RED DEER, CATTLE AND HORSES AT HIGH ELEVATIONS IN THE ANDEAN PRECORDILLERA: HABITAT USE AND DEER DENSITY

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ABSTRACT: Red deer (Cervus elaphus) were introduced to Patagonia and now form a continuous population along the Andes mountains. No information on habitat use and density of red deer in high altitude mountains and simultaneous habitat use by cattle and horses was available. We surveyed an area in Nahuel Huapi National Park for major plant communities and by analyzing pellet group distribution determined that mallins at high elevation were highly preferred by red deer, cattle, and horses (57%, 74% and 47% of total pellet group densities, respectively). Usage of lenga forest was <10% for all herbivores, but the combined pressure may impact natural rejuvenation of forest species. Similarly, steppe above tree line was used <10% by all herbivores, but we predict that red deer usage will increase substantially if population densities increase. The steppe below lenga forest was equally preferred by deer and horses at 18% while the valley received intermediate usage, particularly from horses. As these herbivores differ substantially in body size and digestive system (ruminant and hindgut digestion), they are expected to fill most niches provided by the heterogeneous vegetation with some overlapping. Major plant communities were differentiated for an area of 135 Km². Using pellet group densities, assuming a deposition rate of 16 groups/deer/day, and assuming 1 year for pellets to disappear, we estimated the absolute red deer density at 1.44 deer/100 ha which can be considered moderate (range: 0.3-3.4 deer/100 ha according to habitat type). From the perspective of habitat and forage quantity, we predict that deer density will increase in time, unless mortality rates are increased through harvesting. Considering the experience from its native range, management goals should aim at maintaining the density of red deer at the present level while decreasing the density of cattle and horses.

RESUMEN: Ciervo colorado y ganado vacuno y equino en la precordillera de los Andes: uso de hábitat y densidad. El ciervo colorado (Cervus elaphus) fue introducido a Patagonia y ahora se presenta como una población continua a lo largo de la cordillera de los Andes. No existe información sobre el uso de hábitat y la densidad del ciervo colorado en la altura de la cordillera ni sobre el uso simultáneo del hábitat por ganado y caballos. En este estudio se clasificaron las comunidades principales de vegetación en un sector del Parque Nacional Nahuel Huapi y por medio del análisis de la distribución de heces se determinó una alta preferencia para los mallines de altura por ciervo colorado, ganado y caballos (57%, 74% y 47% del total de las densidades de grupos de heces, respectivamente). El uso del bosque de lenga fue <10% para todos los herbívoros, pero la presión combinada podría afectar la recuperación natural de las especies vegetales del bosques. También la estepa arriba de la zona boscosa fue usada <10% por todos los herbívoros, pero se predice un aumento en su uso si la población del ciervo colorado continúa creciendo. Ciervo y caballos prefirieron la estepa abajo del bosque de lenga (18%), mientras que el valle recibió un uso intermedio, particularmente por caballos. Debido a las diferencias sustanciales entre tamaño corporal y sistema digestivo (rumiante versus digestión cecal) de estos herbívoros, se supone que ocupan casi todos los ambientes provistos por la vegetación heterogénea aunque con alguna superposición. Se diferenciaron las comunidades vegetales principales para un área de 135 km². Usando la densidad de grupos de heces, asumiendo una tasa de defecación de 16 grupos/ciervo/día, y asumiendo 1 año hasta que un grupo desaparece, se estimó una densidad promedio de 1,44 ciervo/100 ha. Esta densidad se puede considerar moderada (rango: 0,3-3,4 ciervo/100 ha según tipo de hábitat). Desde el punto de vista de cantidad de hábitat y forraje se predice un aumento de la densidad de ciervo, a menos que aumente la tasa de mortalidad por medio de la caza. Considerando la experiencia con ciervo en su ambiente nativo, los objetivos de manejo deberían dirigirse a mantener la densidad actual del ciervo y bajar las densidades de ganado y caballos.

