

# Habitat use by endangered huemul (*Hippocamelus bisulcus*): cattle, snow, and the problem of multiple causes

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## Abstract

Habitat use by huemul (*Hippocamelus bisulcus*), an endangered deer, was studied at two adjacent periglacial sites of south-coastal Chile. Fiordo Témpano (cattle site) was cattle-free in 1990, after a winter of little snow, but 20 cattle were concentrated on its 2.7 km<sup>2</sup> grassland in 1995, after a winter of deeper snow. Estero Bernardo (control site) was cattle-free and studied in 1995 only. During spring at the cattle site, deer were observed using rocky slopes both years but grassland in 1990 only. During spring at the control site, deer used rocky slopes and grassland-type habitats daily. At the cattle site, fecal pellet-group densities suggested that winter use of grassland was substantial during 1990 only, and winter use of old-growth forest relative to grassland was much greater in 1995 than in 1990. At the control site, pellet-group densities suggested that winter use of grassland-type habitats was greater than of old-growth forest. Cattle, a concomitant increase in hunting, and snow likely contributed to habitat use differences between years at the cattle site. Although my study could not untangle the relative contributions of multiple causes, results cautiously suggest that excluding cattle from periglacial sites may be important to conserve huemul, and that winter use of old-growth forest should be a research priority. © 2001 Elsevier Science Ltd. All rights reserved.

**Keywords:** Cattle; Habitat use; *Hippocamelus bisulcus*; Huemul; South-coastal Chile

## 1. Introduction

Ecosystems are complex, and the challenge of untangling multiple causes pervades ecological research (Hilborn and Stearns, 1982), including applied studies (Underwood, 1994). The problem is difficult to solve even in carefully designed field experiments, and may be insurmountable by the limited data sets of most studies on endangered species in remote areas. Underwood (1994) argued that without replicated surveys and at least two control sites, impacts from human activities may be hidden by natural factors. Conversely, without proper controls a population decline or habitat shift at the impact site cannot be attributed conclusively to human impacts (Underwood, 1994). While the rigour of Underwood's design is appealing, it is unattainable when there is no warning that human activity will occur

in areas used by little-known species, and financial constraints force research to be short-term. Undoubtedly, studies with adequate resources should strive for rigour leading to strong inferences. Researchers of endangered species, however, often must evaluate when a data set is good enough to be useful. While opportunistic observations of unexpected events will not untangle multiple causes, they could provide insights that contribute to the conservation of obscure and threatened species. Here I present such a case for huemul *Hippocamelus bisulcus*, an endangered, mid-sized deer endemic to the southern Andes (Povilitis, 1979; Groombridge, 1993; Smith-Flueck and Flueck, 1994, 1995).

Huemul have a wide distribution in Chile and Argentina, where they occupy mountainous terrain ranging from open habitats in areas of low precipitation to sub-antarctic rainforests (Cabrera and Yepes, 1960; see Povilitis, 1998 for a map of their past and present range). Most surviving huemul, however, likely occur along Chile's southern coast, where isolation, rugged topography, and inclement weather maintain low human densities (see Frid, 1994, 1999). Photographs of

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the deer and habitats at periglacial coastal sites can be found in Frid (1991, 1997, 1999). Ecological work on huemul has been minimal, but aspects of the species' life history and ecology are described by Povilitis (1979, 1998 and references cited therein), Frid (1994, 1999), and Smith-Flueck and Flueck (1997). Poaching, habitat destruction, and conflicts with cattle (*Bos taurus*) have been proposed as the principal threats to the species (Povilitis, 1983, 1998; Smith-Flueck and Smith, 1995).

During 1990 I studied habitat use by 22 individual huemul at Fiordo Témpano, a remote and roadless periglacial site in Bernardo O'Higgins National Park, south-coastal Chile (Frid, 1994). During observations, huemul spent almost equal amounts of time on rocky slopes and on grassland, and spent little time in other habitats. The proportions of time spent on either rocky slopes or grassland, however, depended on age–sex class. Adult males used grassland almost exclusively, while adult females and juveniles spent one third and two thirds of the time in that habitat, respectively. Rocky slopes were used primarily by adult females, particularly those with neonates. I did not see huemul using the forest during spring, but fecal pellet-group densities suggested that deer had spent similar amounts of time on grassland and old-growth forest during the previous winter (Frid, 1994).

