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Natural mortality patterns in a population of southern Argentina huemul *(Hippocamelus bisulcus)*, an endangered Andean cervid

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1 Introduction

Huemul *(Hippocamelus bisulcus)* populations may have been reduced by as much as 90% since colonization of southern South America by Europeans (Redford and Eisenberg, 1992), and there may be as few as 600–700 individuals left in Argentina and approximately 1.500 in Chile (Smith-Flueck, 2000). Furthermore, as of 1992, the Argentine population was found to be fragmented into at least 63 separate small subpopulations (Serret, 1992), along approximately 1.300 km of the Andes mountains. Thorough studies on Argentine subpopulations are absent, but their distributions and sizes appear to continue to decline. It can be hypothesized that there are problems with either reproduction, mortality or both. Mortality patterns of huemul may be affected by various important factors such as nutrition, disease, and predation. Nutrition can be a limiting factor during harsh winters, particularly where the historic winter range has been disturbed, such as through logging or human settlements. The effect of diseases on population dynamics has never

Fig. 1. Male huemul *(Hippocamelus bisulcus)* Photo: authors

been studied in huemul. The most important native predator is the puma *(Puma concolor)*, but human hunting and domestic dogs may also be important. Illegal hunting and death through dogs (which accompany livestock herdsmen) still occur today. During the study period reported here alone, we became aware of two illegal trophy hunters, each taking an adult male. In both cases, the subpopulations consisted of only a few individuals, and thus the deaths of these males could be particularly devastating to the remaining subpopulation. Although there is no doubt that the impact of death through hunting and dogs will remain an important factor for several subpopulations, the impact from puma predations has been obscure. A popular belief is that puma play an important role in the decline of huemul populations, but it has never been convincingly demonstrated. Although the puma is the major predator of huemul, their coexistence for thousands of years indicates that a local huemul population driven to extinction would be an unlikely consequence of this predator-prey relationship. The surveying of one subpopulation resulted in the collection of remains and carcasses from several huemul, which allowed us to investigate for the first time the importance of nutrition, disease and predation on their population ecology.

2 Materials and methods

The surveyed area is located in the watershed of Lago La Plata in the province of Chubut, southern Argentina (44°50'S, 71°45'W) (Fig. 2). Phytogeographically, the area is situated in the subantarctic province and is characterized by mature and dense forests consisting primarily of the lenga tree *(Nothofagus pumilio)*, with the understory mainly composed of small shrubs such as *Maytenus disticha, Gaultheria mucronata, Myoschilos oblongum* and *Berberis serrata-dentata*. This type of vegetation occurs from lake level at 900 m elevation up to 1.300 m elevation and exists on mountain slopes as well as in valley bottoms.

