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HUEMUL HERESIES: BELIEFS IN SEARCH OF SUPPORTING DATA. 3. REPRODUCTION

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ABSTRACT

The general absence of recovery of remnant huemul populations (*Hippocamelus bisulcus)* hinges on factors affecting the population dynamics. We analyze recent published findings about reproduction and behavior with regard to their possible implications. The life history of huemul is characterized by age at maturity of one year with evidence that fawns may also breed. Reports of twinning need confirmation, but it occurs in congeneric taruca *(H. antsensis)* and other Odocoilines. Huemul breed every year and frequently raise fawns successively. Life cycle calculations should apply these parameters because unrealistic parameters may cover up ongoing processes and lead to spurious conclusion. Sexual segregation in huemul is facultative, similar to many other cervids and reflects relationships between populations and their environment. Dominance group breeding systems were described several times without indications of territoriality, as with taruca. Recently, huemul bucks were characterized as territorial all year, life-long, defending and monopolizing female groups and two 'territorial' bucks sired most offspring. These two bucks though sired only 26% of fawns in their respective social groups. In their area, 'territorial' bucks bred about as many wandering females than resident females, whereas 32-45% of fawns from resident females were sired by outside males. Furthermore, when applying one year as the age at maturity rather than three years, there were unaccounted fawns and possibly <50% of all neonates were sampled. Overall, these data do not support territoriality in huemul. Regarding movements, extant huemul occupy flat grasslands, and at times nearly exclusively so, while historically huemul occurred up to 270 km from forests and in rolling topography. The claim that 5 km of open valley inhabited with guanaco (*Lama guanicoe*) present a barrier to huemul causing genetic isolation is unwarranted: moreover, huemul coexist with guanaco currently and historically. Erroneously considering landscape features as barriers and underestimating reproductive capacity may distract from discovering the factors underlaying the lack of recolonizations generally observed in currently reduced huemul populations.

Additional keywords: Hippocamelus bisulcus, reproduction, sexual segregation, territoriality, resource defense, genetic isolation.

INTRODUCTION

Securing reliable data is difficult on species highly reduced in numbers and remaining mainly in remote refuge areas. In the accompanying paper (Part I. Historical and zooarcheological considerations, this issue) we analyzed information regarding historical conditions which influence the current interpretation of the biology and ecology of huemul (*Hippocamelus bisulcus*). Part II addresses antlers, group size and density, predation, diet, competition, and diseases. These papers together aim to improve our understanding of huemul and its conservation. Here we analyze older and more recent sources and focus on issues related to reproduction, sexual segregation, resource defense, and genetic isolation to reveal discrepancies. We show that current beliefs do not stand up under close scrutiny.

METHODS

We reviewed literature via Cross-Search of ISI Web-of-Knowledge and 17 external databases, three books and three dissertations on huemul, historic and grey literature available in a collection containing 286 entries, plus publications on other related deer species to allow a comparative approach to analyze and interpret huemul literature, including questionable information, which continues to be used to describe huemul.

RESULTS

Reproduction

The general lack of recovery among huemul populations raises immediately the question about population dynamics including vital rates, and other parameters which are essential to diagnose factors limiting recovery. Age at maturity of huemul has been asserted to be three years, although without supportive data (Corti *et al.* 2009). However, irrefutable evidence exists that huemul breed as yearlings (Texera 1974; Guineo *et al.* 2008; Vidal *et al.* 2011). Furthermore, there is good evidence to show that even fawns can breed (Anon. 1936; Texera 1974; Vidal *et al.* 2011), as is known for other Odocoilines including *Odocoileus* and *Rangifer*. Given the above evidence, it is therefore unrealistic to classify females < 3 years old as juveniles and base calculations of intrinsic population growth rates on 'adult' female huemul (Wittmer *et al.* 2010). Other parameters misrepresented regard claims by Garcia *et al.* (2008) that available information indicates that females have only a fawn every second year, unless the fawn dies early on. However, indisputable evidence shows that huemul breed every year (at least in six consecutive years; Aldridge 1988) and frequently raise fawns successfully during several successive years (Guineo *et al.* 2008; Vidal *et al.* 2011). Lastly, huemul have been reported to have twin fawns (Housse 1953; Whitehead 1993), as is known to occur in the sister species taruca *(H. antisensis)* under good conditions (Barrio 2010), as well as in *Odocoileus*. No recent cases are known and twinning needs to be confirmed.