Key words: *Cervus elaphus*, cattle, horses, exotics, national parks, conservation, population density, habitat use.

Palabras clave: Cervus elaphus, ganado vacuno, ganado equino, exóticos, parque nacional, conservación, densidad poblacional, uso de hábitat.

INTRODUCTION

Although the history of initial introductions of red deer (Cervus elaphus) in Patagonia is fairly well known (reviewed in Flueck and Smith-Flueck, 1993), little information is available on subsequent developments. In addition to some local introductions in Chile, deer have also invaded Chile from several Argentine populations (Ortiz, 1992) and thus red deer represent continuous populations across the Andes (Flueck et al., 1995a). However, there is a lack of basic information for both countries about the use of Andean high-altitude habitat by red deer, cattle and horses. Considering that several national parks in both countries border the political boundary and include much of the red deer distribution, this paper has implications for park management policies in both countries. Furthermore, the highaltitude Andean environment is considered to be prime habitat for the severely endangered native deer (huemul, Hippocamelus bisulcus) (Ruckley and Fairweather, 1997; Smith-Flueck and Flueck, 1997). Although red deer continue to expand into areas with huemul, the effects of their presence on huemul populations has vet to be evaluated.

In the southern cone of South America, red deer are able to survive in dense rain forests, ecotones, and also the dry Patagonian steppe (Flueck et al., 1995a). Within some habitats along this precipitation gradient, the negative impact of red deer on plant communities has been described (Veblen et al., 1989, 1992). However, prior to this study there was no ecological information available of red deer at higher elevations. This study therefore aimed

to provide insight to deer density and habitat use by deer, cattle and horses in a high altitude summer range based on pellet surveys (Loft and Kie, 1988; Telfer 1988; Edge and Marcum, 1989). Habitat selection of similar guilds of herbivores including cervids, bovids and equids has been studied before (Hansen and Clark, 1977; Telfer, 1988; Gordon, 1989a,b). Sympatric large herbivore species tend to use their environment in different ways. These differences are determined by animals factors including body size, structure of the incisor arcade, gut morphology and function, sex and reproductive state; and by environmental factors including relative abundance and quality of plant material, climate, and topography.

MATERIALS AND METHODS

Study area

The study area is near Lago Traful in the Nahuel Huapi National Park and consisted of two sites in order to include sufficient areas of all habitat types (Fig. 1). The topography is primarily mountainous with most features formed by glacial processes. The majority of soils originating from volcanic processes are young. Towards the east, the volcanic material has been modified by fluvial and cofluvial transportation of material. The dominant climate is temperate with main precipitation occurring between April and September. There is an abrupt precipitation gradient from west to east due to the rain shadow effect of the Andes which results in a strongly defined vegetation structure and floristic composition. The study site 'Cerro Tapayo' is between 1600 and 1800 m elevation, while the site 'Río Minero' is between 1100 and 1700 m.