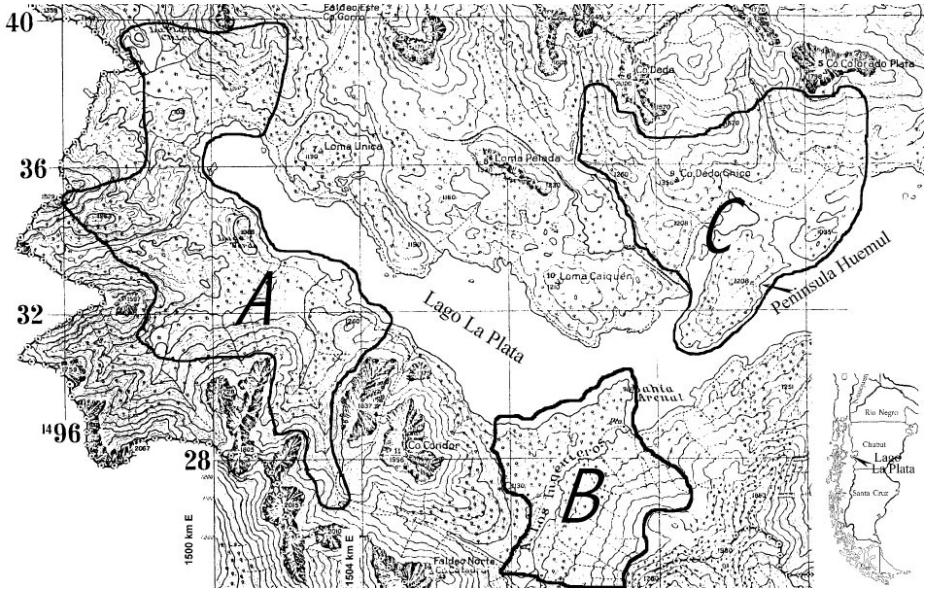

Fig. 2. Study areas: A) huemul population southwest of the lake near border to Chile, B) area which no longer contains huemul, C) huemul population northeast of the lake

The mean annual precipitation is 1.000 mm according to an isohyetal map, however there are large annual and seasonal variations among localities (DIMITRI, 1972). The mean temperature during the months of June and August varies between –4 to –2°C with mean precipitation between 300–400 mm, principally as snow.

The surveys for huemul remains were conducted between 1993 and 1999. Areas from the lake shore up to 100 m inland were searched. Upon finding signs of a dead huemul, a circular area of approximately 50 m was searched intensely and all remains were collected. All signs were registered during the surveys, including the presence of fecal pellets, tracks, and shed antlers of huemul as well as feces, tracks and other signs of puma. Between 1993 and 1996, an area north of Lago La Plata was studied three times, centering on the Peninsula Huemul. Similar studies were conducted south of the lake in 1998 and 1999 (Fig. 2). Subsequently, the collected materials were analyzed in the laboratory to confirm the species, sex, age and the cause of death.

Whenever possible, femur bone marrow fat content was determined. Marrow was removed from the central portion of intact femur bones and weighed. The sample was then dried at 45°C in a drying oven and re-weighed until the dry weight stabilized (NEILAND, 1970). The percentage of fat was expressed as dry weight divided by fresh weight. To determine the age of individuals, the cementum annuli of the first incisor, the molar ratio, and tooth wear were used (TABER, 1971; TEXERA, 1974). When no teeth were present, adults were separated from juveniles by the condition of the epiphyseal plate of long bones. Ages of some males were also determined by comparing the dimensions of the pedicels to males whose age had been determined using their teeth. Bones were also analyzed to establish a methodology to identify the sex of headless carcasses as has been accomplished for North American deer (EDWARDS et al., 1982; ADRIAN, 1992). Sex was determined when possible in all adults without skulls based on features of the pelvis (suspensitory tuberosity, shape of ischial arc, size of ventromedial border of acetabulum, thickness of pubic arc and ilio-pectineal eminence), shape of the posterior portion of the sacrum, and dimensions of the radius and metacarpal.

Predation was verified by looking for dental or claw marks left on the bones. Predation by puma or dogs, the only two large predators capable of taking a deer, was distinguished according to WADE and BOWNS (1982); they each leave distinguishable predation signs on carcasses. Finally, the total number of remains in relation to man-days spent collecting in the field was compared for the two study areas. These results were then compared to results from studies conducted on other populations to evaluate the importance of the number of dead huemul found at Lago La Plata.

3 Results

The bones or carcasses of a total of 19 different individuals were found and collected. The surveys to collect the specimens on the northern side of the lake (Peninsula Huemul) represent a total of 36 man-days (M/D), whereas the surveys to the south represent 57 M/D. Of the 19 separate remains found, 18 were found in the northern study area while only one was found in the southern study zone.

The sex was positively determined for 12 individuals. For the 11 adults, 55% were females and 45% were males. The one subadult with sex determined was a male. The sex could not be determined for any of the calves. All remains could be classified to an age group (Fig. 3). Of the 19 remains, 4 were calves, 2 were subadults and 13 were adults (≥ 2 years old). Four of the carcasses determined to be adults had too few bones to age with precision. Of the 6 collected males, only 4 had skulls and none had antlers, indicating that these males died after shedding their antlers during winter.