Sexual segregation
Huemul social structure is said to differ from other cervids. In contrast to other cervids, it is commonly stated that mixed-sex groups occur not only during the rut, but continuously and throughout the whole year (Povilitis 1983, 1985; Vila *et al.* 2010). However, in addition to mixed-sex groups, sexual segregation, including single animals, and multiple male (Fig. 1) and female groups, has also been documented (Serret and Borghiani 1997; Frid 1999; Wensing 2005). In one population, the sexes were mainly segregated with adult males and females associating only twice out of 104 group sightings (Frid 1994).

The degree of segregation between the sexes (social or spatial separation) is highly variable between different cervid populations (reviewed in Putman and Flueck 2011 as follows). In red deer (*Cervus elaphus*), with sexes usually considered to be highly segregated outside the rut, in some populations even among mature animals, only 18-20% of stags and 50-56% of hinds were seen in segregated parties. In other populations some males leave the rutting area but migrate to areas that contain females all year and loose groups may form. In some fallow deer (*Dama dama*) populations, males remain in female areas long after the rut and in largely open landscapes, or in populations with few adult males; aggregations containing adults of both sexes remain frequent throughout the year. In white-tailed deer (*Odocoileus viginianus*), some populations formed mixed groups year round; among mule deer (*Odocoileus hemionus*), mixed groups of adults also occurred all year, making up 13-30% of all groups encountered. In roe deer (*Capreolus capreolus*), home ranges of adult males and females overlap all year and mixed-sex groups can be common all year. Moose (*Alces alces*), considered a rather solitary species, may nonetheless occur in mixed groups throughout the year, with mixed-sex groups being more in populations with proportionally more females. Thus, the pattern of mix-sex groups described in huemul as being so unusual, in actuality also occurs in numerous other cervids, and conversely, several cervids including huemul form single-sex groups, with several known factors accounting for this variation.

Territoriality
Breeding systems are particularly important in small populations (Stephens and Sutherland 1999) and thus we evaluate contradictory evidence about the huemul mating strategy. The dominance group mating system is the only one which has been observed for huemul until recently (Povilitis 1985; Diaz and Smith-Flueck 2000; Wensing 2005; Fundación RA Philippi 2009). This consists of multi-male aggregations in which one male is dominant over all others and achieves most matings. Subordinate males are tolerated in the group, male aggression is relatively low compared to other systems (Aldridge 1988; Serret 2001), and territoriality is not exhibited. During a 10 year study, no indications of huemul being territorial with active defense were found (Guineo *et al.* 2008). The sister species taruca also exhibits a dominance system and lack of territoriality (Barrio 2010).

In contrast, huemul bucks were recently claimed to be strongly territorial, thus displaying behavioral characteristics unusual for most cervids (Corti *et al.* 2009, 2010). According to Maher and Lott (1995), territoriality is achieved by expelling potential competitors from a defended area, with defense behaviors taking place at the boundaries, which includes scent marking, displays, retreats, chases and fights, and agonistic or aggressive behavior in general. Corti *et al.* (2009) considered huemul bucks as

being territorial, defending their area during all seasons, and life-long. Furthermore, they asserted that these territorial bucks defended and monopolized female groups in specific areas and sired most offspring, while non-territorial bucks rarely sired offspring (Corti *et al.* 2009). Specifically, eight of 16 sampled sexually mature bucks present during 2005–2007 sired no offspring, and 44% of fawns were sired by only two bucks. Thus, a few bucks sired most of the fawns for several consecutive years with the same groups of females (Corti *et al.* 2009).

Territorial behavior as described by Corti *et al.* (2009) for huemul would indeed be unusual among cervids. Instances of territoriality described in cervids so far relate to male behavior during the rut in only a few species (reviewed in Putman and Flueck 2011). Red and fallow deer can adopt a strategy of defending very small mating territories, which is determined by population density and resource patchiness. In the only cervid with delayed implantation, roe bucks often maintain larger breeding territories, especially in forests, but not in open-field habitats. Territorial roe bucks will mark the periphery and interior of their area. However, adult males of all these facultatively territorial cervids also may occur in mixed groups year round with highly variable group sizes depending on density, habitat and sex structure, which determine the type of breeding system adopted (Putman and Flueck 2011). However, no other cervid is known to exhibit territoriality during the whole year as claimed for huemul (Corti *et al.* 2009).