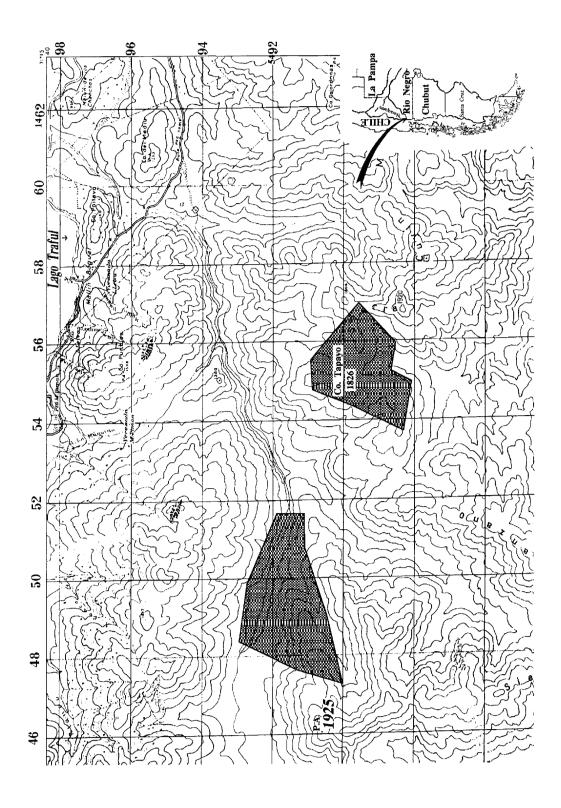


Fig. 1. Locations of the Cerro Tapayo and Rio Minero study sites.

Vegetation description

The vegetation in the study area was classified into four distinct types with seven sub-types. A description of each type and sub-type was made by direct observations, collection of plant specimens from the study area and with reference to a vegetation map for the Nahuel Huapi National Park (Mermoz and Martin, 1986). Individual species were identified using Flora Patagonia (Correa, 1984), Flora of Tierra del Fuego (Moore, 1983), and Flora Silvestre de Chile; Zona Araucana (Hoffmann, 1991).

Two or more line transects were placed within each vegetation type or subtype (Table 1). A particular transect might have passed several vegetation types. For instance, a transect through a "mallin" had plots in wet mallin, dry mallin, and transition zone. In total, 22 transects with 203 plots at Cerro Tapayo and 10 transects with 194 plots at Río Minero were sampled (Table 1). Sampling of the vegetation took place in a circular plot of 5 m diameter. The length of the transect and the number of sampling plots depended on the size and the homogeneity of the vegetation type. For instance, mallins were small and sampling plots were placed every 15 steps whereas in large patches of steppe or forest they were placed at 30 steps along the transects. Direction and spacing varied according to topography, vegetation type and size of patch and was determined at the site (Turner, 1984; Table 1). Transects were placed 50 m apart if the width of the vegetation patch permitted, but in small patches, as is common with mallins, the two transects were placed such that the mallin was divided into three parts of similar size.

A general description of the vegetation in each plot was made by using four plant growth forms: graminoides, herbs/forbs, shrubs, trees, and bare ground. The abundance (in %) of each group was noted down and totaled 100%. In the lenga forest (*Nothofagus pumilio*), where multiple strata of vegetation were present, the abundance of each growth form was estimated, however the total can be more than 100%. The diameter and height of trees were also estimated. Based on the description of the vegetation in each plot, they were assigned to one of the following vegetation types:

Wet mallin, dry mallin, and transition. The mallins and transition are dominated by graminoides and forbs and have a vegetation cover which generally exceeds 80%. Elevations were 1600-1700 m for all three vegetation types.

Wet mallin is defined as exhibiting running water or inundated soils all year round. Cyperaceae, Juncaceae and other wetland species, such as *Caltha sagittata* (Ranunculaceae) and *Limosella australis* (Scrophulariaceae) dominate in the wet mallins. Of the graminoides, *Carex canescens* and *Carex macloviana* (Cyperaceae) and *Juncus depauperatus* (Juncaceae) are the most prevalent species. There are also many introduced species in this vegetation type. *Trifolium repens* (Leguminosae), *Phleum commutatum* (Gramineae) and *Cerastium arvense* (Caryophyllaceae) are the most common introduced species. This introduction is perhaps due to the presence and heavy use by domestic livestock throughout the study area.

When there is no running water nor inundated soils most of the year, the area is defined as dry mallin. The vegetation of the dry mallin is similar to wet mallin, but has more xeric graminoid and forb species, such as *Festuca pallescens* (Gramineae), *Hordeum chilense* (Gramineae), and *Ranunculus peduncularis* (Ranunculaceae). There is also a small percentage of shrubs present, all of which are found in the surrounding steppe.

