 2000; Mittermeier et al., 2003).

Lenga is a medium shade-tolerant species, regenerating from seedling banks in gaps (Donoso, 1993; Cuevas & Arroyo, 1999). Gap formation might happen naturally through the death and consequent fall of one or more old trees or due to blowdowns (Donoso, 1993; Rebertus et al. 1997). However, openings in the forest canopy can emerge from forestry practices as well. In Tierra del Fuego, forests practices are based on the “shelterwood” system, a method that opens the canopy to allow light penetration to induce regeneration (Martínez-Pastur et al., 2000).

Regeneration of lenga is presumed to be hampered by browsing by guanacos (*Lama guanicoe* Müller), a native ungulate, and possibly by the American beaver (*Castor canadensis* Kuhl), an introduced rodent (Arroyo et al., 1996 ;Dodds, 1997; Martínez-Pastur et al., 1999a; Anderson et al., 2006; Martínez-Pastur et al., 2006). Guanacos are generalist herbivores which consume a wide variety of plant species, lenga being part of their diet in Tierra del Fuego (Raedeke, 1980; Raedeke & Simonetti, 1988; Puig et al., 1997), reaching around 10% of their annual diet (Appendix 1).

Currently, there is no agreement regarding the effect of guanacos on lenga regeneration. In harvested forests, guanacos are regarded as a threat to forest regeneration (Arroyo et al., 1996; Dodds, 1997), while browsing upon seedlings

is also regarded high in virgin forest (Martínez-Pastur et al. 1999a; Pulido, et al. 2000). Furthermore, guanaco browsing upon lenga regeneration seems higher at forest edges and gaps (Cuevas, 2002; Cavieres & Fajardo, 2005). The introduced American beavers (*Castor canadensis*) have negative effects on riparian *Nothofagus* forests. In Tierra del Fuego National Park (Argentina), flooding by beaver meadows prevents tree regeneration even after beaver abandonment (Martínez-Pastur et al., 2006). In Navarino Island (neighboring to Tierra del Fuego), beavers significantly reduce tree canopy cover up to 30 m away from the stream edge, almost eliminating seedlings of lenga (Anderson et al., 2006).

Browsing upon lenga seedlings and saplings however, has not been simultaneously compared considering the potential effects of logging, beaver presence and reduction in canopy cover, being all factors presumed relevant in the interaction between herbivores and lenga. Therefore, differences in browsing intensity and impact upon lenga regeneration can not be properly assessed, and an assessment at the landscape level is needed. In these terms, if forest intervention facilitates browsing upon lenga seedlings and saplings, in logged forest they should suffer a greater occurrence and intensity of browsing. Similarly, if beavers feed upon or facilitate guanaco access to lenga seedlings, in forests with presence of beaver there could be an additional herbivory pressure, depicting higher browsing activity compared with forest without beavers. Furthermore, if a reduction in canopy cover is causing increased browsing upon seedlings, regeneration ought to sustain similar browsing activity at forest borders, gaps and logged forests, which would differ from continuous un-logged forests.

In this work, we evaluate the impact of guanaco on lenga regeneration in Tierra del Fuego at the landscape level in a) forests with and without forestry managements, b) with presence/absence of beavers and c) in distinct locations

at a landscape level (i.e. edge, gap and core area) in un-logged forests, covering the heterogeneity of the forests.

AREA DESCRIPTIONS

The study area is located near Estancia Vicuña ($54^{\circ} 8' 19''\text{S}$, $68^{\circ} 42' 17''\text{W}$) at Karukinka, a protected area of about 300.000 ha in Tierra del Fuego Island, owned and administrated by Wildlife Conservation Society (Saavedra, 2006). Currently is an area free from sheep raising (Figure 1).

