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Ranging behaviour of huemul in relation to habitat and landscape

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Abstract

The huemul *Hippocamelus bisulcus* is an endangered species of deer occupying temperate woodland habitats in the Andes of southern Chile and Argentina. Continuing declines due to a combination of hunting and habitat loss have created a need for more conservation measures. However, current information on ranging behaviour, dispersal and seasonal movements is very limited. Three sites were therefore selected in Aysén, Chilean Patagonia, to study the movements and habitat associations of huemul. Although seasonal migrations in elevation had been reported previously for the species, we found the extent of seasonal movement limited, much less than that reported for other deer species in mountainous environments. Huemul selected mid-slope elevations, and the winter ranges of most animals overlapped summer ranges. The extent of the seasonal movements that were undertaken were, however, the greatest at the highest site and insignificant at the lowest site. Previously published information shows that habitats used by huemul follow a latitudinal gradient in elevation (reducing *c.* $100\,\mathrm{m}\,^{\circ}\mathrm{S}^{-1}$ in latitude), and our results suggest that seasonal movements are likely to be greater in sites above this line. The mean range size differed between sites, ranging from 357 to 656 ha (mean 444 ha; median 506 ha). These estimates excluded long-distance (>5 km) movements, which were infrequent.

Introduction

The huemul *Hippocamelus bisulcus* is an endangered species of deer with a geographic range restricted to the temperate regions of southern Chile and Argentina (Wemmer, 1998). Comparisons between historical accounts and current status suggest that the status of the species has deteriorated dramatically, involving substantial reductions in abundance and geographic range (Díaz & Smith-Flueck, 2000; Flueck & Smith-Flueck, 2005).

Huemul are a medium-sized deer, with a mean body weight of *c.* 70 kg. Their primary habitat is temperate woodland dominated by lenga *Nothofagus pumilio* on Andean mountain slopes between 36° and 54° south (Aldridge & Montecinos, 1998). Within this range, winter conditions can be severe, with mean monthly temperatures below 0 °C and snow depths exceeding 1 m. Huemul are known to undertake seasonal migration, making use of habitats in higher elevations during summer and lower elevations in winter (Povilitis, 1998), behaviour that is typical in other deer populations in mountainous environments (Mysterud, 1999). However, huemul exist in environments that make study difficult, and current information on movements, as well as ranging behaviour in general, is limited, based largely on small sample sizes or unmarked animals (Povilitis, 1985; Díaz & Smith-Flueck, 2000).

We therefore undertook a study based on radio telemetry with the objectives of establishing daily and seasonal movement patterns and habitat use. To assess potential between-site differences, we collared animals in three areas in Aysén (Region XI), Chile.

Study sites

We used three study sites:
1. Tamango forest reserve (47°11′S, 72°29′W) has vegetation communities that are transitional between the southern beech forests to the west and pampa to the east. It contains a mixture of deciduous and evergreen forest dominated by lenga *N. pumilio* and coigüe *Nothofagus dombeyi* and a mosaic of shrubland (dominated by ñirre *Nothofagus antarctica*) and open ground, some of which resulted from fires between 1942 and 1945. The altitudinal range of the vegetated zone is 160–1100 m, *c.* 23% of which has a gradient of over 45° with rocky outcrops. The 6925 ha reserve is surrounded by private sheep and cattle ranches to

the north, east and west, and the lake and river Cochrane to the south and south-east. The mean maximum temperature in January is 19.7 °C and mean minimum in July (the coldest month) is −1.7 °C. Annual precipitation is 805 mm.

2. La Baguala (47°08′S, 72°12′W) is also a forest reserve located 20 km east of Tamango and north of lake Cochrane, with a similar altitudinal range (160–1100 m), but steeper slopes (30% of the area has a gradient of over 45°). Lower slopes are dominated by grassland (*Stipa* sp. and *Festuca* sp.) and shrubs *Embothrium coccineum*, *N. antarctica*. Patches of forest (lenga and coigüe) occur mid-slope, interspersed with grass and shrubs. Upper slopes are dominated by *Krümholz* (stunted lenga) and rocky outcrops. Both mid and upper slopes also contain successional communities, resulting from previous forest fires.