Fig. 3. Cause of death of huemul whose age could be determined, from Lago La Plata, province of Chubut, Argentina

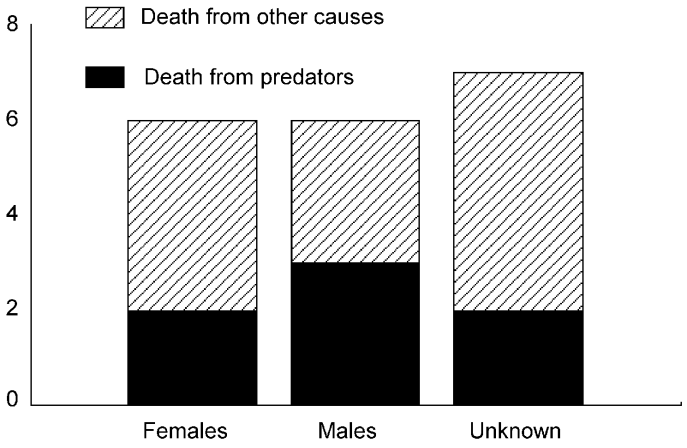

Fig. 4. Cause of death of huemul whose age could be determined, from Lago La Plata, province of Chubut, Argentina

Based on the state of the bones and the quantity of soft tissue present, it was estimated that these animals died from between a few months to a maximum of 4 years before being found. Thus, all animals found to the north of the lake died between 1989 and the end of the winter 1995. The single animal found in 1998 on the south side died 2–4 years earlier.

Of the individuals examined, 37% had clear signs of predation by puma, which caused 50% of the death among calves, 50% among subadults and 31% among adults (Fig. 3). Twenty-nine percent of adult females and 50% of adult males had signs of predation (Fig. 4). Only one individual had clearly died from a cause other than predation, which was not possible to be determined. Of the remaining 11 animals which died from unknown causes, ten had too few bones to draw conclusions. Although one male was found as a nearly complete carcass, there were no typical signs of puma predation. There were some tooth marks and perforations on the frontal and maxillary bones, but the carcass did not show other typical signs of a predator. Possibly the male was attacked by a puma and somehow escaped to the water, where he died. His body was found washed ashore by waves.

The marrow of the femur of 3 individuals was analyzed. The fat contents of the marrow of a calf 6 to 10 months old, a male of 3,5 years old and an animal of 15 to 20 months old were 91%, 88% and 98%, respectively. The calf and the male showed signs of predation.

A male 3,5 years old found north of the lake was killed by a puma; he had an acute infection in the upper maxillary bone, possibly from actinomycosis. The bone near the roots of both molars M_3 was partially destroyed. A similar problem was found in the only individual found to the south, an adult female who died of unknown causes. Instead, the M_2 of the mandible was involved, but the bone was not as severely affected as in the other case. The only other pathology observed was in an older male found during the summer of 1996. He had a deformed inner hoof on the front left leg. The presence or absence of ecto- and endoparasites could not be evaluated due to the advanced stage of decomposition of the remains. However, examination of red deer *(Cervus elaphus)* (n = 323) in similar habitat has not revealed any ectoparasites to date (FLUECK, unpubl. data).

All the huemul remains were found within a 100 m strip along the shore of the lake, below the 1000 m elevation. Twelve of the 19 (63%) specimens were found on or bordering the beach, or in the water. On several surveys conducted up to above treeline, no remains were found. In at least 3 cases with the cause of mortality unknown, illegal hunting has to be considered due to the location of the remains. Two animals, a subadult of unknown sex and a 4-year old male with most of the skeleton minus the head, were found along an old logging road. The third was a 2,5-year old male with intact skull and no signs of predation found in an old logging camp. There were a total of 7 old logging camps along a 5 km stretch of the study area on the north side of the lake. Several of these have been used by fishermen in recent years. According to the few local inhabitants, there are no feral dogs and no signs were found to indicate their presence. However, signs of puma were found on the north as well as south side of the lake, including feces and tracks as high as 1.400 m elevation. Fresh puma signs were observed next to fresh huemul tracks as well.

