

Fascinating Life Sciences

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Deer of the World

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Huemul *Hippocamelus bisulcus* (G. I. Molina, 1782)

34

Jo-Anne M. Smith-Flueck, Robin Gill, and Werner T. Flueck

Abstract

This comprehensive chapter covers various aspects of the biology and natural history of the huemul (*Hippocamelus bisulcus*), including names, taxonomy, subspecies and distribution, descriptive notes, habitat, movements and home range, activity patterns, feeding ecology, reproduction and growth, behavior, disease and status in the wild and in captivity. The chapter includes a distribution map, several photos of the species, and a list of key literature.

Common Names

English: Patagonian huemul, Chilean huemul, huemul deer, south Andean deer, guamul, guemal, Chilean guemal; **Spanish:** huemul patagónico, ciervo patagónico, venado patagónico, ciervo andino del sur, huemul chileno; **French:** cerf des Andes du sud, huemul des Andes meridionales; **German:** Andenhirsch, Südandenhirsch; **Indigenous people:** shoonem, shoan, huamul, güemul, yekchal, schenam.

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Taxonomy

Huemul are in the order Artiodactyla, family Cervidae, and subfamily Odocoileinae. The genus *Hippocamelus* contains two extant species, *Hippocamelus bisulcus* (huemul) and *Hippocamelus antisensis* (taruka).

The pre-Columbian distribution of huemul has its roots in founding stock, likely of the *Odocoileus* line (Morejohn & Dailey, 2004), which dispersed through the Panama land bridge during the Great American Interchange. Paleozoological and biogeographical evaluations indicate that extant *Hippocamelus* spp. became established in the mid to late Pleistocene, likely dispersing south on the eastern side of the Andes through continuous savanna habitat as several periods of glaciation would have kept them away from the Andes (reviewed in Flueck & Smith-Flueck, 2012a). Pleistocene fossils of an Odocoileini, *Hippocamelus sulcatus*, considered by paleontologists to be an extinct chronospecies of the two extant *Hippocamelus* species, have been excavated from the plains of Uruguay, Argentina, and southern Brazil (Eisenberg, 2000; Barrio, 2013; Chimento et al., 2019; Alcarez & Francia, 2013). This time period coincides with glaciers covering the Andes, which would account for the lack of fossils in higher elevations. The relationship of *H. sulcatus* to the fossil deer *Odocoileus lucasi* remains to be resolved, although it is speculated that the former is a descendant of the latter; some consider *Odocoileus lucasi* to be the ancestor of *Hippocamelus bisulcus* (Heckeberg, 2020). Importantly, *Navahoceros* was long considered the probable ancestor of *Hippocamelus* spp. until Morejohn and Dailey (2004) determined it to be a “nomen nudum,” confirming instead that the fossil specimens were those of the misidentified *Odocoileus lucasi*. Thus, *Navahoceros* never existed.

Recent mammalian habitats in the Andes and foothills were only established since the last major glaciation about 11–13,000 years ago, and were occupied by fauna coming from the Patagonian region east of the Andes, which, not having been glaciated, served as a refuge for many species.

Frailley et al. (1980) identified and dated an antler of *Hippocamelus* sp. (maybe ancestor to *H. antesensis*), in southern Bolivia (Tarija Basin, 22°S) to middle Pleistocene, though the excavation site's age was later recalculated to be late Pleistocene (Coltorti et al., 2007). *H. bisulcus* is known from archeological sites in Argentina (Díaz, 2000) and in Chile from late Pleistocene and early Holocene, between 30 and 34°S [0.5 km from Pacific coast] (Moreno et al., 1994; Frassinetti & Alberdi, 2001; Canto et al., 2010). Evidence suggests that *Antifer* sp. and *H. bisulcus* immigrated to central Chile from Argentina at 38°S after the last glaciation event, an area characterized by significant lowering of the Andean Cordillera and westward penetration of the Patagonian steppe toward the Alto Biobio river area (Moreno et al., 1994). More recently, huemul are represented in pictographs at Cueva de las Manos and near Rio Pinturas in southern Argentina, dated to ca.4600–2300 BP and 8000 BP, respectively (Díaz, 2000).

As for phylogenetics, results from Heckeberg's (2020) study agree with earlier studies that show polyphylies for three Odocoileine genera *Hippocamelus*, *Mazama*, and *Pudu* and for both species of *Odocoileus*. The taxonomy and evolutionary history of Odocoileini remains enigmatic, partly because of the scarce Plio- and Pleistocene fossil record, and because more morphological and molecular markers, particularly nuclear and cytogenetic data are needed (Heckeberg, 2020; for more details on *Hippocamelus* see also Chap. 1).