3. Candonga (46°14′S, 72°26′W) is owned by a private logging company. The altitudinal range of vegetation occurs between 600 and 1100 m and is dominated by lenga forest up to the tree line. Several glaciers are present and the zone is characterized by very steep terrain; 60% of all the area has a gradient of over 45°. Ground vegetation cover throughout the valley is relatively sparse, having not fully recovered following an ash fall from an eruption of mount Hudson in 1991.

Because of their protected status, Tamango and La Baguala were patrolled regularly by park guards and grazing and illegal hunting were prevented. In Candonga, grazing by cattle occurred during the summer months at a density of *c*. 1 cow km^{-2}. European hares *Lepus europaeus* occur at all three sites and guanaco *Lama guanicoe* are present in La Baguala, at a density of *c*. 1.7 km^{-2}, and were present occasionally at Tamango. On the basis of drive counts made by the park guards, the population density of huemul during the study was estimated to be *c*. 2.0 km^{-2} in Tamango and between 1.4 and 1.9 km^{-2} in La Baguala. The density in Candonga was unknown, but was considered to be lower than at the other sites.

Methods

Capture and marking

Between September 2000 and November 2002, 16 adult huemul (at least 1 year old) were captured using tranquilizing darts and equipped with radio collars. Five (3♂, 2♀) of the collared animals were caught in Tamango, seven in La Baguala (3♂, 4♀) and four in Candonga (3♂, 1♀). The majority (14) of these animals were fitted with conventional VHF collars with an activity sensor and a range of *c*. 6 km (13 manufactured by Sirtrack®, Havelock North, New Zealand; one by Telonics®, Mesa, AZ, USA). Two animals in La Baguala (1♂, 1♀) were fitted with 12-channel GPS collars (Sirtrack®), which were also equipped with VHF transmitters. The two GPS collars were programmed to log the position of the deer every 6 h and continued recording for 3 and 4 1/2 months, respectively. The VHF collars weighed 350 g and the GPS collars weighed 500 g, which is *c*. 0.5–0.7% of the average body weight of an adult huemul. Four of the collared animals died during the study: one from drowning, one was shot illegally and two were killed by puma *Puma concolor*. At the end of the study, the collars were left on the animals to obtain further evidence of mortality.

Radio telemetry

Monitoring of the collared animals started in September 2000 in Tamango and continued for 36 months, and in La Baguala and Candonga it was started in 2002 and continued for 24 and 19 months, respectively. Animal position was determined either by triangulation or by visual observation, after using the radio signal to locate the animal. Reliable triangulation proved to be difficult in the rugged terrain, but the majority (83.8%) of the positions obtained from VHF collared animals were verified by a visual sighting. Huemul were found to tolerate approach to between 10 and 100 m, enabling visual observations to be made with minimal disturbance. In total, 1853 locations were obtained, of which 757 were verified by visual sightings, 143 were obtained solely by triangulation from VHF signals and 953 were obtained from the two animals equipped with GPS collars.

Analysis

Estimates of home-range size were calculated from 95 to 50% probability contours obtained from kernel estimates (Worton, 1989) and 100% minimum convex polygons (MCP), using software developed for Arcview 3.1 (Hooge & Eichenlaub, 1997). Movements of more than 5 km were infrequent (representing $<0.3\%$ of observations) and were therefore regarded as either temporary or permanent dispersal. After excluding these excursions and cases where sample size was limited by fatality, the mean number of observations used to estimate range area was 69 for VHF collars (range 24–119) and 489 for GPS collars (range 372–606).

The distance between summer (21 December to 20 March) and winter (21 June to 22 September) ranges was calculated from the distance between mean grid reference co-ordinates in each season. Overlap between summer and winter ranges was calculated from minimum capture polygons from the ratio of (overlapping area × 2)/(summer area-winter area). Finally, the possible effect of sample size on both range area and proportional overlap was investigated by regression analysis.

Because the altitudinal range available to the radio-collared animals differed between sites, we first investigated selection for altitudinal zones (in 200 m intervals) using the log of the ratio of proportional use/availability (Aebischer, Robertson & Kenward, 1993). Analysis of sex and seasonal differences in use of elevations was carried out separately for animals with VHF collars, which yielded data with irregular time intervals and GPS collars, which provided fixes every 6 h. For animals with VHF collars, data were analysed using a correlated error mixed model fitted using REML. For animals with GPS collars, a daily mean elevation was calculated and then analysed using a first-order moving average (MA(1)) time series model. For each animal with a GPS collar, three possible functional responses were considered: (1) a linear trend; (2) a season ramp; (3) a season step. These tested whether movement in elevation was simply gradual, gradual followed by stabilization or thirdly an abrupt movement, respectively.