4 Discussion

4.1 Determination of sex and age of huemul remains

As in other New World cervids, huemul also possess dimorphic sexual characteristics. The males have a body frame larger than the females and exhibit cranial pedicels supporting the annual antler growth. Furthermore, sex can be determined by the presence or absence of the suspensitory tuberosity of the pelvic bone, features of the pelvic bone and sacrum, and the size of the large leg bones (SMITH-FLUECK, 2001).

4.2 General circumstances of the mortality cases

All remains were found below the elevation of 1.000 m and within 100 m of the lake shore. All male skulls were from animals which died during the winter, some time between the shedding of hard antlers and the new growth. Although little information exists about the timing of shedding and regrowth of antlers (SMITH-FLUECK, 2000), we assume that it would be similar to other temperate cervids which shed antlers throughout the winter and start regrowth shortly thereafter, until the beginning of spring. As all males died during the winter to early spring, we can assume that the majority (if not all) of the other animals also died during the same period. For temperate cervid populations it is common that the mortality rate is highest during the winter, when they are the most stressed and the energy deficit reaches its maximum. Only occasionally, as in populations with very high densities, can food shortage create problems during the spring/summer period and cause increased mortality rates (FLUECK and SMITH-FLUECK, 1996). However, it is unlikely that food shortage was a problem in the Lago La Plata population as was indicated by very healthy body

conditions, based on marrow fat content. Two of three healthy deer were killed by puma and thus were not selected due to poor health. In contrast, in only 3 cases was there clear evidence of health problems and 2 were killed by puma. However, it seems improbable that any of these latter individuals died directly or indirectly from the disease due to its mild nature.

4.3 Differences in mortality rates between the two study sites

The number of huemul found dead per man-days was vastly different from the northern to the southern side of Lago La Plata. When comparing these results to similar studies of other populations (SERRET, 1995; SERRET and BORGHIANI, 1998), the probability of finding a dead huemul north of the lake was 25 times higher than in the south or in Los Glaciares National Park, and 6 times higher than in Perito Moreno National Park. This concentration of dead huemul could be explained by a punctual event such as an epidemic. However, the remains from the northern area are from animals which died within a time frame from approximately 1989 to 1995, therefore, the possibility of a punctual event is excluded.

What reasons could account for these large differences between the northern and southern study areas? One possibility could be a difference in deer density. However, results based on fecal pellet density in both zones (SMITH-FLUECK, 2001) and in the other populations (SERRET, 1995; SERRET and BORGHIANI, 1998; VIDOZ, 1998) show that this is not the case. Our suggestion is that the habitat of these two study areas have different functions for the survival of huemul. For those living northeast of the lake, there are two principal winter habitats to consider: low areas near the shore line or grasslands further east at even lower elevations. It is very common among cervids living in ecotonal areas to select the lower grassland areas for winter grounds (GAFFNEY, 1941; MADSON, 1961); the same pattern has been noted for huemul in Perito Moreno National Park (SERRET and BORGHIANI, 1998). However, the huemul from the area northeast of the lake no longer have the opportunity to migrate east to reach these lower laying grassland areas, as these areas are now under intense anthropogenic use and the habitat has been changed substantially. The only alternative is to migrate down to the shoreline which consists of mature lenga forests. The huemul using the areas south of the lake are found mainly in the southwestern part. For their seasonal migration, they have easy access to several valleys which go west towards the Cisne river in Chile, dropping down to elevations of 250 m (CONAF, 1989). These valleys are so low that the lenga forest changes to the evergreen coihue forests (*Nothofagus dombeyi* and *N. nitida*), with evergreen bamboo *(Chusquea coleu)* in the understory; the presence of huemul in these valleys has been previously confirmed (CONAF, 1989). As a consequence, the area southwest of the lake would experience less use by huemul during winter, whereas huemul in the area northeast of the lake remain there during the entire winter, which is normally the period of highest mortality among cervids.