Distribution

Present

Huemul are endemic to the Southern Cone of South America, with past and present distributions only in Argentina and Chile. There are no recognized subspecies. The huemul currently only inhabits the Andes of Southern Chile and Argentina (Fig. 34.1). The 100 or more subpopulations likely occupy much less than 500 km² (Jiménez et al., 2008). Currently, the most northern and southern subpopulations are in Chile at 36°40'S and 53°50'S, respectively (Vila et al., 2006). The nearest group to the northernmost subpopulation is about 425 km further south, which at 40°30'S is Argentina's most northern current subpopulation (Jiménez et al., 2008). The southernmost subpopulation in Argentina today is 50°73'S (Vila et al., 2006). In both countries, subpopulations are highly fragmented with 60% of them containing as few as 10–20 individuals (Jiménez et al., 2008). Lower elevations on both sides of the Andes and most valley bottoms no longer contain huemul. The present distribution is significantly reduced from that of the past (Fig. 34.1) (Díaz, 1993, 2000; Zuliani et al., 2023) and the population continues to decline.

The degree of isolation of subpopulations and its effects remains unclear.

Past

The distribution of huemul during the Holocene was at least from latitude 30°S to 55°S in Argentina (Fig. 34.1), a linear distribution of nearly 2800 km. Historical reports and fossil records provide evidence that huemul not only occupied the Patagonian ecotone between the forest and steppe (Vila et al., 2010), but also inhabited the Patagonian steppe reaching to the Atlantic coast (Flueck et al., 2022, 2023). Presence of huemul on Tierra del Fuego (Fireland) also has been verified (Díaz, 2000; Flueck & Smith-Flueck, 2012a). The post-Columbian period resulted in large changes through the introduction of feral livestock and horses, the latter increasing the mobility of indigenous people. The general displacement of huemul from the eastern portion of their historical distributional range is reviewed in Flueck and Smith-Flueck (2011b, 2012a) and HTF (2012).

Descriptive Notes

The huemul, a telemetacarpalian deer of medium size (Fig. 34.2), is similar to the taruca in build and cranium, but stands slightly taller and lacks the distinguishing white throat patch of the taruca. Only a few morphological measurements are available from live individuals or skeletons of huemul. Sexual dimorphism is pronounced, and differentiating between sexes and ages is feasible. Due to similarity in general appearance between individual adults, particularly the females, with no significant variation in natural markings, studies requiring individual identification benefit by marking (Garay et al., 2016a), although sometimes individuals have been distinguished by their body color patterns, facial markings, antler configurations, scars (Povilitis, 1983, 1985; Corti et al., 2010), and, questionably, tail and rump patches of females (Frid, 1999).

Body measurements [Smith-Flueck, 2000, (Gill unpublished data); all measurements are for adults]:

Head and body length: males 140–175 (141–180 $n = 6$) cm; females 140–157 (149–169 $n = 2$) cm.

Shoulder: males 79–100 cm; females 78–97 cm.

Chest girth: males 97–114 (96–111 $n = 7$); one female 114 (91–108 $n = 5$) cm.

Hind foot length: males 40–47 cm; females 36–43 cm.

Ear length: males 15–20 (20–27 $n = 3$) cm; females 16–18 (23 $n = 1$) cm. They resemble the mule deer, *Odocoileus hemionus*, with their long ears.