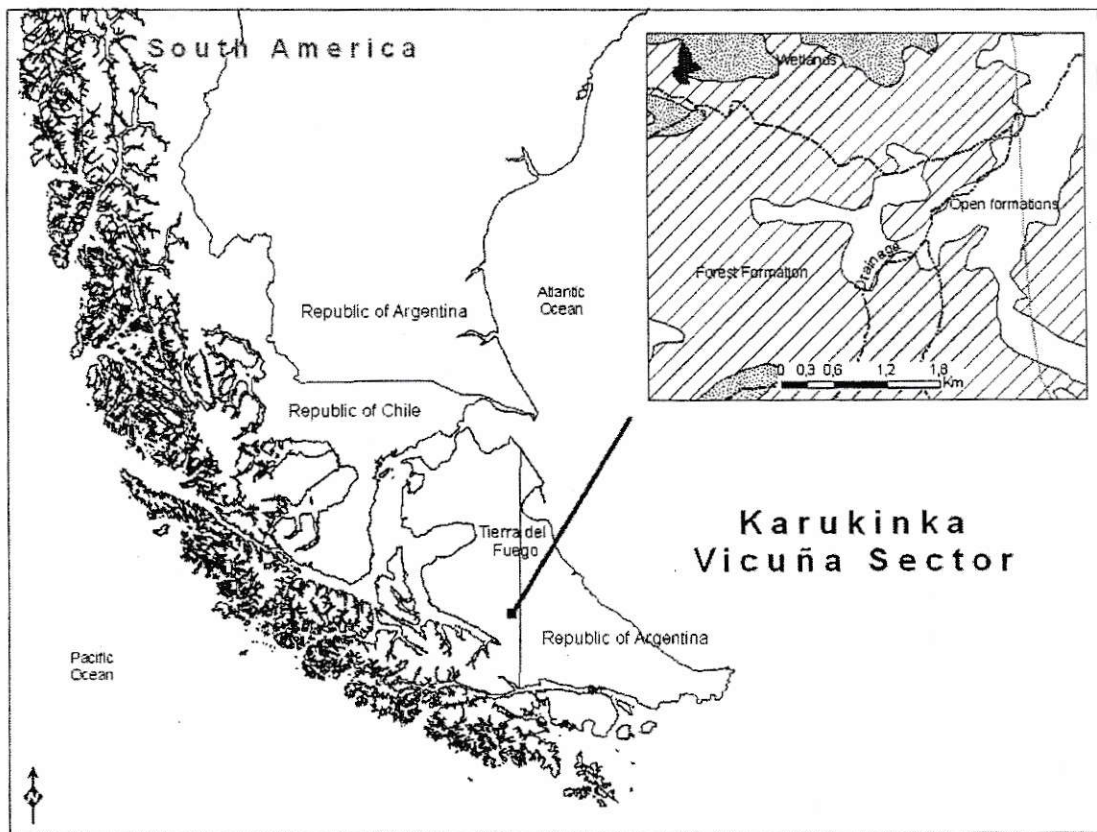


Figure 1: Location of study area ($54^{\circ} 8' 19''\text{S}$, $68^{\circ} 42' 17''\text{W}$)

The study area is mainly flat but crossed by low mountainous cords, whose peaks rarely exceed 1,000 m (Pisano, 1977). Average temperature of the warmest month is 9.6°C and that of coldest month is -4.2° C (values from Pampa Guanaco Station, 54° 07' S - 68° 42' W). Annual precipitation ranges from 400 to 620 mm and much of the winter precipitation falls as snow (Pisano, 1977). Forests are dominated by lenga. Ñirres (*Nothofagus antarctica*) also occurs at borders between forest and open areas (Pisano, 1997). Besides the forests, there are open areas covered by Patagonian steppe, *Sphagnum* bogs and wetlands containing *Carex* (Lizarralde et al., 2004).

Lenga forest are monospecific regarding tree composition and shrub diversity in the understory is low (Moore, 1983; Martínez-Pastur et al., 2006). Among them, *Berberis buxifolia* and *Empetrum rubrum* are the most frequent woody understory species. Several grasses and herbs are common, like *Schizeilema ranunculus*, *Osmorhiza* sp., *Dyspopsis glechomoides* as well as some bryophytes. There is almost no introduced species in forests except for *Cerastium arvense*.

During the last decades part of the area was exploited by logging and livestock raising in open areas. As consequence, the landscape is dominated by lenga forest (most of them previously logged) and open areas, principally Patagonian steppe. Forest intervention in the study area occurred through the "shelterwood system" eight years ago. Specifically, the shelterwood system occurs through a progressive intervention of the forest, removing first 60-70% of the basal area and later the remnant canopy is cut after saplings have been established (Pulido et al. 2000). Harvested forests in the study area were intervened until the first cut, retaining 30-40% of the original basal area.

METHODS

We distinguished six situations within lenga forests. First, four situations were discriminated following a factorial design which includes the presence and absence of beaver (in addition to the presence of guanaco which is present in all cases), and the occurrence of logging: 1) logged forest with beaver (LF-B), 2) logged forest without beaver (LF-no B), 3) un-logged forest with beaver (no LF-B), and un-logged forest without beaver (no LF-no B). To test whether the effects of reduction in canopy cover on browsing activity and characteristics of regeneration are analogous in harvested situations and natural conditions, we also distinguish between 5) canopy gap (gap) and 6) border (border) in un-logged forest.

LF-B and non LF-B situations were considered for forests located within 15 m from stream edges with beaver present, as beaver impact might reach 95 m from the stream (Martínez-Pastur et al., 2006). Areas located within 15 m from the edge into the forest were considered forest border. No LF-no B was considered for forests located at least 150 m from the nearest border to also constitute a core area, avoiding edge effect (Laurance, 2000). Only natural caused gaps of at least 100 m² were considered in the analysis.