In contrast, during the summer, use of the area southwest of the lake was intense (44% of feces found were fresh), whereas only 1% of feces were fresh on the north side near the lake, indicating that the resident population on the north side was very reduced and the majority migrated to higher elevations. This difference is probably due to the fact that the northeast portion of the lake has easy access (due to a dirt road) and thus receives higher human activity at lower elevations (e.g. campers, fishermen, tourists) during the summer season. Thus, the influence of human activity may explain the difference in the quantity of huemul remains found between the two areas, particularly with respect to available winter range.

4.4 The impact of puma

The puma population of this region has a direct relationship with the huemul population. However, this relationship is not necessarily negative with respect to the viability of the huemul population. The puma and huemul have coexisted for many millennia, implying a stable predator-prey relationship. One can assume that huemul always lived at low densities in the pristine forests of mature lenga due to the dispersed sources of concentrated food. Furthermore, it has never been shown that a puma population caused the extinction of a huemul population. At least in these virgin forests, it is doubtful that they could extirpate the last huemul, as protective cover is plentiful, which makes discovery and attacking of this prey more difficult and more so if considering the generally small size of the huemul groups. Also, it is clear from many studies of puma and North American deer that they have coexisted over long periods.

It is to no surprise that puma feed on huemul. In most of its distribution in North America the puma feeds primarily on cervids (CONNOLLY, 1978), with ungulates constituting up to 70% of its diet (IRIARTE et al., 1990). RAU et al. (1995) found that pudu *(Pudu pudu)* and guanaco *(Llama guanoceo)* comprised 15% of the puma diet in Chile. All puma scats found in a study by Cerro Ventisquero, province of Rio Negro (Argentina), contained huemul hair (SMITH-FLUECK and FLUECK, 1997). Remains of huemul with signs of puma predation were also found in the National Parks of Nahuel Huapi, Perito Moreno and Los Glaciares (SERRET, 1995; ADMINISTRACIÓN DE PARQUES NACIONALES ARGENTINA, unpubl. data).

The predation cases found in the present study occurred over a period of six years and were likely not an unusual phenomenon, particularly as the population appeared to be in good condition and at higher density than in most other studied populations. A certain amount of predation is to be expected and puma may regulate huemul (SMITH-FLUECK, 2001). Under pristine situations, large predators have not been known to exterminate ungulate species; only human hunting or modification of habitat have resulted in such situations (CONNOLLY, 1978). Severe winters, though, may amplify mortality rates through predation and may have accounted for these observations, as the winters between 1989 and 1992 were harsh.

The impact of large predators, such as the puma, on their prey depends on various factors. On one side, the attack success rate is generally very low; the rates for wolves *(Canis lupus)* and lynx *(Lynx lynx)* are 20% and 5%, respectively (TESTA et al., 2000). This allows for a great opportunity for adaptation by the prey species. Moreover, large predators can only regulate the deer population if they regulate themselves intrinsically and if there are alternative prey species (ERLINGE et al., 1984). A variety of social mechanisms exist which prevent these predators from reaching densities where they could eliminate the prey species. This includes dispersion (MECH, 1987), the intra- and interspecific killing of predators (HORNOCKER, 1970; SLOUGH and MOWAT, 1996; SPREADBURY et al., 1996; KUNKEL et al., 1999), territoriality and reduced reproduction. The social system of territoriality separates large predators (as individuals or social groups) either in time or in space (GORMAN and TROWBRIDGE, 1989; SANDELL, 1989). This has been shown to be the case for puma (SEIDENSTICKER et al., 1973; HORNOCKER and BAILEY, 1986; SPREADBURY et al., 1996). The emigration of subadults also plays a major role (WASER, 1996). There is intense fighting when a new individual intends to overtake a home range which is already occupied (BELTRAN et al., 1992). As the food sources diminish, several types of aggressive behavior start to increase. Interspecific killing among puma has been documented on numerous occassions, including the killing within family units (LINDZEY et al., 1988; ANDERSON et al., 1992). These diverse mechanisms are in place so that there is an intrinsic upper limit to puma density. Even an increase in the food supply will not result in a further increase in puma above that intrinsic limit. In general, puma densities are low and home ranges very large (FLUECK, 2000).