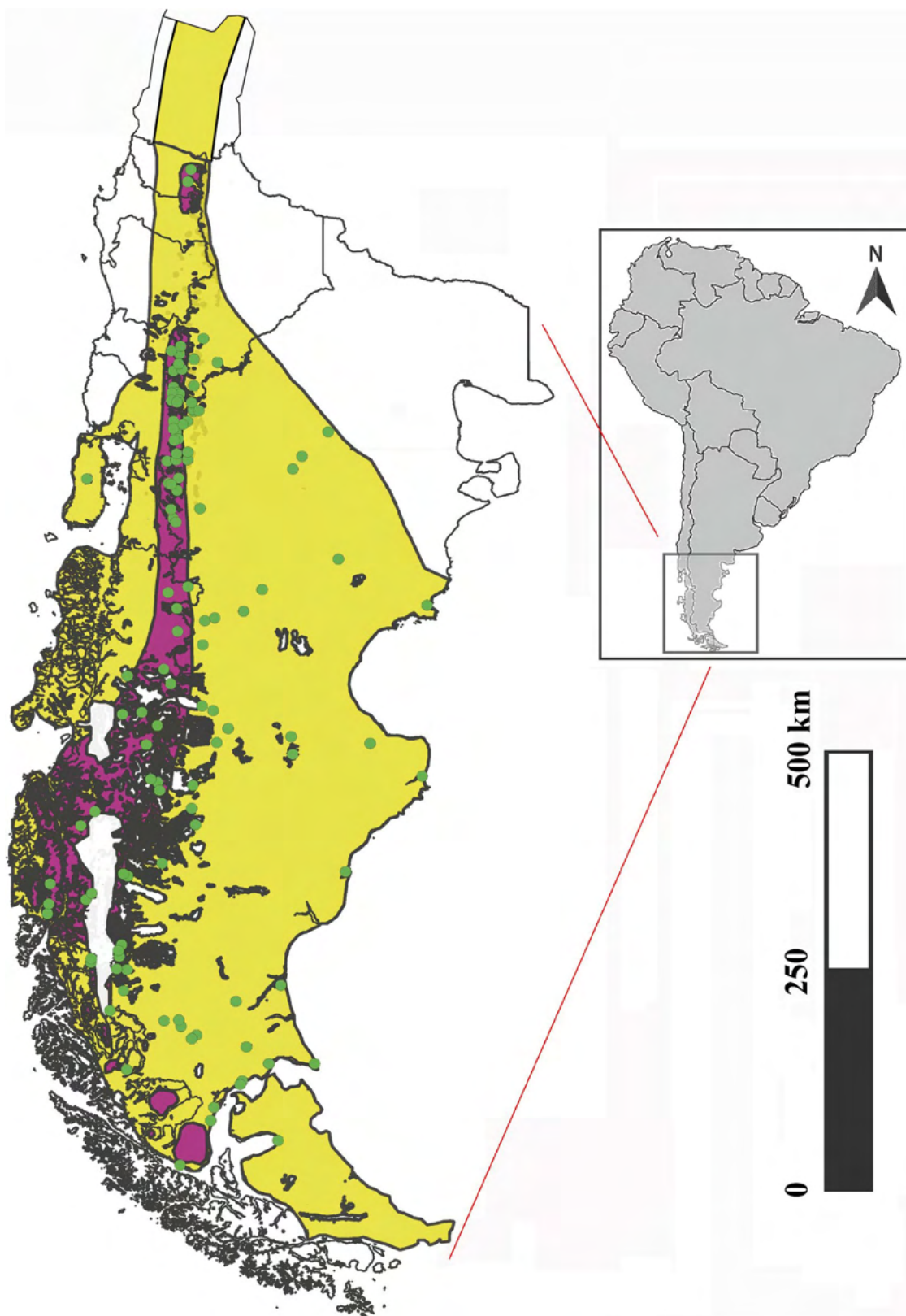


Fig. 34.1 Historical distribution (yellow: Flueck et al., 2022); current distribution (purple: Jimenez et al. 2008), unsuitable areas (internal white zones indicating bare ice fields, rocky slopes without vegetation,

or lakes), and historical locations (green dots), based on reports by naturalists, shed antlers, and archaeological samples (Figure taken from Flueck et al., 2022)

Fig. 34.2 Characteristic features of male and female adult huemul (photos by Smith-Flueck and Flueck)



Tail length: males 12–16 cm; females 11–16 cm.

Body mass: Estimates for unidentified adults fall between 70 and 100 kg (Whitehead, 1993; Drouilly, 1983). One adult male was 90.7 kg (Osgood, 1943). Recent weight recordings, however, suggest lower averages: In situ captured males and females in Chile weighed 55–76 kg ($n = 3$) and 70–72 kg ($n = 2$), respectively (R Gill unpublished data), and from the same population both sexes averaged 69 kg ($n = 9$; Bustos et al., 2003): males and females weighed 69.5 kg ($n = 6$) and 67.3 kg ($n = 3$), respectively. At Huilo Huilo Reserve, adult males and females weighed between 83 and 89 and 73 and 78 kg, respectively (Vidal unpublished data). In Argentina, one captured male weighed 79 kg; he died 9 months later at the end of autumn of malnutrition (Smith and Flueck unpublished data).

Dental formula: I 0/3, C 0/1, P 3/3, M 3/3; 32 teeth total (Smith-Flueck, 2000). Timing of milk and permanent teeth eruption varies considerably among cervids (Smith-Flueck, 2000) with huemul newborns having all milk teeth already showing at birth (Texera, 1974).

Coat: The coat, a solid color, molts from yellow, reddish-brown in summer to grayish-brown in winter, with a white strip along the lower lip, another small white patch on the hind quarters under the tail, and white to light gray hair inside rather large ears similar in size to the mule deer (Fig. 39.2); hairs are undulated and length ranges from 5 to 7 cm and 3 to 4 cm in winter and summer, respectively, although length occurs up to 19 cm (Flueck unpublished data). Huemul rely on their fur to thermoregulate in the harsh Patagonian climatic conditions with the winter coat providing complete insulation down to a critical temperature of -50°C (Texera, 1974). Only adult huemul males have a dark-brown Y-shaped design extending along the muzzle to slightly above the eyes (Fig. 34.2). In some males, this chevron pattern is much darker and more striking. Fawns are born with unspotted thick wooly coats of a coffee-brown color in

various tonal gradients over the body (Texera, 1974), likely serving as camouflage protection, and perhaps having evolved while inhabiting the more open steppe environment during the Pleistocene. Taruca, with a similar evolutionary origin, also have spotless fawns. Hoof growth in young huemul fawns, measured from the hairline along the abaxial ridge to the growth line, can be used as an aging tool (Flueck & Smith-Flueck, 2005).