I returned to the area in 1995 and found, by interviewing local people, that in 1991 a resident of Puerto Edén, the nearest human settlement, had illegally introduced 18 cattle into the 2.7 km<sup>2</sup> grassland of Fiordo Témpano. Cattle were brought by boat and released at the site without establishing a permanent human presence. Cattle introductions and poaching of huemul are common in remote national parks, as Chile lacks the infrastructure to enforce conservation laws (Povilitis, 1986; Frid, 1997).

Cattle was only one of at least three factors potentially causing habitat use by huemul to differ between years at Fiordo Témpano. Snowfall was much greater in 1995 than in 1990, and the cattle introduction may have been associated with increased poaching. Cattle at high density (Loft et al., 1991), deep snow (Schoen and Kirchhoff, 1990), and hunting by humans (Kilgo et al., 1998) are known to affect habitat selection of other odocoilid deer.

In this study I contrast habitat use by huemul at Fiordo Témpano before and after cattle were introduced, and compare these observations to a cattle-free control site, Estero Bernardo. My opportunistic, short-term study cannot untangle the relative contributions of multiple factors. Nonetheless, given the endangered status of huemul and lack of other studies, my results are useful for assessing habitat shifts by huemul, and provide an opportunity to address the use of opportunistic data to the conservation of obscure and endangered species.

## 2. Methods

### 2.1. Study sites

Data were collected at Fiordo Témpano (ca. 48°40'–43' S, 73°59'–74°3' W) and Estero Bernardo (ca. 48°34'–37' S, 73°36'–32' W), Bernardo O'Higgins National Park, southern Chile. Fiordo Témpano was the site of the cattle introduction, while Estero Bernardo was cattle-free and used as a control. Both sites are periglacial, coastal and roadless. These sites are ca. 8.5 km apart, but separated by very rugged terrain. The climate is cool and wet year round, and is influenced by a large, adjacent ice-cap (Zamora and Santana, 1979). Analyses of huemul social organisation and other ecological aspects of each site can be found in Frid (1994, 1999).

Fiordo Témpano consists of a 13.3 km<sup>2</sup> watershed. Approximately 62% of the watershed appeared to be poor habitat for huemul, consisting of rocky alpine terrain which was largely under snow cover at the time of data collection, and of low elevation wetlands. Principal habitats are described below. [Note that percent covers presented below, which were estimated from 1:60,000 aerial photographs using a planimeter, are based on watershed size and differ from those in Frid (1994), which were based on the portion of the watershed that was systematically surveyed.]

1. *Grassland* is  $\leq 110$  m above sea level and contiguously covers ca. 20% of the watershed. It is an open habitat on the relatively flat valley bottom. Dominant vegetation includes graminoids and the perennial herb *Gunnera magellanica*. The latter is the principal food of huemul during spring at the study sites (Frid, 1994, and unpublished data). The habitat has little shrub cover and almost no trees.
2. *Low elevation rocky slopes* cover ca. 3.3% of the watershed, and are located on the periphery of grassland below 200 m above sea level. They consist of steep rocky outcrops mixed with vegetated ledges that often are sloping and narrow. The plant composition of ledges is very similar to that of grassland, including abundant *G. magellanica*.
3. *Old-growth forest* covers 15% of the watershed, from about 110 to 400 m above sea level. It is found only on the two mountain slopes that bound the grassland (one east-facing and one west-facing). It consists of closed canopy forest dominated by southern beeches (*Nothofagus betuloides*), and *Drimys winteri* is an important tree of the sub-canopy. Mean ( $\pm$ S.D.) basal area, estimated with a cruising gauge, was  $211 \pm 89$  m<sup>2</sup>/ha ( $n=107$  plots). This estimate is for the 1.3-km<sup>2</sup> forest patch on the east-facing slope, where we sampled densities of huemul fecal pellet-groups (see later). On the west-facing slope forest patches are smaller

and appeared to have lower basal areas. *G. magellanica* is rare in the forest, and the understory is largely a tangle of fallen logs and dense underbrush through which cattle are unlikely to travel.