Another mechanism affecting the predation pressure on a particular prey species is *prey switching* (ADAMS et al., 1995; BALLARD et al., 1997). For instance, as the density of the major prey species diminishes, the predator may adjust by changing its diet rather than increasing its effort on the declining species. Generally, within the scale of their distribution, predators of large herbivores are not limited by food to the point where they compromise the survival of their prey species. For example, in the Granite Mountains, USA, puma predation reduced mountain sheep *(Ovis canadensis)* populations to low densities and kept them there for 3 years. Then, predation pressure dropped to where the sheep populations increased by 15% annually during the remaining 3 years of the study (WEHAUSEN, 1996). What we do know about the interplay between predator-prey is that the complex system of predators and prey of large body size has existed for approximately the last 12 million years (VAN VALKENBURGH, 1995).

The huemul found dead in this study died principally as a result of puma predation. The relative density of huemul on the north side of Lago La Plata indicates the presence of an important population, with puma a likely natural factor affecting the population dynamics.

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Summary

The huemul *(Hippocamelus bisulcus)*, an endangered deer living in the Andes of southern South America, numbers 600–700 in Argentina, from at least 63 fragmented subpopulations. Very limited information exists on most populations, but there are indications that the distribution and population sizes continue to diminish, possibly through reduced reproductive rates, elevated mortality rates or both. This is the first analysis of the population ecology of a subpopulation in Argentina, made possible through the only existing compilation of numerous remains of dead huemul (n = 19). Surveys were conducted between 1993 and 1999 to locate and collect remains, which were found concentrated at lower elevations. The sex ratio of adults and subadults (n = 12) was 1:1, but could not be determined for fawns. Clear signs of predation was found in 37% of all deer: 50% among calves, 50% among subadults and 31% among adults. These signs occurred in 29% of adult females and 50% of adult males. Deaths occurred during winter as judged by the state of the male skulls, which indicated the phase of the antler cycle. Femur fat content of 3 deer averaged 93%. Predation signs frequently were clearly from puma *(Puma concolor)*, which is the only natural predator of huemul. The high predation rate, high marrow fat content and no indications of deaths resulting from disease corroborate the pristine state of the of mature lenga *(Nothofagus pumilio)* forest. The area with a concentration of huemul carcasses appears to be the huemul's major winter habitat.

Key words: huemul; *Hippocamelus bisulcus*; *Puma concolor*; population dynamics; mortality pattern; habitat

Zusammenfassung

Natürliche Mortalitätsmuster in einer Population des südargentinischen Huemul (Hippocamelus bisulcus), einer gefährdeten Cervidenart der Anden

In Argentinien leben noch 600 bis 700, auf mindestens 63 fragmentierte Subpopulationen verteilte Individuen des Huemul, einer gefährdeten Hirschart der Anden des südlichen Südamerika. Über die