Male behavior makes up only part of the mating strategy. Female roe deer commonly acquire extra-pair matings (Foerster *et al.* 2003). Although roe bucks often maintain breeding territories, up to 55% of females in one study performed excursions outside their usual home ranges during the peak of the rut, ranging from 0.6 to 3.0 km, and lasting for several days (Lovari *et al.* 2008; Richard *et al.* 2008). Moreover, Vanpé *et al.* (2009) found 14% of polytocous litters sired by more than one buck. Multiple paternity also occurs in *Odocoileus virginianus* (DeYoung *et al.* 2002), where recent studies refuted the prevailing assumption that male reproductive success is highly skewed toward a small number of mature, dominant bucks (DeYoung *et al.* 2009). In fact, physically immature males (1.5 and 2.5 years of age) collectively fathered 30–33% of offspring in all studied populations, even where mature males were present. The same flexible mating strategies also occurs in huemul, where subordinate males did all the siring in consecutive years in areas of supposedly territorial males, females being bred by neighboring males, and females moving into areas of other males to return after mating (Corti 2008; Povilitis 1983, 1985; Wensing 2005).

Evidence for territoriality in huemul bucks
Huemul bucks being territorial during the entire year (Corti *et al.* 2009) is unusual among cervids, with implications for population genetics. Based on the original source, 41 marked huemul (20 with radio-collars), observed at least once per month between late March 2005 to December 2007, were the basis to determine interactions and group membership (Corti 2008). These observations resulted in 25.7 spatial points on average from 18 males and 23 females to determine home range sizes and spatial overlap. In the following we analyze several lines of arguments to claim territoriality among huemul bucks.

Territoriality based on dominance. According to (Corti 2008), "adult males were considered territorial if they appeared dominant to other males and held a specific area. Non-territorial adult and juvenile males were considered subordinates". However, dominance was not defined and there was no information as to how it was measured.

Territoriality based on spatial overlap. Observations of males resulted in 7-20 spatial points/male, therefore, not all individuals were seen every consecutive month (Corti 2008). The 50% core area of dominant males (based on 15.6 spatial points on average) was considered to represent the defended territory or exclusive area of mating, averaging 55.7 ha (range 25-114 ha). However, as these spatial points were collected during a period of 2.5 years and with large time intervals in between readings, the delimited core areas and overlaps do not indicate spatio-temporal relationships. Moreover, little or no overlap of home ranges does not constitute evidence of territorial defense behavior (Grant *et al.* 1992). In addition, 50% of the 'territorial' males had their core areas overlapping with another 'territorial' male (Corti 2008). Notably, the claim of life-long territoriality was based on 3 adult males remaining in the same area until death (2-3 years).

Territoriality based on behavior. Very few interactions among 'territorial' males were seen, and therefore "cannot establish conclusively that they defend areas against other males" (Corti 2008).

Instead the degree of home range overlap was used to deduce territorial behavior. However, home range overlap in cervids is strongly tied to animal density and vegetation structure (Jepsen and Topping 2004; Kjellander *et al.* 2004; Tufto *et al.* 1996). Actual interactions between huemul bucks during the rut were documented as 'territorial' males chasing subadults 5 times, and one observation of parallel walking of two 'territorial' males at the apparent boundaries of two territories. Parallel walking, however, is common among many cervids, unrelated to territoriality, and interpreted as assessment of the opponent, leading either to fighting or withdrawal (Clutton-Brock *et al.* 1979). A 'territorial' male with a broken forelimb, and a juvenile male with both a broken rear leg and antler were considered evidence of aggressive territorial behavior during the rut. This seems unlikely given that no direct interactions between 'territorial' males were ever seen (Corti 2008), that juveniles do not engage in fights with mature males (Thomas *et al.* 1965; Ozoga 1972; Geist 1981; Anderson and Wallmo 1984; Povilitis 1983, 1985; Guineo *et al.* 2008), and the general absence of such reported injuries from rutting in other cervids. Although accidental falls of rutting males might result in broken legs, a more plausible scenario would be a pursuit by dogs (Packard 1947), which frequently occurred in the study area (Corti 2008). The fraying of trees and shrubs was interpreted as territorial marking, referring to behavior of roe deer during the mating season (Johansson and Liberg 1996). However, the common behavior of non-territorial cervids to rub antler and forehead against stems of trees and bushes has been described as innate extra-rut behavior, velvet shedding, marking behavior, and conspecific communication. *Odocoileus*, and likely the related huemul, have much less glands in the forehead skin than territorial *Capreolus* (Quay and Müller-Schwarze 1970, 1971). Intensive rubbing and thrashing, also called horning, is known for huemul (Geist 1998), and is very common in *Odocoileus*, yet this genus is non-territorial.