Variables sampled

Sampling of seedlings and saplings of lenga was performed in November 2006 using 0.5 m² quadrants, at six randomly located replicates for each situation, except for virgin core forest where five replicates were done. Occurrence and intensity of browsing was assessed as the browse rate index (BRI; Veblen et al., 1989). This index estimates the browsing level by visual inspection of the percentage of foliage removed expressed into five categories: 0 = no browsing (0%); 1 = low (1-25%); 2 = moderate (26-50%); 3 = high (51-75%); 4 = very high (76-100%); y 5 = death due to browsing. This index has already been used to

study the effect of guanaco browsing in lenga regeneration (Cavieres & Fajardo, 2005). Height, basal diameter of individual seedlings and total number of seedlings were also registered in each quadrant sampled.

Techniques (statistical analysis)

To test differences in occurrence of browsing between forest types considered, a Contingency Table Analysis was used. The test of multiple comparisons of proportions was conducted when differences were found (Zar, 1999). According to previous occurrence of logging and beaver presence, differences in BRI were evaluated through the Scheirer-Ray-Hare Test (Sokal & Rohlf, 2003). On other side, regarding to the effect of reduction in canopy cover in seedlings of un-logged forests (i.e. border, gap and core areas), differences in BRI were evaluated through the Kruskal-Wallis Test.

In case of average height, basal diameter and density of seedlings factorial analysis of variance was applied to test differences according to previous occurrence of logging and beaver presence. Since height data do not fulfil normality, the Scheirer-Ray-Hare Test was applied in that case. Differences in these above-mentioned three variables between gaps, and border and core areas of un-logged forest were evaluated through the Kruskal Wallis test and a *posteriori* test was applied (Dunn Test) when differences were found.

RESULTS

Regeneration characteristics of lenga

a) Average height of seedlings

Average height of seedlings was significantly higher in logged forests compared to un-logged ones (Figure 2). In contrast, average height was not different according to beaver presence (Tables 1 & 2). In un-logged forests, height of seedlings at canopy gaps, borders and core areas were not significantly different ($H = 0.63$; $P = 0.73$; $N = 17$).

b) Basal diameter of seedlings

Basal diameter of seedlings was significantly higher in logged forests compared to un-logged forest; contrary, according to beaver presence, basal diameter of seedlings did not differ (Table 3). In un-logged forests basal diameter of seedlings was significantly higher in canopy gaps than core areas ($Q = 15.69$; $Q_{0,05(3)} = 2.39$) and also in borders compared to core areas ($Q = 14.71$).

c) Density of seedlings

Density of seedlings was not significantly different between logged and un-logged forests, neither according to beaver presence (Table 3), nor between borders, canopy gaps and core areas of virgin forests ($H = 0.48$; $P = 0.79$; $N = 17$).

Browsing upon lenga seedlings

a) Occurrence of browsing

Occurrence of browsing was heterogeneous across the different types of forests considered ($\chi^2 = 478.73$; $P < 0.01$; $N = 2356$) (Figure 3). Browsing is more frequent in logged forest than in un-logged forests. The three forest types without beaver and logging (core area, gap and border) have similar occurrence

of browsing and together differ from forests with logging and with beaver (Table 4).

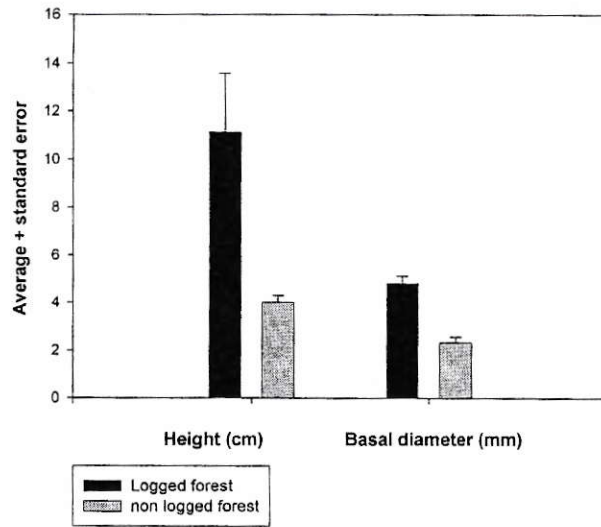


Figure 2: Height and basal diameter of seedlings according to logging effect in Tierra del Fuego

Table 1: Size patterns in lenga regeneration in Tierra del Fuego according to forest situations (values are mean \pm standard error)

	Height (cm)	Basal diameter (mm)	Density (seedlings/m ²)	Quadrants	n (total seedlings)
LF-B	7.42 \pm 1.48	4.56 \pm 0.44	136.33 \pm 57.55	6	409
LF-no B	14.89 \pm 4.24	5.07 \pm 0.45	139 \pm 25.69	6	417
no LF-B	4.69 \pm 0.18	2.93 \pm 0.18	205.67 \pm 54.44	6	617
no LF-no B	3.2 \pm 0.25	1.62 \pm 0.07	170.4 \pm 77.48	5	426
Gap	7.79 \pm 3.12	4.15 \pm 1.35	76.33 \pm 35.37	6	229
Border	4.9 \pm 1.37	4.31 \pm 1.31	86 \pm 40.9	6	258