meisten dieser Bestände ist nur sehr wenig bekannt. Es gibt jedoch Hinweise darauf, dass sowohl die Verbreitung als auch die Größe der Bestände rückläufig sind, vermutlich infolge abnehmender Reproduktionsraten und/oder erhöhter Mortalität. Basierend auf der Zusammenstellung von Totfunden (n = 19, Konzentration in unteren Höhenstufen) des Zeitraums 1993 bis 1999, wird hier erstmals eine Untersuchung zur Populationsökologie einer argentinischen Subpopulation des Huemul vorgelegt. Das Geschlechterverhältnis bei adulten und subadulten Individuen betrug 1:1, für Kälber konnte es nicht bestimmt werden. Deutliche Hinweise auf Prädation als Todesursache fanden sich bei 37% aller Individuen (Kälber 50%, Subadulte 50%, Adulte 31%). 29% der adulten Weibchen und 50% der adulten Männchen wiesen Anzeichen eines Todes infolge Prädation auf. Bei den Männchen konnte anhand des Schädelbefundes (Phase des Geweihzyklus) auf einen Tod während des Winters geschlossen werden. Der Fettgehalt des Knochenmarks im Oberschenkelknochen dreier Individuen betrug im Mittel 93%. Die an den Kadavern gefundenen Prädationszeichen konnten vielfach dem Puma *(Puma concolor)* zugeordnet werden, dem einzigen natürlichen Feind des Huemul. Die hohe Prädationsrate, der hohe Fettgehalt des Knochenmarks und das Fehlen von Anzeichen für Krankheiten als Todesursache belegen den ursprünglichen Zustand des Lenga *(Nothofagus pumilio)* Waldes. Das Gebiet mit der Konzentration der Huemul-Kadaver scheint das Haupt-Winterhabitat des Bestandes zu sein.

Schlüsselwörter: Huemul *(Hippocamelus bisulcus)*, Puma *(Puma concolor)*, Populationsdynamik, Mortalitätsmuster, Habitat

Résumé

Phénomènes de mortalité naturelle dans une population d'Huémul d'Argentine du Sud (Hippocamelus bisulcus), un cervidé des Andes menacé

L'Huémul *(Hippocamelus bisulcus)*, une espèce de Cerf menacée vivant dans les Andes de l'Amérique du Sud, présente un niveau de population de quelque 600 à 700 têtes en Argentine, constituée d'au moins 63 sous-populations fragmentées. On dispose de très peu d'informations à propos de la plupart de ces sous-populations mais il est des indications comme quoi leur distribution et leur taille continuent à diminuer, sans doute en raison d'un taux de reproduction réduit, d'un taux de mortalité élevé ou des deux à la fois. Ceci constitue la première analyse démécologique d'une sous-population argentine, rendue possible par la seule compilation existante de restes de huémuls retrouvés morts (n = 19). Des recherches ont été menées entre 1993 et 1999 pour localiser et collecter des restes, retrouvés pour la plupart en des endroits situés à faible altitude. La sex-ratio des adultes et sub-adultes (n = 12) se situe à 1:1, mais n'a pu être déterminée pour les faons. Des traces évidentes de prédation ont été trouvées dans 37 % des cas : 50 % parmi les faons, 50 % parmi les sub-adultes et 31 % parmi les adultes. Ces traces concernaient 29 % de femelles adultes et 50 % de mâles adultes. Les mortalités intervinrent au cours de l'hiver, comme il ressort de l'état des crânes des mâles, lesquels indiquaient la phase en cours du cycle des bois. La teneur en matières grasses du fémur de 3 sujets était de 93 % en moyenne. Souvent, les traces de prédation pouvaient clairement être attribuées au Puma (Puma concolor), seul prédateur naturel de l'Huemul. Le taux de prédation élevé, la teneur élevée en graisse au niveau de la moëlle et l'absence d'indications de mortalités résultant de maladies corroborent le pristine état de la forêt de Lenga (Nothofagus pumilio) parvenue au stade de pleine maturité. L'espace où se concentrent les carcasses de l'Huemul apparaît constituer l'habitat majeur de l'espèce au cours de l'hiver.

Trad.: S. A. DE CROMBRUGGHE

Mots clefs: Huémul *(Hippocamelus bisulcus)*, Puma *(Puma concolor)*, dynamique de population, taux de mortalité, habitat

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