Estero Bernardo is a watershed of ca. 25 km<sup>2</sup>. This surface area and percent covers given later are presented to give the reader a general description of the site. The watershed, however, is not as well defined by topography as at Fiordo Témpano, and some important habitats are discontinuous and part of a complex fine-grained mosaic. A more precise site description would require detailed landscape analyses that are beyond the scope of this paper. Habitats relevant to this study were:

1. *Grassland-type habitats* are found near sea level on the valley bottom, and cover ca. 22% of the watershed. These open habitats generally resemble the grassland at Fiordo Témpano, but there are three notable differences. First, they include flat rocky areas with little vegetation other than moss, and thus *G. magellanica* is patchier than at Fiordo Témpano, ranging between microsites from extremely abundant to absent (see Frid, 1999). Second, low shrubs (<1 m tall and mainly *Pernettya* spp.) are more abundant than at Fiordo Témpano. Third, grassland-type habitats are the dominant matrix in a mosaic that includes clumps of tall shrubs (1–2 m tall and mainly *Pernettya* spp.), a forest patch, and a lake and river. The latter divide the valley bottom into two sections, with the larger being to the east.
2. *Low elevation rocky slopes* cover ca. 13% of the watershed, are below 200 m above sea level and found mostly on the valley sides. The 200 m elevation threshold is arbitrary but represents the elevations that were systematically surveyed for huemul. They resemble low elevation rocky slopes in Fiordo Témpano, but in parts of the study areas they are interspersed with steep forest. *G. magellanica* is abundant.
3. *Old-growth forest* below 400 m above sea level covers ca. 22% of the watershed. The 400 m elevation threshold is arbitrary but was chosen because I considered that it contained the forest type that we sampled for basal areas; see later. It is dominated by *N. betuloides*, and *D. winteri* is an important tree of the sub-canopy. It generally resembles forest at Fiordo Témpano (including absence of *G. magellanica*), except that it is more fragmented by rocky slopes. Most forest patches are along the valley sides, but some are in the valley bottom. Basal areas were measured only on the 2-km<sup>2</sup> forest patch where we sampled densities of huemul fecal pellet-groups, and had a mean ( $\pm$ S.D.) value of  $140 \pm 45$  m<sup>2</sup>/ha ( $n = 45$  plots).

Much of the remainder of the study site that is not described earlier contains a higher-elevation mix of rocky slopes and steep forest, and alpine areas under snow cover.

## 2.2. Study seasons

Fieldwork was conducted at Fiordo Témpano from 26 October to 20 December 1990 (the cattle-free year: Frid, 1994), and from 20 to 24 October 1995 (the year with cattle). At Estero Bernardo, data were collected from 25 October to 15 November 1995 (Frid, 1999). To avoid bias, I considered direct observations of huemul for only the first 5 days of data collection during the longer studies. All observations presented here correspond to equivalent stages of early spring.

Plant phenology and weather were documented only qualitatively. At Fiordo Témpano substantial differences between the springs of 1990 and 1995 were not apparent. Snowfall during the winters preceding fieldwork, however, were very different. At sea level in Puerto Edén, at a linear distance of ca. 55 km from the study sites,  $\leq 30$  cm of snow accumulated for less than a week during the winter of 1990, while during the winter of 1995 about 60 cm of snow persisted for approximately 1 month (Puerto Edén residents, pers. comm.) Unfortunately, there are no weather stations near the study area and more precise records are lacking. Puerto Edén is not located near any glaciers; influence from the adjacent ice-cap likely caused even greater snow accumulation at the study sites.

## 2.3. Direct observations of huemul and cattle

Huemul were observed during foot surveys. At both sites I attempted to spread survey effort evenly across grassland-type and rocky slope habitats, but at Fiordo Témpano surveys were somewhat biased in favour of grassland. Because of visual obstructions, forests were not sampled for direct observations of huemul.

On 20 October, 1995, five observers walked the grassland of Fiordo Témpano to survey cattle. Due to the small area and openness of this habitat, I am certain that all cattle were counted. Habitats adjacent to grassland, including rocky slopes and forest, were surveyed for cattle signs (scats and tracks) and/or presence during 2 days of 1995.

## 2.4. Fecal pellet-group data for huemul

I used fecal pellet-group density recorded in early spring as an index of habitat use by deer during the previous winter (Kirchhoff and Schoen, 1983; Kirchhoff, 1990 and references cited within). Densities were estimated by counting pellet-groups on line transects that were stratified in grassland-type habitats or

old-growth forests. Each transect was divided into plots that were 20 m long by 1 m wide ( $n=45\text{--}142$  plots per transect; see Table 1) and adjacent to each other (Kirchhoff, 1990). Independence issues related to sampling design are discussed later.