Table 2: Two way Anova for ranked average height of seedlings, according to logging and beaver effect (The Scheirer-Ray-Hare Test) in Tierra del Fuego

Dependent variable	S.S.	d.f.	M.S.	H	P
<i>Height of seedlings</i>					
Logging	616.08	1	616.08	12.98	<0.01
beaver	4.46	1	4.46	0.09	0.76
logging x beaver	155.51	1	155.51	3.28	0.07
Error	268.03	19	14.11		
Total	1044.08	22			

b) Browsing intensity

Browsing was significantly higher in logged forests (2.08 ± 0.12) than un-logged forests (1.26 ± 0.24), and in forests with beavers (2 ± 0.13) than forests without beavers (1.35 ± 0.26) (Figure 4, Table 5). In contrast, browsing intensity did not differ between border, canopy gap and core area of un-logged forests (Kruskal-Wallis test: $H = 3.72$; $p = 0.16$; $N = 17$).

Table 3: Two way Anova for basal diameter and density of seedlings (seedlings/m²), according to logging and beaver effect in Tierra del Fuego

Dependent variable	S.S.	d.f.	M.S.	F	P
<i>Basal diameter of seedlings</i>					
Logging	36.91	1	36.91	54.05	<0.01
beaver	0.91	1	0.91	1.33	0.26
logging x beaver	4.7	1	4.7	6.88	0.02
Error	12.97	19	0.68		
Total	55.49	22			
<i>Density of seedlings</i>					
Logging	14496.01	1	14496.01	0.84	0.37
beaver	1518.23	1	1518.23	0.09	0.77
logging x beaver	2055.63	1	2055.63	0.12	0.73
Error	328143.87	19	17270.73		
Total	346213.73	22			

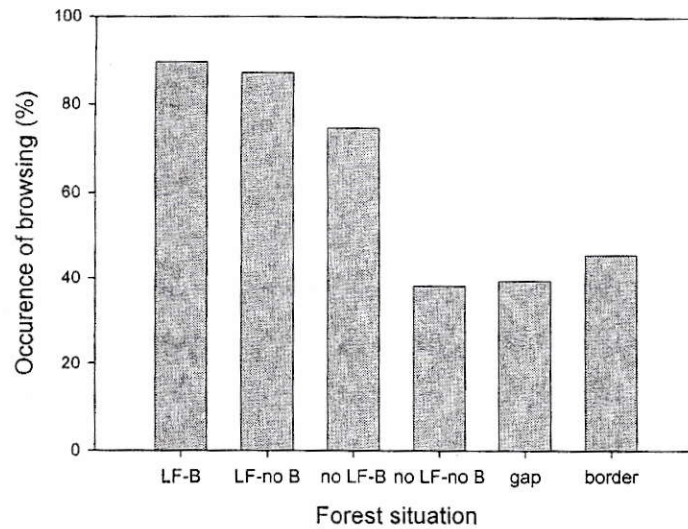


Figure 3: Occurrence of browsing in individual seedlings on different types of forests in Tierra del Fuego

Table 4: Test of multiple comparisons for occurrence of browsing on different types of forests in Tierra del Fuego

Comparison	q	difference
no LF-no B & LF-B	23.66	yes
no LF-no B & LF-no B	22.27	yes
no LF-no B & no LF-B	16.87	yes
gap & LF-B	19.38	yes
gap & LF-no B	18.19	yes
gap & no LF-B	13.27	yes
border & LF-no B	18.05	yes
border & LF-B	16.69	yes
border & no LF-B	11.56	yes
no LF-B & LF-B	8.95	yes
no LF-B & LF-no B	7.31	yes
no LF-no B & border	2.66	no
no LF-no B & gap	0.46	no
gap & border	1.9	no
LF-no B & LF-B	1.55	no

$$q_{0.05(6)} = 4,03$$

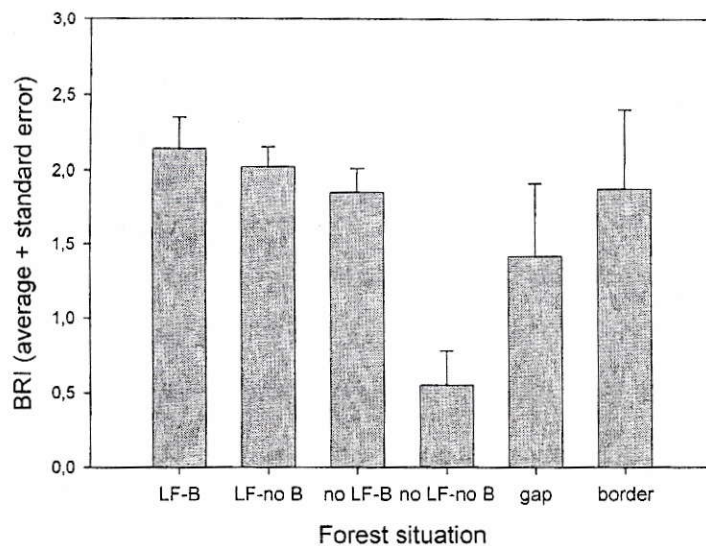


Figure 4: BRI on different types of forests in Tierra del Fuego

Table 5: Two way Anova for ranked BRI, according to logging and beaver effect (The Scheirer-Ray-Hare Test) in Tierra del Fuego