Vegetation type	Cerro Tapayo	Río Minero	Length (m)
wet mallin	17 (3)		79,79,34
dry mallin	19 (4)		124,34,34,23
transitional zone	46 (4)		158,147,135,90
high elev. Steppe	68 (6)	60 (4)	540,450,383,383,270,270,180,180,113,90
lenga forest	53 (5)	57 (2)	675,608,383,293,225,158,135
low elev. Steppe		35 (2)	450,338
valley		42 (2)	540,405
Total	203 (22)	194 (10)	

Table 1. Number of plots sampled per vegetation type, number of transects (in parenthesis) in which at least one plot of that type was sampled, and length of transects (m).

The immediate surrounding vegetation of the mallin areas is called 'transition'. This vegetation type is very similar to the vegetation called 'high pasture lands' on the vegetation map of the Nahuel Huapi National Park (Mermoz and Martin, 1986). The high pasture lands are also described as dominated by graminoids, but with less than 80% total cover and with a larger percentage of shrubs than in the mallins. Again, *Festuca pallescens* (Gramineae) and *Poa* spp. (Gramineae) are by far the dominant species. Most forbs are low growing and of the composite family.

High elevation steppe. One of the main vegetation types is high elevation steppe. This type is dominated by grasses, forbs, and shrubs. It generally has no more than 80% total vegetation cover, but no more than 50% bare ground. It is generally found above tree line on young soils with a high percentage of volcanic ash, rock and other coarse textured materials. The strong exposure to winds results in a low growing and sturdy steppe vegetation.

The dominant shrub species include *Gautheria pumila* (Ericaceae), *Discaria chacaye* (Rhamnaceae), *Baccharis rhomboidalis* (Compositae) and *Chiliotrichum rosmarinifolium* (Compositae). Of the grasses the main species are *Festuca pallescens* and *F. monticola* (Gramineae) and *Poa scaberula* and *P. stepparia* (Gramineae). Many low growing matforming forbs are also present, with *Oreopolus glacialis* (Rubiaceae) perhaps the most common, but *Senecio* spp. (Compositae) and other composites also contributed significantly to the cover.

The species diversity and composition changes according to exposure, elevation, soil type and substrate material. These findings and description of vegetation types are very similar to that of the National Park vegetation map (Mermoz and Martin, 1986).

Lenga forests. The third vegetation type sampled at Cerro Tapayo was the Lenga forest which is a mixture of stands of different ages and can be divided into two types: 'Lenga forest' with trees higher than 2.5 meters and with an open under story, and 'Lenga thicket' with trees lower than 2.5 meters and so thick and twisted as to not allow any under story development. These two types are described separately in the vegetation map for the Park (Mermoz and Martin, 1986), but for the present study the two were lumped together since very little Lenga thicket was sampled.

The dominant over story was lenga while the under story contained some of the same species of graminoides, forbs and shrubs as were found in the surrounding steppe and transition type. In addition, there were a few more mesic shrubs and forbs, however representing less than 40% of the total vegetation. These species included *Ribes* magellanicum and *R. cucullatum* (Grossulariaceae) and *Azara mycrophylla* (Flacourtiaceae). Of the forbs, *Calceolaria crenatafolia* (Scrophulariaceae) and *Viola maculata* (violaceae) were more common.

The lower elevation lenga forest was sampled near Río Minero at an elevation of 1500 m where the under story was much more closed. There were stands of bamboo (*Chusquea culeou*, Poaceae) and also a high percentage of *Berberis serratodentata* (Berberidaceae). In addition, a larger area was covered by forbs and graminoides, including *Codonorchis lessonii* (Orchidaceae), *Uncinia lechleriana* (Cyperaceae), *Acaena pinnatifida* (Rosaceae), *Osmorhiza depauperata* and *O. chilensis* (Umbelliferae). Overall, these forests have a closed canopy of 60% or more. The trees range from 2.5 m to 20 m in height with diameters reaching 70 cm.