Transects were sampled during similar dates both years and at both sites (Fiordo Témpano: 27 October–1 November, 1990, and 21–23 October, 1995. Estero Bernardo: 30–31 October, 1995). Because field effort focused on behavioural data (Frid, 1994, 1999), only one transect was sampled per habitat during each sampling period. Specifically, during both years at Fiordo Témpano only the 1.3-km<sup>2</sup> forest patch of the east facing slope and the centre of grassland were sampled. Transect locations were approximately the same both years. At Estero Bernardo only the centre portion of grassland-type habitats located west of the river and one large forest patch (ca. 2 km<sup>2</sup>) were sampled.

The assumption that pellet-group densities estimated during early spring adequately index deer use during the previous winter has been rigorously tested by Kirchhoff (1990) for Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in Southeast Alaska, but has yet to be tested for my study area. South-coastal Chile, however, resembles southeast Alaska biogeographically (Alaback, 1991), and it is reasonable to expect pellet-group deterioration rates, the major factor affecting data interpretation, to be similar in both places.

With one exception (old-growth forest in 1990), pellet-group data had a negative binomial distribution. Thus, mean density and degree of aggregation of pellet-groups were compared between years and sites using the methods of White and Eberhardt (1980). Though not optimal, the test involving data without a negative binomial distribution likely is still valid (G. C. White, pers. commun.). Specifically, significant differences between years or sites were based on likelihood ratio statistics for comparisons between three sets of alternative models (White and Eberhardt, 1980):

1. *Test 13*: populations are different vs. the null hypothesis that populations have common  $m$

(mean density) and separate  $k$  (degree of aggregation) values.

2. *Test 24*: populations have separate  $m$  and common  $k$  values vs. the null hypothesis that populations are the same.
3. *Test 14*: populations are different vs. the null hypothesis that populations are the same.

Note that analyses compared two other sets of alternative models which, based on results of tests 13 and 24, were redundant (White and Eberhardt, 1980) and are not reported for brevity.

Data presented in Table 1 assumes that plots within a transect represent independent samples of the given habitat or year, which is questionable because plots were adjacent to their nearest neighbour in the transect. However, preliminary analysis in which data from every second plot was deleted (such that plots within a transect were 20 m from their nearest neighbour) showed the same patterns as presented in Table 1. While results from this preliminary analysis were non-significant due to reduced sample size and lower statistical power, they suggest that had plots been independent my conclusions would still be supported.

### 3. Results

#### 3.1. Observations of cattle at Fiordo Témpano

Twenty cattle (four calves, two adult males, six adult females, two juveniles, and six unclassified individuals > 1 year old) were present during late October, 1995. These animals were very feral, and ran away when observers approached within a distance of 300–500 m. Several animals seemed to be in poor physical condition (ribs visible). In addition to observing live animals, we found two skeletons. Trampling of vegetation by cattle appeared substantial but was not quantified.

Cattle were seen on grassland only. Cattle signs (scats or tracks) were abundant in this habitat and were not observed on rocky slopes or inside the forest. Some cattle sign was present on a wetland area adjacent to

Table 1  
Mean pellet group densities by site, habitat and year

Year	Mean pellet groups/ha $\pm$ 95% confidence limits ( $n$ = number of 20 $\times$ 1 m plots)			
	Fiordo Témpano		Estero Bernardo	
	Grassland	Old-growth forest	Grassland-type habitats	Old-growth forest
1990	123 $\pm$ 50 ( $n$ = 142)	187 $\pm$ 98 ( $n$ = 107)	Not sampled	Not sampled
1995	46 $\pm$ 30 ( $n$ = 131)	247 $\pm$ 127 ( $n$ = 91)	605 $\pm$ 271 ( $n$ = 56)	311 $\pm$ 191 ( $n$ = 45)

grassland, but appeared to be rare. The study area is surrounded by rugged mountains, glaciers, sea water, and extensive swamps, making cattle dispersal unlikely.