Dependent variable	S.S.	d.f.	M.S.	H	P
<i>BRI</i>					
Logging	358.13	1	358.13	7.45	0.01
beaver	235.28	1	235.28	4.9	0.03
logging x beaver	48.61	1	48.61	1.01	0.31
Error	415	19	21.84		
Total	1057.02	22			

DISCUSSION

Lenga forests, in general, are an important habitat for guanacos in Tierra del Fuego. Forests are used as a refuge and sleeping area (Franklin, 1983), but also as a feeding source. Guanaco feeds on lenga almost all year except in winter (see results in Appendix 1), because lenga is a deciduous tree and guanacos feed only leaves of lenga leaving branches intact (Arroyo et al. 1996). Nonetheless lenga is a species of high occurrence in the diet, lenga and ñirre together represent around 10% of the annual diet (Appendix 1).

When assessed simultaneously all types of environments, browsing is actually higher in harvested forests compared with ones without logging intervention. In fact, in logged forests most of regeneration is constituted by thick saplings with deformed stems and vigorous growth of lateral branches due to the loss of apical dominance, typical signs of saplings under continuous browsing (Dodds, 1997; Martínez-Pastur et al., 1999a). In contrast, browsing is low in un-logged forests, the lowest between all forest types considered. According to Pulido et al. (2000) guanaco browsing in lenga forests intervened would be lower than un-logged forests because seedlings are protected by harvest residues; in the study area this situation is not widespread except for some isolated seedlings protected by large trunks.

Regeneration in logged forests and canopy gaps of un-logged forests is composed by thicker seedlings than non managed forests (in logged forests seedlings are also taller), where seedling banks are expected to be activated by more light penetration at soil level (Donoso, 1993; Dodds, 1997; Martinez-Pastur et al., 1999b). These results support the gap regeneration strategy described in literature (Donoso, 1993; Arroyo et al. 1996) and the effect of induction in regeneration growth caused by the shelterwood system (Martínez-Pastur et al. 1999b). Thicker and taller seedlings offer more foliage than smaller and thinner

seedlings; then, guanacos might be attracted to intervened forests due to a higher development of lenga and consequently more lenga foliage availability. While this ought to apply to gaps and possibly borders and as well, given the area of these habitat is ostensibly lower than logged forests in the study site, guanacos reach them less often rendering a lower browsing pressure upon seedlings at these open sites. In fact, browsing at our gaps was remarkably lower than browsing reported by Cavieres & Fajardo (2005), in an area without logging. This would signal that the effect of higher browsing in canopy gaps, and possibly in borders, is cancelled when there are harvested forests nearby, which offer greater availability of seedling and saplings.

Guanacos have inhabited Tierra del Fuego over more than 8,000 years (Sarno et al., 2001) and the cycle of regeneration of lenga forest is 300 to 500 years (Rebertus & Veblen, 1993), then guanacos and lenga forests have coexisted for centuries. Therefore, historically guanaco has not been an impediment to the regeneration of lenga forests. The apparent forestry problem appears when forests are intervened. High browsing activity in logged forests probably will cause a higher frequency of sympodial trees, reducing the logging value of the forest. Indeed, Martinez Pastur et al. (1999a) for almost a decade ago indicated that the guanaco should be a factor to consider within the forest management plans. In technical terms, the installation of fences which exclude the guanaco, as has been done by a forestry company in Tierra del Fuego with successful results, seems required.

Regarding the beaver effect, browsing was also significantly higher in forest with beavers. This suggests that the effect of beavers on the regeneration of the lenga is not only indirectly by changing soil conditions across flooding, but directly enhancing the browsing, possibly because beavers, as guanacos, feed on lenga regeneration or because beaver meadows in some way enhances guanaco access to seedlings. These effects are locally confined to the riparian

forests. Then, its impact on lenga forest would not be as significant as logging effect.

In summary, the process of regeneration and future establishment of lenga forests in Tierra del Fuego is shaped by abiotic factors, such as light penetration at understory or quantity of water in the soil, and by biotic factors like browsing by guanacos and beavers. Therefore, to ensure a successful establishment of regeneration and consequently the future restoration of forests, either for productive or for conservation purposes, forest variability in a landscape context must be considered in planning and management of lenga forests.