Territoriality based on skewed parentage. According to Corti (2008), the huemul mating system was polygynous, with males defending several estrus females sequentially, and 13% of mature males siring 44% of all fawns. This highly skewed male reproductive success was implied to support the existence of a territorial breeding system (Corti *et al.* 2009). Highly skewed reproductive success would indicate that few 'territorial' huemul were able to monopolize breeding by maintaining strong associations with many females within their reduced core mating area. However, simple ratio association indices were very weak and ranged from 0.00 - 0.03 for males and 0.01 - 0.03 for females, indicating that most huemul spent only short periods of time in small groups or were solitary, especially adult males (Corti 2008). Furthermore, at only 1.7 huemul/km^2, the supposedly exclusive 50% core areas (56 ha on average) would require a clumped distribution, where groups of females would have to remain principally in these reduced areas of a given 'territorial' buck. In contrast, in other cervids at low density and few males, females started to wander in search of breeding opportunities (Labisky and Fritzen 1998; Lovari *et al.* 2008; Richard *et al.* 2008), multiple fathers are common (DeYoung *et al.* 2002; Vanpé *et al.* 2009), and non-dominant males frequently have breeding success (DeYoung *et al.* 2009). Huemul actually exhibited similar variations as the deer in these other studies: a) one of seven 'territorial' males never sired any fawns; b) one subordinate male entered the area of a 'territorial' male in two consecutive years and sired all fawns; c) five females had offspring sired by males inhabiting neighboring areas; d) and three females were directly observed leaving their areas and moving into areas of other males before returning to their ranges after mating (Corti 2008). Huemul groups in other areas (Povilitis 1983; Wensing 2005) and taruca (Barrio 2010) were also found to be very fluid with members coming and going, and Povilitis (1985) described a female getting courted by two or three males intermittently, another female being mainly courted by one male but mounted by another male, a dominant male chasing a subordinate male after the latter had mounted a female, and dominant males leaving the females for prolonged times in apparent search for other estrus females. Thus, the skewed breeding success among male huemul reported in Corti *et al.* (2009) seems at odds with these other observations and is evaluated below.

Determination of skewed reproductive success. Several possible biases need to be considered when determining the reproductive success of 'territorial' huemul bucks. Due to limited genetic variability, incomplete sampling, and probably genotyping error, it was not possible to assign paternity at high confidence, and was considered to possibly generate a large bias (Corti 2008). This bias was reduced as much as possible by assigning only putative fathers as those that were near the area of a mother; yet indices of overlap of fathers' 50% core area with mothers' home range were low (average of 0.29, range 0.00- 0.67) (Corti 2008).

Based on Corti (2008), relative success of 'territorial' males breaks down to siring only about 45% of observed fawns in their social group, while siring another 41% of fawns to wandering females, and

importantly, their social groups also 'lost' 32-45% of the observed fawn crop to outside males. Moreover, one of seven 'territorial' males did not sire any fawns during the 2 years: all fawns stemmed from a subordinate male coming in from another social unit. Within social units, 22% of females got bred by other males, 11% of females were either bred by the 'territorial' or other males, and 33% of female had no data. The 13% of mature males (two 'territorial' bucks) siring 44% of all fawns (Corti *et al.* 2009) were responsible for only 26% of the fawns in their respective social groups.

However, when applying the age at maturity of one year (Guineo *et al.* 2008; Vidal *et al.* 2011) instead of 3 years, there are potentially 28 fawns unaccounted for, apart from the 23 sampled ones (Table 1). Thus it is probable that less than 50% of all neonates were sampled which adds another source of bias.