### 3.2. *Huemul at Fiordo Témpano*

During the first 5 field days of 1990 (26–30 October), 1–3 deer were observed to use grassland daily. Of seven known individuals, four (two adult males, one adult female, one yearling female) used this habitat at least once. Huemul were seen on rocky slopes during 3 of 5 days, with each observation representing a different adult male not seen on grassland.

During the 5 field days of 1995 (20–24 October), huemul were not observed on grassland. A total of 6–7 deer (four females, 2–3 males; one male may have been sighted twice) were seen on rocky slopes during 3 of 5 days.

Mean density of huemul fecal pellet-groups did not differ substantially between old-growth forest and grassland in 1990 (Table 1, Frid, 1994). During 1995, however, it was five times greater in old-growth forest than grassland [Table 1: tests 13, 24, and 14 (see Section 2), respectively: Chi-square = 12.97, d.f. = 1,  $P \leq 0.0003$ , Chi-square = 15.27, d.f. = 1,  $P \leq 0.001$ ; Chi-square = 15.31, d.f. = 2,  $P \leq 0.005$ ]. Furthermore, mean density in grassland was 2.7 times lower in 1995 than in 1990 (Table 1: tests 13, 24, and 14, respectively: Chi-square = 6.15, d.f. = 1,  $P \leq 0.01$ , Chi-square = 7.081, d.f. = 1,  $P \leq 0.008$ ; Chi-square = 7.23, d.f. = 2,  $P \leq 0.03$ ).

### 3.3. *Huemul at Estero Bernardo*

During the first 5 days of surveys at Estero Bernardo (25–29 October, 1995), we saw 4–6 huemul using grassland-type habitats daily. These observation included eight of nine individuals identified during that period (three adult males, two adult females, two yearlings and a subadult male). During 4 of 5 days we saw 1–2 deer using rocky slopes. The latter observations included two known adult males, of which one was seen only on rocky slopes.

Mean pellet-group density was twice as large on open habitats than in old-growth forest. The difference approached significance, which is notable given the small sample sizes at this site [Table 1: tests 13, 24, and 14 (White and Eberhardt, 1980), respectively: Chi-square = 2.77, d.f. = 1,  $P \leq 0.1$ , Chi-square = 3.03, d.f. = 1,  $P \leq 0.08$ ; Chi-square = 3.29, d.f. = 2,  $P \leq 0.2$ ).

## 4. Discussion

Results suggest that huemul at Fiordo Témpano (cattle site) used grassland substantially less in 1995 than in 1990. I observed deer on this habitat daily during 1990, but observed only cattle and no deer during

1995. Because observations were made during only 5 days in 1995, evidence is based largely on fecal pellet-group density (assumed to represent winter use) on grassland being 2.7 times lower in 1995 than in 1990. Fecal-pellet group data also suggested that winter use of forest relative to grassland was much greater in 1995 than in 1990.

North American studies have found relationships that might explain habitat use differences between years at Fiordo Témpano. White-tailed deer (*Odocoileus virginianus*) in Florida decreased their use of open habitats and increased use of areas with visual cover during the hunting season (Kilgo et al., 1998). Sitka black-tailed deer in southeast Alaska decreased use of open habitats and increased use of high-volume old-growth forest during winters of greater snow accumulation (Schoen and Kirchhoff, 1990). Old-growth forests were selected because they provide a combination of greater canopy cover (which intercepts snow) and greater biomass of understory forage (Alaback, 1982; Schoen and Kirchhoff, 1990 and references cited therein). Studies in North America also found that, when cattle concentrations are low, mule deer (*O. hemionus*) can coexist with cattle and even benefit from nutritious forage regrowth following cattle grazing (Peek and Krausman, 1996). Cattle in high concentrations, however, can displace mule and white-tailed deer from preferred habitats (Loft et al., 1991; Galindo-Leal et al., 1993; review in Peek and Krausman, 1996). Such displacement could decrease access to preferred forage (Loft et al., 1991; review in Peek and Krausman, 1996). Cattle also may damage habitats through increased soil erosion, alteration of plant species composition, and other mechanisms (review in Fleischner, 1994).