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APPENDIX 1:
**GUANACO (*LAMA GUANICOE* MÜLLER) DIET IN CENTRAL-SOUTH
TIERRA DEL FUEGO**

INTRODUCTION

The guanaco (*Lama guanicoe*), a wild South American camelid, is a generalist herbivore that feeds on a wide variety of types of forage (Raedeke, 1980; Raedeke and Simonetti, 1988; Puig et al., 1997). The diet of guanacos changes seasonally, as the use and preference for woody species increases when the availability of grasses and forbs decrease (Puig et al., 1997; Baldi et al., 2004). In Tierra del Fuego, grasses and forbs comprise between 60% and 90% of their diet (Raedeke, 1980; Bonino & Pelliza-Sbriller, 1991), and consumption of forage species is strongly linked to its availability (Raedeke, 1980).

Conservation status of guanacos in Patagonia has varied during the last two centuries. In the second half of the nineteenth century domestic livestock was introduced in Patagonia, within it in Tierra del Fuego, which triggered a decline in the population of guanacos by competition for resources with these herbivores and the resulting conflict with ranchers (Montes et al., 2006). After these events, conservation programs of guanacos were initiated in the area with successful results (Franklin et al., 1997), allowing such an increase of the population that in Chilean part of Tierra del Fuego, in particular, regulated harvests for productive purposes have been permitted by Government institutions.

Given this recovery in the population size, several authors note that lenga (*Nothofagus pumilio*) regeneration in Patagonia (the main timber resource of South of Chile and Argentina) is hampered by guanaco browsing (Arroyo et al., 1996; Dodds, 1997; Martínez-Pastur et al. 1999). Therefore, it is particularly important to know current food habits of guanacos in Tierra del Fuego.

METHODS

Sample of faeces of 37 individuals of guanaco were collected from lenga forests in Karukinka. Eight samples were collected in spring (November 2006), nine in summer (January 2007), ten in autumn (April 2007) and ten during winter season (July 2007). Samples were fresh faeces from dung piles or single depositions belonging to single individuals. Botanical composition of guanaco diet was determined through microhistological analysis, carried out in the Laboratorio de Microhistología, Instituto Nacional de Tecnología Agropecuaria (INTA), Bariloche (Argentina).

Plant species in faeces were then classified according to life-form in: woody plant (trees + shrubs), forb, grass, grass like, hemiparasite and moss species. Plant species diversity from faeces of guanacos grouped by season was calculated using Shannon index. Differences in species richness and diversity between seasons were evaluated through an Analysis of variance and a *posteriori* test was applied (Holm-Sidak test) when differences were found.

RESULTS

The annual diet was composed by 43 species of vascular plants and one moss species (*Sphagnum* sp.), belonging to 24 families. 19 plants were identified to species, 19 were identified only to genus, three species in family taxa and three species were not identified (a forb species, a fruit of a forb species and a shrub species). The category *Nothofagus* spp. corresponds to the sum of *Nothofagus pumilio* and *Nothofagus antarctica*, because of the impossibility of further discrimination (Table A.1).

The most specious samples of faeces (one collected in spring and the other during summer) contained 19 plants while the least diverse sample was collected during winter which contained 12 plants consumed. Species richness and plant diversity in guanaco diet decreases in winter (Table A.2). In fact, differences between seasons in these variables were statistically significant

Table A.1: Occurrence of plant species in guanaco faeces of all seasons sampled in Tierra del Fuego (e.g. faeces with plant species present/all faeces collected x 100)

Life form species	Frecuency (%)				
Grass species		continuation:		continuation:	
<i>Alopecurus magellanicus</i>	100	<i>Empetrum rubrum</i>	97.3	<i>Erodium cicutarium</i>	2.7
<i>Bromus</i> sp.	5.41	<i>Senecio alloeophyllus</i>	18.92	<i>Gunnera magellanica</i>	83.78
<i>Festuca gracilima</i>	16.22	non identified shrub	10.81	<i>Osmorhiza</i> sp.	43.24
<i>Holcus lanatus</i>	13.51			<i>Plantago</i> sp.	2.7
				Ranunculaceae species	8.11
<i>Poa</i> sp.	100	b) Tree species		<i>Ranunculus</i> sp.	37.84
<i>Stipa</i> sp.	8.11	<i>Maytenus</i> sp.	2.7	Rosaceae species	8.11
<i>Trisetum</i> sp.	43.24	<i>Nothofagus betuloides</i>	27.03	<i>Rubus geoides</i>	72.97
		<i>Nothofagus</i> spp. (*)	72.97	<i>Rumex</i> sp.	16.22
Grasslike species		Forb species		<i>Veronica serpyllifolia</i>	2.7
<i>Carex</i> sp.	100	<i>Acaena</i> sp.	8.11	<i>Viola</i> sp.	13.51
<i>Eleocharis</i> sp.	59.46	<i>Achillea millefolium</i>	2.7	non identified forb	16.22
<i>Luzula chilensis</i>	70.27	<i>Arjona patagonica</i>	5.41	non identified fruit	2.7
<i>Marsippospermum grandiflorum</i>	13.51	Asteraceae species	35.14		
Woody species		<i>Blechnum penna-marina</i>	43.24	Hemiparasite species	
a) Shrub species		<i>Callitriche</i> sp.	8.11	<i>Misodendrum</i> sp.	86.49
<i>Baccharis magellanica</i>	2.7	<i>Capsella bursa-pastoris</i>	5.41		
<i>Berberis</i> sp.	83.78	<i>Cerastium arvense</i>	67.57	Moss species	
<i>Chilotrichum diffusum</i>	27.03	<i>Cotula scariosa</i>	21.62	<i>Sphagnum</i> sp.	78.38