Table 1. Offspring production during the 2 years, based on the age at maturity of 1 year and assuming successful breeding each year (capture data are from Corti 2008)

	n	Sampled fawns	Missing fawns
Females resulting in fawn captures each year	6	13[A]	
Females resulting in only one captured fawn	10	10	10
Females resulting in zero captures	9	0	18
Total		23	28

[A] One female resulted in 3 sampled fawns over 3 years.

Genetic isolation
Mate finding or genetic isolation can be affected by physical isolation of subpopulation. Genetic isolation requires either absolute barriers, or an absence of immigration due to other factors, including lack of conspecifics through a discrepancy between maximal dispersal distance and separation between neighboring populations. It can also result from neighboring populations being too small to produce dispersers as this is influenced by the Allee effect on behavior (Stephens and Sutherland 1999) and population density (e.g. Kokko and Lopez-Sepulcre 2006).

To support claims of genetic isolation, a valley 5 km wide was asserted to present a barrier to huemul (Corti *et al.* 2009), due to being flat and open (Fig. 2). Yet the habitat shouldn't present an obstruction to huemul movements. Extant huemul are known to occupy grasslands, and coastal populations used open bottom grasslands 48% of the time, and males nearly exclusively so (Frid 1994, 1999). Data from historic huemul distribution show that they still occurred up to 270 km away from forests and in flat or rolling topography (see Part I. Historical and zooarcheological considerations, this issue), and during glacial maxima huemul occupied flat and rolling areas void of forest to the east of the Andes (Armesto *et al.* 2010). Furthermore, the valley contains guanaco *(Lama guanicoe)*, a species that coexists with huemul adjacent to that study area and also further south (Guineo *et al.* 2008). Commonly the two species were sympatric in the past; such that Prichard collected a guanaco and huemul with two consecutive shots (Prichard 1902; Hatcher 1903; Osgood 1923). In contrast to the claim regarding a barrier, a description of the nature reserve containing this valley states that a "population of huemul deer [that] occupies the valley and neighboring Huemul Reserve" (www.conservacionpatagonica.org/patagonia_huemul.htm).

To further support supposed genetic isolation, a very limited dispersal capacity of huemul was asserted (Corti *et al.* 2009). Dispersal of huemul has been determined to be 8 km during a 2-3 year study, based on one subadult female (Gill *et al.* 2008), which was used to claim that the study population cannot receive dispersers from a population 10 km away, and gene flow thus was absent (Corti *et al.* 2009). However, given low densities, very small groups and short-termed studies (Gill *et al.* 2008), this one dispersal distance might not present the norm for huemul dispersal behavior and unlikely represents a maximum. Huemul certainly disperse effectively considering their rapid postglacial occupancy of a huge region of South America (30-55°S) (Diaz and Smith-Flueck 2000). *Odocoileus virginianus* disperse 50 km on average (but may exceed 200 km, Brinkman *et al.* 2005); the small *Capreolus capreolus* disperse 120 km and 51 km on average in northern Sweden and in interior areas of Norway, respectively; and *Alces alces* disperse a minimum of 20 km and up to 150-200 km (reviewed in Hjeljord 2001).

DISCUSSION

Age at maturity of wild and captive huemul is undoubtably at one year, with good evidence that fawns may breed as well. Several well known factors affect the age at maturity, usually through food limitation, as reflected in proportionally smaller offspring and juvenile weights below the norm (reviewed in Putman and Flueck 2011). The low-density huemul population claimed to have females sexually mature at three years does not appear to be food-limited as evidenced by a several-fold increase during 3-4 decades and sizes of male skulls (n = 8, Blue Thomas, pers. communication 2006). Reports of twinning in huemul, as known for the congeneric taruca and other Odocoilines, needs confirmation. Also, huemul clearly breed every year and frequently raise fawns in successive years. For calculations of intrinsic growth rates or life tables we recommend these parameters be used. Applying unrealistic parameters may cover up underlaying processes and lead to spurious conclusions, such as underestimating reproductive potential and consequently, underestimating mortality events, or overvaluing other processes.