Lower elevation steppe. In the area near Río Minero, two low steppe areas were sampled. These areas are the result of previous fires some 20 or more years ago, and are now being colonized by steppe vegetation. In addition to the upland steppe vegetation, some more xeric plant type were present. Mulinum spinosum (Umbelliferae) constituted a large part of the vegetation together with Festuca pallescens (Gramineae) and Poa scaberula (Gramineae) and other grass species. Common shrubs included Discaria chacaye (Rhamnaceae) and Baccharis rhomboidalis (Compositae). The forbs were a mixture of introduced exotics and natives; Anemone multifida (Ranunculaceae) and Acaena leptocantha (Rosaceae) were common. These areas are in a successional stage which can be recognized by the sprouting Chusquea culeou and patches of Nothofagus antarctica (ñire).

Valley. A mosaic of vegetation was found in the valley of the Río Minero. The mosaic was sampled because no single vegetation type covered an area big enough to be sampled separately. Furthermore, the whole area is disturbed heavily and does not represent a natural vegetation type. Near the river patches of Nothofagus antarctica thickets (Nothofagaceae) and wet mallin types were present. Shrub or scrub vegetation consisting of steppe species was also present. Sparse steppe or dry herbaceous vegetation types (many made up of exotic species) were located further away from the river. It had most of the low elevation steppe species with more introduced plants such as Rumex acetosella (Polygonaceae), Plantago linearis (Plantagina), Hordeum chilense (Gramineae), Holcus lanatus (Gramineae), Poa pratensis (Gramineae) and Trifolium repens (Leguminosae).

Pellet group counting and determination of preferential habitat use

Transects were evaluated during December 1995. The plots used for the vegetation description (r = 2.5 m) were also used to count pellet groups of red deer, cattle, and horses. For deer, a pellet group was counted if it contained more than five pellets. Cattle and horses presented a special problem as they frequently defecate while walking, leaving several piles per defecation. When it appeared that several piles were part of a single defecation they were recorded as one (Turner, 1984; Telfer, 1994). Cattle and horse dung piles were counted if more than half was inside the plot. Any footprints were noted as well as an indication of recent use. Only 17% of plots with tracks also had feces present (n = 107). As these high elevation areas are not used by cattle and horses in winter, and snow usually also limits deer use to lower elevations, the presence of feces represents habitat use from late spring to autumn. The differential use of red deer, cattle and horses for any vegetation type was analyzed by testing for differences in means of pellet group density per vegetation type (White and Eberhardt, 1980; Turner, 1984; Loft and Kie, 1988; Edge and Marcum, 1989). The principle is based on the assumption that the negative binomial distribution adequately models observed pellet group counting data (derived from Bowden et al., 1969; McConnell and Smith, 1970; Stormer et al., 1977). A goodness-of-fit test was used to determine if the data sets follow the negative binomial distribution. Point and interval estimators of the parameters m (mean) and k (measure of contagion) are obtained by the method of maximum likelihood. This results in four different models for describing the different populations: m's and k's differ between population; k is constant but m's differ; m is constant and k's differ; k and m are constant between populations. Hypothesis testing is performed by using likelihood ratio tests to determine which of the models is more adequate.

Estimation of deer density

To estimate deer population size based on pellet group density it is necessary to know the average daily defecation rate and the decomposition rate of the pellet groups. These parameters were adopted from other studies resulting in a less rigorous population estimation, however it serves for a first approximation (Patton, 1992:309; White, 1992).

For the estimation of red deer densities in an area of 13.530 ha surrounding the study site, the pellet group counts and the vegetation map for the Nahuel Huapi National Park (Mermoz and Martin, 1986) were used. The similarity between our vegetation description and the description of the vegetation map of the park allowed extrapolation by placing a grid of blocks of 150 hectares over the vegetation map dividing it into vegetation types and subtypes.