Results

Home-range size

Estimates of mean home-range area were 444 ha (range 314–848; median 506) obtained from the 95% contour of the kernel method and 490 ha (range 258–947; median 602) from the MCP (Table 1). For estimates obtained from the 95% kernel method, there was no significant correlation with sample size ($F = 0.39$; 1,12 d.f.; $P = 0.546$, or with the number of months each animal was tracked ($F = 0.83$; 1,12 d.f.; $P = 0.379$). There was also no difference in estimates for animals equipped with GPS compared with VHF collars (VHF mean: 451 ha; GPS mean: 407 ha; $F = 0.16$; 1,12 d.f.; $P = 0.700$).

In the majority of cases, the distance moved between successive locations was relatively small, more than 70% being <1 km. Only two movements >5 km were recorded (of *c.* 8 km), which were excluded when calculating range areas. One of these movements appeared to be permanent dispersal by a sub-adult female, the other temporary movement in response to disturbance. Including these movements would have yielded much larger range areas: up to 1954 and 2506 ha were obtained for the 95% kernel and MCP methods, respectively.

Home-range area estimates based on the 50% contour ranged from 25.5 to 107.6 ha (Table 1). These averaged only 13.5% (range 5.0–20.7%) of the area covered by the 95% contour, indicating strong selection for particular parts of the home range.

Estimates of home-range area differed between sites, with ranges in Candonga being significantly larger than the other two sites (Table 1). There was no significant difference in range size between males and females (Table 1; site: $F = 15.1$; 2,9 d.f.; $P < 0.001$; sex $F = 0.45$; 2,9 d.f.; $P = 0.519$).

For the majority of animals studied (10 out of 12), a portion of the winter home ranges overlapped the summer home ranges. The proportion of overlap differed between sites ($F = 4.63$; 3,8 d.f.; $P < 0.05$; $r^2 = 49.7\%$) and was the greatest in Tamango (49.7%); La Baguala 28.3% and the least in Candonga (21.6%). There was a significant positive relationship between overlap and winter sample size (overlap = 0.076 sample size; $t = 3.03$; $P < 0.02$), suggesting that overlap would increase if a larger sample had been obtained. The mean distance between mean summer and winter positions was 552 m (range 44–1219 m), less than the median distance moved in 24 h (706 m; $n = 1061$).

Altitudinal range of movement

The altitudinal range available to the radio-collared animals differed between sites, with the highest elevations in Candonga and the lowest in Tamango (Fig. 1). In general, huemul selected mid-slope habitats while avoiding the highest elevations ($\Lambda = 0.3113$; $P < 0.05$). However, there are also differences between sites, with animals in Candonga using higher elevations than the other two sites (Wilk's $\lambda = 0.1276$; $P < 0.05$). At the two highest sites (Candonga and La Baguala), there was a tendency for radio-collared animals to move downslope in winter and upslope in summer (Table 2). The animals in La Baguala fitted with GPS collars also made significant movements upslope between spring and summer (Fig. 2a and b; Table 3). One of these (a female) moved progressively up during the spring, remaining on the upper slopes for most of the summer (Fig. 2a), whereas the other (a male) moved later, more abruptly, and not so high, making occasional forays downslope during the summer (Fig. 2b). At Tamango, no significant seasonal movement occurred. The average altitudinal difference between summer and winter was 204 m in Candonga and 195 m in La Baguala (Table 2).

At one site, Tamango, there was a significant difference in the elevations used between the sexes (Table 2; males: 438 m; females 502 m; SE of the difference: 28 m). The difference was

Table 1 Home-range areas of radio-collared huemul *Hippocamelus bisulcus* between September 2000 and December 2003

			Minimum capture polygon		95% Kernel		50% kernel		Overlap[a]	
Site	Sex	n	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Candonga	M	3	544	124	656	99	84	20.8	0.216	0.126
La Baguala	M	3	575	148	424	31	61	8.0	0.190	0.049
	F	3	638	157	399	17	44	12.4	0.376	0.216
Tamango	M	3	314	28	371	22	43	2.5	0.452	0.240
	F	2	323	17	336	22	53	5.7	0.566	0.102
Mean			490	58	444	37	57	6.4	0.356	

Range areas are mean values (in hectares) calculated for animals of each sex and site. Data obtained during periods when two individuals undertook long excursions (>5 km) have been excluded.