Mixed-sex groups during all seasons, segregation of sexes, single or multiple male and female groups are all expressed in several cervids including huemul. In one huemul population, adult sexes associated in <2% of all group sightings (Frid 1994). Similarly, populations of mature red deer, fallow deer, moose, roe deer, mule deer, or white-tailed deer also have mixed groups all year, at times up to 30% of all groups, most likely reflecting relationships between populations and their environment. Mixed-sex groups in huemul all year are neither a consistent trait nor unique among cervids, instead, variation in social group composition is common, which will assist in reinterpreting the historically much larger group sizes and densities of huemul, use of other habitat types, and potential variations in behavior and ecology (see Part 1 for past biogeography, and Part 2 regarding group size and density).

The huemul breeding system has several important implications. Although only dominance male group systems were described, equivalent to the only congeneric taruca, recently huemul bucks were characterized as strongly territorial during all seasons and life-long, defending and monopolizing female groups and siring most offspring, while non-territorial bucks rarely sired offspring (Corti *et al.* 2009). Spatial overlap was the surrogate for territoriality, but is considered inappropriate (Grant *et al.* 1992). Also, the few spatial points covering 2.5 years do not reveal spatio-temporal relationships, and for huemul it took 600% more spatial points before the estimated home range size became asymptotic (Gill *et al.* 2003). 'Life-long' territoriality was based on three bucks remaining in their area until death (2-3 years), and broken legs in a juvenile and a mature male considered evidence for territoriality, interpretations that we reject. Furthermore, elsewhere another young male was found with a broken forelimb more than 2 months before the rut (Cerda *et al.* 2011). No behaviors commonly associated with territoriality were observed, and 50% of 'territorial' bucks had their core area overlap with other 'territorial' males. The two 'territorial' bucks siring most fawns were though responsible for only a quarter of the fawns in their respective social groups, with many more fawns sired by outside males. Then, 14% of 'territorial' bucks never sired fawns, a subordinate male sired *all* fawns for two consecutive years in the area of a 'territorial' buck, and several females were bred by bucks from neighboring areas or they moved into areas of other males to be bred there before returning. Such fluid membership has been described in several other huemul populations. Additionally, when applying the more realistic age at maturity of one year (instead of 3 years), there are potentially 28 fawns unaccounted for, apart from the 23 sampled ones. Thus it is probable that less than 50% of all neonates were sampled, the remainder may have been lost unnoticed during the perinatal period. Overall, these data do not support territoriality in huemul.

Genetic isolation requires either absolute barriers, or an absence of immigration due to other factors. A valley 5 km wide claimed to result in genetic isolation has a landscape similar to areas which have been and still are used by huemul elsewhere. Limited dispersal capacity was also implied to justify this 5-km wide barriers, based on a single subadult female dispersing only 8 km. However, additional documented movements include a male which moved about 8.5 km for 3 months before returning (Gill *et al.* 2003). These two sole records unlikely represent maximal capacity of huemul which disperse effectively considering their rapid postglacial occupation of a huge region of South America (30-55°S). In comparison, mountain goats (*Oreamnos americanus*) which are true rock specialists with extremely short legs, will still travel up to 25 km during spring and summer to get to low elevation mineral licks, crossing large stretches of habitat considered completely unsuitable for mountain goats, like flat forests (Brandborg 1955; Poole *et al.* 2010). Visits of such highly specific places, and lasting <2 days are clearly a result of vertical traditions which was considered vulnerable to anthropogenic impacts (Poole

et al. 2010). This may also indicate that reduced movements in huemul may be due to past elimination of huemul which by tradition crossed areas later settled by man.

CONCLUSION
Available confirmed reproductive parameters should be used for life cycle calculations to avoid spurious conclusion. Until recently, dominance group mating systems with fluid group memberships, lacking territoriality, was described for several huemul and taruca populations. Recent claims of territoriality during all seasons, where territorial males defend and monopolize female groups and sire most offspring, is not supported by the data. The assessment of potential barriers to huemul movements needs to consider past and current habitat use. Particularly, neither open space nor gentle topography constitute an impediment. Erroneous considerations of landscape features as barriers may distract from discovering the factors underlaying the lack of recolonizations generally observed in currently reduced huemul populations.

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Figure 1. Groups of multiple huemul bucks. The scene is from the book 'Der Kampf der Andenhirsche' (with courtesy of Milada Krautmann).

Figure 2. Valley of 5 km width containing guanaco (*Lama guanicoe*), a species which coexists with huemul adjacent to this area and elsewhere.