(*)=*Nothofagus pumilio*+ *Nothofagus antarctica*

(Table A.3), being winter the season with lowest species richness and diversity and exhibiting significant differences with the rest of the seasons (table A.4).

Table A.2: Plant species richness ($S \pm$ standard error) and diversity (Shannon index, $H \pm$ standard error) in different seasons in faecal samples of guanaco in Tierra del Fuego

Season	S	H
Spring	16.75 \pm 0.59	2.4 \pm 0.02
Summer	16.33 \pm 0.71	2.33 \pm 0.04
Autumn	17.8 \pm 0.36	2.39 \pm 0.04
Winter	13.9 \pm 0.55	2.12 \pm 0.05

Table A.3: One way Anova for species richness and diversity of guanaco faeces in Tierra del Fuego, according to seasonality

Dependent variable	S.S.	d.f.	M.S.	F	P
Species richness (S)					
seasonality	81.03	3	27.01	9.48	<0.01
Error	94	33	2.85		
Shannon-Wiener Index (H)					
seasonality	0.51	3	0.17	10.3	<0.01
Error	0.54	33	0.02		

Monocotyledoneous plant species (grass and grass like) were the main component of the diet ($45.41 \pm 1.6\%$ of individual sample of faeces, average \pm standard error), and three monocotyledons (*Alopecurus magellanicus*, *Poa* sp. and *Carex* sp.) were also the more frequent species in diet, all of them year round (Table 1). Woody plants ($31.65 \pm 4.35\%$) and forbs ($17.06 \pm 4.54\%$) were the second and third most consumed items. Between woody plants two shrubs (*Empetrum rubrum* and *Berberis* sp.) were also frequent besides the hemiparasite of *Nothofagus* (*Misodendrum* sp.). Trees accounted for 16.75% (± 2.78) of guanaco diet and the two deciduous species (lenga and ñirre)

constituted 9.23% (± 3.4) of the annual diet of guanaco, with a peak of 15.21% in summer and no consumption during winter. This last is predictable because lenga is a deciduous species and guanacos feed only leaves of lenga leaving branches intact (Arroyo et al. 1996). Hemiparasites and mosses were the less represented life-forms in annual diet with 4.41% (± 1.11) and 1.51% (± 0.33), respectively (Figure A.1).

Monocots consumption was rather homogeneous during the year. Woody plants and forbs showed greater variability throughout the year and their contributions were complementary. The grasses (Poaceae), the most consumed family, reached a peak of 31% in winter when the availability and palatability of pastures are low.

Table A.4: Test of multiple comparisons for species richness and diversity of guanaco faeces on different seasons in Tierra del Fuego

Comparison	P	Critical Level ($P \leq 0.05$)	difference
<i>Species richness (S)</i>			
autumn vs. winter	1.13×10^{-5}	0.01	yes
spring vs. winter	1.15×10^{-3}	0.01	yes
summer vs. winter	3.57×10^{-4}	0.01	yes
autumn vs. summer	0.07	0.02	no
autumn vs. spring	0.2	0.03	no
spring vs. summer	0.62	0.05	no
<i>Shannon-Wiener Index (H)</i>			
autumn vs. winter	3.63×10^{-5}	0.01	yes
spring vs. winter	4.34×10^{-5}	0.01	yes
summer vs. winter	1.21×10^{-3}	0.01	yes
spring vs. summer	0.22	0.02	no
autumn vs. summer	0.28	0.03	no
spring vs. autumn	0.83	0.05	no

Woody plants, the second general group of plants in consumption, ranged from a peak of consumption of 43.26% in winter to a minimum of 23.75% during the summer, when there is greater availability of herbaceous plants (forbs and Monocots). Both shrubs and trees are consumed during the year, but species composition changes. Among shrubs, *Empetrum rubrum* is the greatest contributor to the diet throughout the year, accompanied by *Chilliotrichium diffusum* only in autumn. Among trees, lenga and ñirre in winter are replaced by the evergreen coigüe (*Nothofagus betuloides*).