Daily deposition rate, necessary for translating pellet group density to deer density, was calculated with published rates (Riney, 1957; Neff, 1968; Collins and Urness, 1979). For the mean annual deposition rate we used 16 pellet groups per day per animal. The rate of disappearance was assumed to be one year considering that pellet groups lasted only 11 months in southeast Alaska (Kirchhoff, 1990). Furthermore, studies of red deer pellet group density in the same region but at lower elevations indicated that on the average, pellet groups last one year (Flueck et al., 1995b). These studies were based on clearing permanent plots repeatedly and comparing the initial standing crop of pellets with subsequent densities in previously cleared plot. Using the pellet group counts of this study, published deposition rate, and the total areas per vegetation type, an estimate of the total deer population for that area surrounding the study sites could be derived.

RESULTS

Pellet Counting

Results of the pellet group counts of red deer, cattle and horses with respect to vegetation types are presented in **Table 2**. A goodness-of-fit test indicates that the data sets adequately fit the negative binomial distribution. The relative usage of different vegetation types by red deer, cattle, and horses is summarized in **Table 3**.

Red Deer. As the main focus was red deer habitat use at high elevations, it is important to look at the mean number of pellet groups per vegetation type. The mean density of red deer pellet groups found in the different vegetation types varied significantly (Chi Sq. 22.21; d.f.=6; P=0.001) (White and Eberhardt, 1980). The parameter k (contagion) differed between vegetation types (Chi Sq.=11.05; d.f.=6, P=0.08) indicating different patterns of habitat use resulting likely from the different cover structure among other things. Overall, the dry mallin and the transition areas were

VEGETATION	N ^o pellet groups per plot					
Туре	Red deer		Cattle		Horses	
	Mean	SE	Mean	SE	Mean	SE
Wet mallin	0.12	0.08	0.06	0.06	0.35	0.15
Dry mallin	0.58	0.16	0.53	0.14	0.42	0.14
Transition	0.41	0.09	0.11	0.09	1.53	0.29
High Steppe	0.16	0.05	0.02	0.01	0.40	0.06
Lenga Forest	0.11	0.03	0.05	0.03	0.09	0.03
Low Steppe	0.34	0.12	0.03	0.03	0.86	0.11
Valley	0.21	0.09	0.14	0.10	1.29	0.20

Table 2. Number of pellet groups per vegetation type for red deer, cattle and horses.

Table 3. Relative usage of different vegetation types by red deer, cattle, and horses.

VEGETATION Types	Red deer %	Cattle %	Horse %
Wet mallin	6	6	7
Dry mallin	30	56	9
Transition	21	12	31
High steppe	8	3	8
Lenga	6	5	2
Low steppe	18	3	17
Valley	11	15	26
Total	100	100	100

most preferred, although the wet mallin may be under-represented due to faster decomposition rates. Although the wet mallins may receive a much higher deer use than measured, it can be stated that the vegetation complex comprising wet/dry mallins and transitional zone is most preferred by deer followed by lower elevation steppe and the valley. In both study sites the lenga forests and the high elevation steppe areas had lower density of pellet groups.

Horses. The mean density of horse pellets found in the different vegetation types varied significantly (Chi Sq.=65.2; d.f.=6; P<0.00001). The parameter k differed between vegetation types (Chi Sq.=9.3; d.f.=6; P=0.158) indicating different patterns of habitat use resulting likely from the different cover structure among other things. The transition areas between dry or wet mallin and the rocky or sandy steppe areas were most preferred, followed by the valley. Overall, horses preferred the wet/dry mallins and transitional zone vegetational complex and the valley and the low elevation steppe areas in that order. Again, the wet mallin may be under-represented due to faster decomposition rates. Almost no pellets were found in the lenga forest.