Given the above studies, it is reasonable to infer that in Fiordo Témpano high concentrations of cattle and greater snow accumulation may have reduced use by huemul of grassland in 1995, and that greater snowfall in 1995 likely contributed to greater winter use of old-growth forest. In addition, the cattle introduction may have increased human presence, and thus risk from hunters. Greater wariness by deer suggested that poaching increased due to the cattle owners visiting the area. In a dramatic contrast to 1990, when I could approach most deer within 5 m or less (see Frid, 1991), huemul in 1995 did not allow us to approach closer than about 200 m. Increased risk from hunters may have caused deer to spend less time on open, riskier grassland and more time in presumably safer habitats, such as rocky slopes (see Frid, 1999) and forest (see Kilgo et al., 1998).

While my study cannot conclusively untangle the relative contributions of multiple factors, I suggest that cattle, on their own or in association with increased hunting, were an important factor reducing huemul use of grassland at Fiordo Témpano. This argument is

based on three observations. First, mean pellet-group densities at Estero Bernardo (control site) were greater in grassland-type habitats than in old-growth forests (though not quite significantly), suggesting that snow cover was not sufficiently deep and/or long-lasting to preclude deer from spending at least similar amounts of time in grassland-type habitats and forest during the winter of 1995. Second, during spring when snow was no longer a potential factor, deer at Fiordo Témpano used grassland daily in 1990 (prior to cattle), but during observations exclusively used rocky slopes in 1995 (after cattle were introduced). Third, the latter observation was in sharp contrast to Estero Bernardo, where in 1995 I saw 4–6 huemul using open habitats of the valley every day. Collectively, both sets of cattle-free direct observations (Fiordo Témpano in 1990 and Estero Bernardo in 1995) suggest that the absence of huemul on grassland during the spring of 1995 at Fiordo Témpano was very unusual, and possibly linked to cattle and/or a concomitant increase in risk from hunters.

Regardless of the mechanisms involved, lower use of grassland during 1995 at Fiordo Témpano may have reduced foraging opportunities during spring. During the spring of 1990, huemul on grassland spent an average of 87% of their feeding time eating *G. magellanica*, which at Fiordo Témpano was scarce outside of grassland and rocky slopes (Frid, 1994). Although *G. magellanica* also was abundant on rocky slopes, where in the spring of 1990 huemul spent an average of 83% of their feeding time eating it, the area of grassland is six times larger than that of low-elevation rocky slopes (Frid, 1994). Theoretical models predict that habitat shifts that decrease access to preferred forage potentially could reduce reproductive success (Sutherland, 1996). Furthermore, empirical evidence strongly suggests that declines in snowshoe hare (*Lepus americanus*) populations are largely a consequence of body condition and fitness decreasing because increased predation risk induces a shift to habitats with lower food quality (Hik, 1995). Similar mechanisms could affect huemul populations following habitat shifts caused by cattle introductions or other human activities.

Most of Bernardo O'Higgins National Park is very rugged and swampy, and periglacial valleys — which tend to be better drained — are the only likely places for introducing cattle. Other cattle introductions within the park occurred also in periglacial valleys occupied by huemul (Povilitis, 1986; Puerto Edén residents pers. comm.). Periglacial valleys were important to huemul in the absence of cattle and contained abundant *G. magellanica* at both study sites (Frid, 1994, 1999). Peek and Krausman (1996) have pointed out how mule deer and cattle may coexist when cattle grazing intensity is low, and that cattle-stocking can be manipulated to enhance mule deer habitat. Peek and Krausman (1996), however, base their argument on studies conducted in relatively

more productive habitats of the continental United States. Their conclusions could be inapplicable to the subantarctic conditions of south-coastal Chile, where relatively productive valleys are small, few, and naturally fragmented by low elevation glaciers, sea water, and extremely rugged topography. Furthermore, poaching is an important factor endangering huemul (Povilitis, 1983, 1998), and cattle introductions bring a concomitant increase in human presence and associated hunting.

A long-term study of several huemul populations may have been able to use the experimental design of Underwood (1994) to unravel the relative contribution of cattle to changes in habitat use at Fiordo Témpano. My opportunistic observations fall short of strong inference. Nonetheless, given the endangered status of huemul and the lack of other studies, results cautiously suggest that removing cattle from Fiordo Témpano and preventing further cattle introductions to periglacial valleys is important to conserve huemul on the mainland of south-coastal Chile. They also suggest that more work is needed not only to test this hypothesis, but also to understand whether old-growth forests are important to huemul during winters of deep snow accumulation.

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