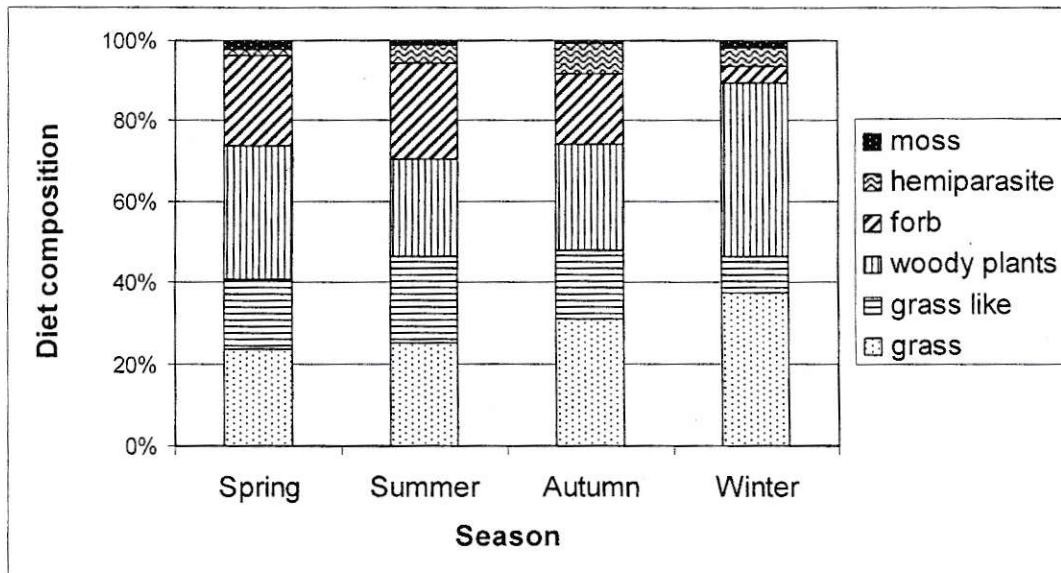


Figure A.1. Seasonal food habits of guanacos in Tierra del Fuego according to life form of plants, based on faecal samples (n = 37)

Forbs contribution in guanaco diet during the year, by their side, behaved according to their environmental availability; they were mostly consumed in spring and summer while in winter consumption fell to 4.1%. *Rubus geoides* and *Gunnera magellanica* are the main forbs consumed during the year, except for winter when consumption of all forbs falls and only *Blechnum penna-marina* exceeds 1% of diet.

DISCUSSION

The guanaco in central-south of Tierra del Fuego behaved as a generalist herbivore with the ability to change the proportion consumed between different groups of plants and also change species composition during the year, agreeing with Raedeke (1980), Raedeke & Simonetti (1988), Fernández-Baca (1991) and Puig et al. (1997). Almost the entire year guanaco was mainly a grazer herbivorous (consuming grasses, grass-like plants and forbs), but in winter when much of the vegetation is covered with snow and the availability of herbaceous plants is scarce, guanacos change their habits by increasing the participation of woody species (Puig et al., 1997; Baldi et al., 2004).

Species composition and richness of guanaco diet was similar to the 40 species reported by Raedeke (1980), while diversity (Shannon index) was slightly lower than results of forest-steppe ecotone reported by Bonino & Pelliza (1991). This similarity is expected, since both studies were also conducted in Tierra del Fuego, particularly in the central part of the island in an area of ecotone between the forest and steppe. Our results show less involvement of grasses and greater participation of woody plants than results of Raedeke (1980) and Bonino & Pelliza (1991). These annual differences are explained mainly for a less participation of grasses in summer and a bigger participation of woody plants during all year and particularly in winter.

Discrepancies of our results with those previously published in Tierra del Fuego could be explained by environmental availability, as in the central-south area of the island (where our study was conducted) landscape is dominated by forest formations. The most consumed species of trees, shrubs and forbs are also dominant species in lenga forests, while more selective monocotyledoneous plants are dominant species in open areas. These results show that guanaco

behaved like non selective feeder reaffirming its character of generalist herbivore.

The comparative low preference of grasses might be because there is also a comparatively smaller proportion of steppe (where grasses are abundant) and higher proportion of forest respect to the central part of the island. As we mentioned, the peak of grass consumption occurred in winter when curiously availability and palatability are low, but probably grasses are selected over winter to optimize mix of herbaceous and ligneous plants because forbs availability is even lower. It is important to note the emergence of *Nothofagus betuloides* in the diet during the winter. The study area is dominated by deciduous forests of lenga while evergreen forests appear further south, near Lake Deseado (c.a. 30 km from the study area), so guanacos during winter move long distances to meet their nutritional needs.

Regarding the high consumption of woody plants and the concern over the potential negative impact of guanaco on the lenga regeneration, it is important to stress that nearly half of woody plants consumed are shrubs and deciduous woody species (lenga and ñirre) contribute less than 10% of the diet.

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