Cattle. The mean density of cattle pellets varied significantly between the different vegetation types (Chi Sq.=23.5; d.f.=6; P=0.0006).The parameter k differed between vegetation types (Chi Sq.=17.2; d.f.=6; P=0.009) indicating different patterns of habitat use resulting likely from the different cover structure among other things. Cattle preferred

the wet/dry mallins and transitional zone vegetational complex and the valley, in that order. Again, the wet mallin may be under-represented due to faster decomposition rates. Lenga received some use but both high elevation and low elevation steppe received the least amount of use.

Estimation of density of red deer

The population densities of red deer were estimated for the study areas and the direct surrounding areas (Table 4). In the vegetation map of Mermoz and Martin (1986), the low elevation steppe was not differentiated as such (scale 1: 250,000), however since this vegetation type was sampled, we assumed that at least one grid block was covered. The "ñire forest" and "low forest and thickets" were not sampled in the two sampling areas, but were distinguished in the map of Mermoz and Martin (1986). Although no plots were sampled in these vegetation types, their structure suggests that the number of pellet groups would be very low at best (it is very difficult to walk through a ñire forest or low forest and thicket).

The overall density of red deer in this high altitude habitat in the Andes mountains was thus estimated conservatively at 1.44 deer per 100 ha, ranging from 0.3 to 3.4 deer/100 ha according to habitat type (**Table 4**).

DISCUSSION

Habitat use by red deer, cattle and horses

This study mainly reflects habitat use during late spring through autumn due to snow accumulation in winter in these higher elevations, when animals move to low elevations. The relative use by all three herbivores of wet mallin was similar, however cattle preferred the dry mallin most, followed by deer and horses, and it was also the vegetation type most frequently used by cattle (Table 3). The transition zone was most preferred by horses followed by deer and cattle, and it was also the most frequently used vegetation type by horses. In contrast, the vegetation type most preferred by deer was the dry mallin. High steppe was preferred equally by deer and horses followed by cattle. Preference for drier sites by horses has been observed elsewhere (Turner, 1984; Gordon, 1989a,b). The lenga forest received the lowest use by all herbivores which can be explained by the low forage base in these forests. However, it would be important to investigate if this combined level of use of lenga forests is affecting natural rejuvenation of lenga and other shrub species. The low elevation steppe was equally preferred by deer and horses

Veg. Type	Tot. Area in hectares	N° Plots sampled	Pellet groups per plot	groups/ ha/yr	deer/ ha/yr	Nº deer in area/year
All mallins	933	82	0.39	198	0.034	31.72
High steppe	2799	128	0.16	83.5	0.014	40.02
Lenga forest	4946	80	0.14	71.3	0.012	60.34
Lenga thickets	560	30	0.03	17	0.003	1.68
Low steppe	93	35	0.34	174.7	0.030	2.78
Valley	3079	42	0.21	109	0.019	58.50
Ñire forest	933	0				
Low forest and thickets	187	0				
Total	13530	397				195

 Table 4. Estimation of deer densities in different vegetation types and extrapolation of population size for the study and surrounding area of 13530 ha.

followed by cattle, while the valley was most preferred by horses followed by deer and cattle with similar use.

Cattle are expected to select habitat types with an abundance and availability of plant material with low lignin content in order to meet their metabolic requirements as a large ruminant. This is reflected in this study by their high preference for dry mallins, transition and valley (56%, 12%, 15% of time, respectively). Red deer on the other hand are mixed feeders and will eat both graminoids and browse. They differ from cattle by a higher preference for the transition zone and particularly the steppe habitat (26% versus 6% in cattle). However, the general low usage of high elevation steppe by deer could be the result of the present low density and it would be important to monitor the usage of this vegetation type during the likely future increase of deer density in that area. Other steppe areas in this region have been shown to reach deer populations densities of 50 deer/100 ha (Flueck et al., 1995b). The preference of horses for drier site may be related to hindgut digestion requiring large amounts of forage to pass the digestive system even when of lower quality and explains the selection for habitats with availability of high plant biomass (Gordon, 1989a, b).