[a]Calculated from (overlapping MCP area × 2)/(summer MCP area+winter MCP area).

MCP, minimum convex polygons.

not significant at La Baguala; however, comparison was limited to VHF data only and did not include all animals. There were insufficient observations from collared females at Candonga to make the comparison between sexes worthwhile.

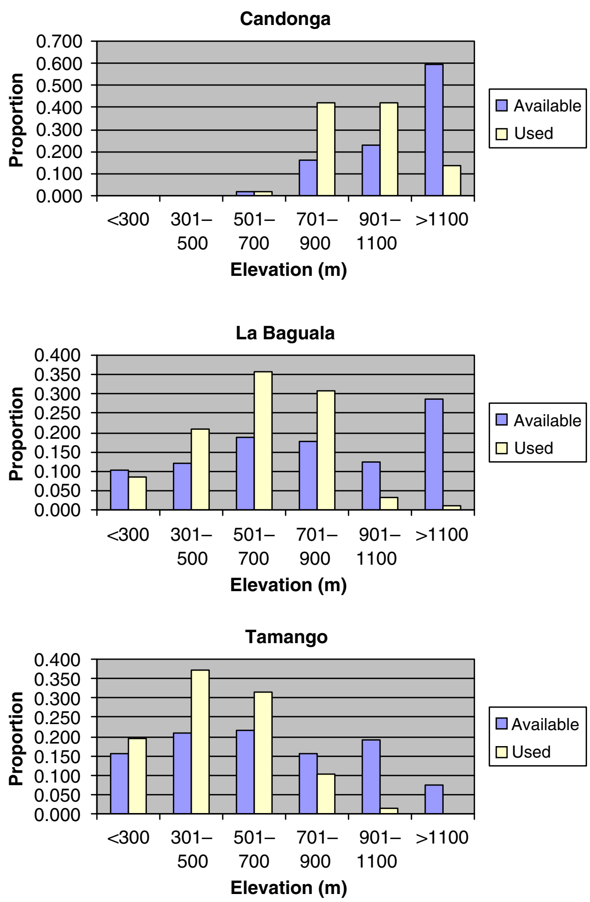

Figure 1 Elevation profile of each site in comparison with the mean use of each elevation class by collared huemul *Hippocamelus bisulcus* at each site.

Relationship between altitude and latitude

Information obtained from previously published studies reveals a tendency for huemul to use higher elevations in more northerly latitudes (Fig. 3). For this analysis, the median of the upper and lower altitudinal limits of habitats used by huemul were regressed against latitude. The relationship between median altitude and latitude is significant, and suggests that habitat use moves down *c.* 107 m in elevation with an increase of 1° in latitude south ($F = 27.86$; 1,11 d.f.; $P < 0.001$; elevation = $5765 - 107.3 \times$ latitude).

Discussion

The results obtained from the huemul marked in this study indicate that they undertake either a modest seasonal migration or none at all. Both lateral and altitudinal distances between summer and winter were relatively small in relation to the size of average daily movements, and in most cases, winter home ranges overlapped or formed part of, summer home ranges. There is a huge difference between the seasonal movements recorded in this study and those moved by deer in many populations in mountainous environments in the north temperate or boreal regions. Black-tailed deer *Odocoileus hemionus* have been reported to move up to 51 km and more than 1000 m in elevation between summer and wintering areas in California (Loft, Bertram & Bowman, 1989; Livezey, 1991), and red deer *Cervus elaphus* may move up to 68 km and 350 m in elevation in Norway (Albon & Langvatn, 1992). Siberian roe deer *Capreolus pygargus* have been found to move even further, up to 200 km, including hazardous river crossings (Danilkin, Darman & Minayev, 1992).

Nonetheless, altitude has a strong influence on movements and habitat use in huemul. Among the three sites used in this study, seasonal movements were greater and home-range area was larger with less overlap between summer and winter at the highest sites. Further, the two sites where we recorded the most seasonal movement (Candonga and La Baguala) lie above the regression line of altitude on latitude and the third site, Tamango, lies below it. This outcome is consistent with

Table 2 Summary of analyses to assess the influence of season and sex on the elevations used by huemul *Hippocamelus bisulcus* in the three study areas

						Mean elevations			
Site	No. of animals	Factor	d.f.	Wald/d.f. ratio	*P*	Summer	Autumn	Winter	Spring
Candonga	3	Season	3	15.31	<0.001	1039a	1057a	834b	932b
						Summer	Autumn	Winter	Spring
La Baguala	5	Sex	1	0.01	0.936				
		Season	3	16.77	<0.001	669a	613a	474b	478b
		Sex season	3	0.09	0.968				
						Males	Females		
Tamango	5	Sex	1	5.62	0.018	438a	502b		
		Season	3	0.02	0.997				
		Sex season	3	0.31	0.821				

Results reveal the significance of factors used in an REML model using VHF data. Factor levels with the same letter (a or b) within each site are not significantly different from each other.

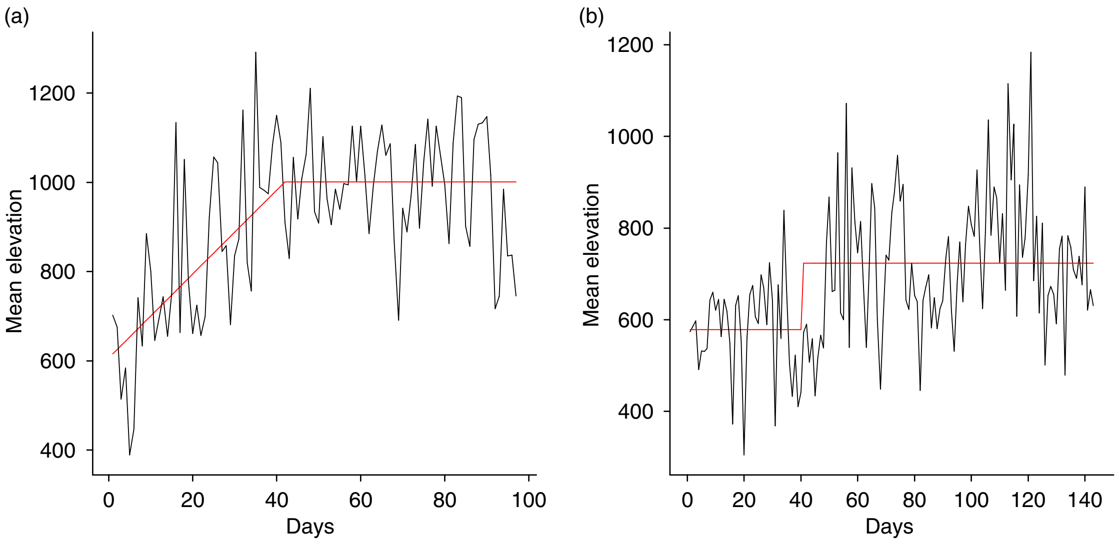

Figure 2 Mean daily elevation of GPS-collared animals at La Baguala following capture. The parameters of the models fitted appear in Table 3. (a) Female 30, caught 10 November. Season ramp model fitted. (b) Male 34, caught 11 November. Season step model fitted.

Table 3 Summary of time series models fitted to elevation data for huemul *Hippocamelus bisulcus* with GPS collars

	Model	Parameter	Estimate	t
Animal 30	Season ramp	Omega	9.4	7.27
		Constant	917.8	54.72
		Theta (MA)	−0.231	−2.27
Animal 34	Season step	Omega	145.1	4.88
		Constant	683.1	51.07
		Theta (MA)	−0.1829	−2.20

The parameters for the models were: $y_t = \mu + \omega f_t + e_t + \theta e_{t-1}$ where y_t is the mean daily elevation at time t, f_t is the input function (either a season step or season ramp), e_t is the random error term and θ is the coefficient for the moving average time series. For the season step model, the parameter ω is the height of the step while for the season ramp model it is the slope of the ramp. The constant, μ, represents the mean elevation.