Hansen and Clark (1977) found similar diet compositions between cattle, horses and *Cervus elaphus* at high elevation while others reported highest overlap mainly in areas used during spring and summer (Olsen and Hansen, 1977). Although diets may overlap, the herbivores studied here exhibited significant differences in spacial use of habitat.

Red deer density

Pellet group density was sampled following the standing crop of feces method along transects. However, in this method there is no intrinsic knowledge of the time period over which the collected pellet groups had been accumulating. Pellet groups present in a transect at the time of counting are the net result of a dynamic equilibrium between rates of accumulation and rate of decomposition. Studies in the same region indicated that the standing crop of pellet groups can be considered to represent depositions from one year (Flueck et al., 1995b). Densities encountered in wet mallins may be subestimates due to the faster decomposition of pellets in the presence of water (Lehmkuhl et al., 1994). However, wet mallins represent less than 5% of the total area considered and has little consequence for estimating the total population size.

In its native European range, red deer densities have been found most compatible with respect to natural forest regeneration at densities ranging from 0.8 to 3.3 deer/100 ha in Germany (Neumann, 1963), or 0.3 to 2.0 deer/ 100 ha in Poland (Bobek et al., 1984). The estimated range of densities for the present study of 0.3 to 3.4 deer/100 ha can be considered low enough such that the expected impact on the vegetation is relatively low. However, this area has been invaded only recently by red deer and the population appears to be expanding. Just west of the Río Minero study area there is a very low pass connecting to an area further south where red deer were released in about 1924. The first deer appeared just west of the study area in 1973 and since then have spread east. In similar areas but at lower elevation and with red deer present for several decades, densities of up to 100 deer/100 ha have been described as measured along a straight transect of 5 Km, crossing all vegetation types encountered in the present study (Flueck et al., 1995b). From the perspective of the habitat and forage quantity, it can be predicted that red deer density will increase in time, unless the mortality rate is increased through harvesting. At higher density, however, it is likely that red deer not only affect the vegetation but also associated faunal elements (Baines et al., 1994).

The low overall density of red deer of 1.44 deer/100 ha is supported by other observations. For instance, during the study only twice could red deer be seen including a group of three adults and one calf on top of Cerro Tapayo. Local settlers said that deer are seen in greater numbers in autumn (March) when groups of 15 to 20 individuals are common in the study area.

Management Aspects

Red deer were estimated at 195 individuals in 135 km² (Table 4), while the lease using this area runs about 150 cattle and 75 horses (Lagos, pers. comm.). Red deer, cattle, and horses were using the study area substantially; the relative pellet group densities among the three herbivores were 1: 0.5: 2.6 respectively. Combined metabolic body weight would make cattle the largest group of herbivore followed by horses. The combined effect of these groups of herbivores can be evaluated using their relative preference for the given habitat types in the area. Thus, mallin areas receive proportionally most use by cattle while the valley area was most used by horses, but carrying capacity has to be evaluated while considering all species. As these herbivores differ substantially in body size and digestive system (ruminant and hindgut digestion), they are expected to fill most niches provided by the heterogeneous vegetation with some overlapping.

In summary, mallins at high elevation were highly preferred by red deer, cattle, and horses (57%, 74% and 47% of total pellet group densities, respectively). Usage of the lenga forest was less than 10% for all herbivores, but it is not know if the combined pressure has an impact on the natural rejuvenation of forest species. Similarly, the steppe above tree line is used less than 10% by all herbivores, but it is predicted that usage by red deer will increase substantially if the population density increases. The steppe below the lenga forest is equally preferred by deer and horses at about 18% while the valley received intermediate usage, particularly from horses. The absolute red deer density of 1.44 deer/100 ha can be considered moderate. Considering the experience from its native range, management goals should aim at maintaining the density of red deer at the present level while reducing the density of both cattle and horses.

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