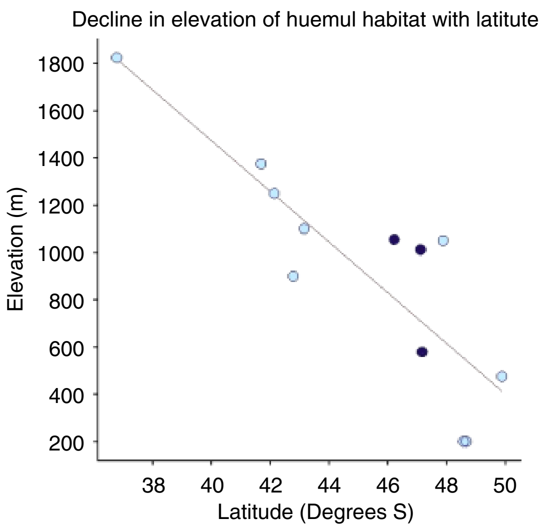

Figure 3 Relationship between elevation and latitude of sites reported to be used by huemul *Hippocamelus bisulcus* in Chile and Argentina. Data represent the median elevation of the upper and lower ranges of habitats used by huemul. Light circles: data from sites reported in Díaz & Smith-Flueck (2000); dark circles: sites used in this study.

the effects that latitude and elevation have on climate and suggests that huemul will have a tendency towards more seasonal movement above this latitudinal gradient, and conversely, more likely to be sedentary below it.

There are at least two benefits for deer undertaking seasonal migrations. The most frequently proposed one is to reduce exposure to adverse weather and deeper snow conditions in winter time (Danilkin *et al.*, 1992; Kucera, 1992; Nelson, 1995; Mysterud, Bjørnsen & Østbye, 1997; Nicholson, Bowyer & Kie, 1997; Holand *et al.*, 1998). Another advantage is that migrating animals can exploit vegetation of higher digestibility and protein content for longer, by following the progression of leaf emergence up slope in spring time (Albon & Langvatn, 1992; Sakuragi *et al.*, 2003). Both these factors could explain the limited altitudinal movements of huemul that did occur.

There are a number of possible explanations as to why huemul do not undertake longer seasonal movements. The terrain in many parts of the range of huemul appears to be steeper than sites reported where deer undertake longer migrations (Loft *et al.*, 1989; Livezey, 1991; Albon & Langvatn, 1992; Mysterud, 1999), and huemul can therefore exploit a greater altitudinal range, if necessary, by moving a shorter distance. Further, the terrain in the region at both higher and lower elevations offers relatively little suitable habitat. Above the treeline at 1100–1200 m, vegetation cover diminishes rapidly to sparsely vegetated areas of rock and ice, without extensive communities of grassland or dwarf shrubs. At lower elevations, grazing and other human activities are commonplace, and the risk of predation may also increase (Povilitis, 1983, 1998; Frid, 1994, 1999, 2001). As a result, the benefits of further migration appear to be limited.

This study has revealed larger home-range sizes than those recorded previously for the species. Previously, seasonal ranges of 36–82 ha had been estimated for huemul in Aysén, although home ranges of up to 700 ha in Chillán had been suggested if the animals are affected by disturbance (Povilitis, 1985; Díaz & Smith-Flueck, 2000). In contrast, we recorded mean 95% kernel ranges of 444 ha, extending up to 1954 ha for a disturbed animal. This difference is likely due to the use of telemetry, which facilitates the location and recognition of animals using the more peripheral parts of their home range. The GPS collars, in particular, revealed that more movements were occurring during periods of a few hours to a few days than had hitherto been appreciated. However, we found that huemul spend much of their time in a smaller core area: mean 50% kernel ranges covered only 57 ha. There are several possible reasons why behaviour is focused in this way on a core area; however, further investigation is needed to determine how different parts of the home range are being used and the functional significance of this.

In addition to differences in seasonal movement, we also found between-site differences in range size. In common with migratory behaviour, considerable variation in range size has been reported among other deer species, both among individuals as well as between populations (Danilkin, 1996; Strohmeyer & Peek, 1996; Holand *et al*., 1998). Some variation in ranging behaviour and range size will therefore be expected among other huemul populations. However, because huemul are able to tolerate winter conditions with little or no migratory movement, and habitat conditions at elevation extremes appear to offer little benefit, then it is likely that the pattern of relatively sedentary behaviour we observed in this study will be reflected in other sites. The relatively limited movements made by huemul suggest that subpopulations may easily become isolated and unsustainable if the status of the species continues to deteriorate. Further, the fact that habitat use is focused on valley sides suggests that regional conservation efforts should attempt to maintain connections between these environments to reduce the chance of isolation from developing.

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