Antlers: Only males grow antlers, which start their growth shortly after shedding the prior ones that are cast from June to early September (Smith-Flueck, 2000; Guineo et al., 2008) (Fig. 34.3). Juveniles at 6 months already have their antler knobs of about 1–2 cm in length (Smith-Flueck, 2000; Fig. 34.3); and at one and a half years of age their first set of antlers of one point will reach 6–8 cm in length (Garay et al., 2016a); a yearling male in captivity developed two points (Smith-Flueck unpublished data). Antlers vary from a simple fork to a 5-pointed beam. Antlers with three tines are not uncommon in some localities, representing 43% of samples measured from Chile and Argentina ($n = 47$, Flueck and Smith-Flueck unpublished data). Larger 4-point antlers were more common in the past (Supplementary Fig. 34.1, Flueck & Smith-Flueck, 2011b, 2012b). If antler expression in huemul is homologous to other cervids, then those extant populations with smaller antlers, like those at the coastal periglacial sites (Guineo et al., 2008), are likely subjected to nutritional deficiencies (Vidal, 2010; Flueck & Smith-Flueck, 2011b, 2012b). Maximum antler length: 34.3 cm (Whitehead, 1993).

Lifespan is unknown. At Tomango NR, Chile, one radio-collared male reached at least 14 years of age (Velásquez, pers. comm.). One female, ear-marked as a fawn (Garay et al., 2016a), was last seen when she was 16 years of age in 2019 (F. Barrientos, pers. observation.), shortly before the Sars-CoV2 pandemic began. The park was then closed to everyone, not permitting the park ranger Barrientos to continue his monitoring.

Appendicular bones: Lengths and articular width of appendicular bones are shown in Table 34.1. Huemul are

Fig. 34.3 Antler development: (a) Juveniles at approximately 6 months of age with antler knobs (photos by J. Smith-Flueck); (b) young adult male with one antler recently cast as fresh blood at site where burr was attached, observed 22 July 2020 (courtesy of M. Escobar)

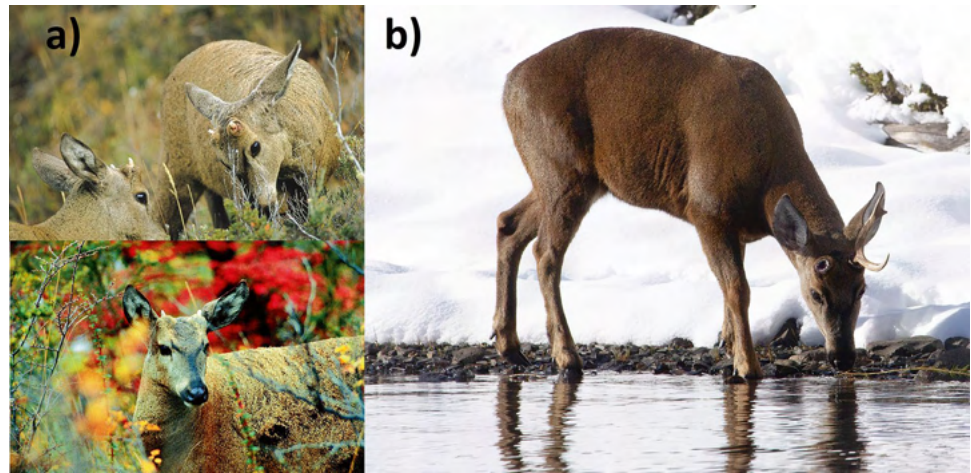


Table 34.1 Length and articular width (mm) of appendicular bones from adult male and female huemul (Flueck & Smith-Flueck, 2011a)

| | Males | | | | | | | Females | | | | | | |
|------------|-------|--------|-----|--------|-----|----------|-----|---------|--------|----|--------|------|----------|------|
| | n | Length | SD | Distal | SD | Proximal | SD | n | Length | SD | Distal | SD | Proximal | SD |
| Humerus | 7 | 237 | 69 | 47.2 | 1.6 | 65 | 3.1 | 2 | 217 | | 43 | | 50.8 | 1.06 |
| Radius | 10 | 214 | 53 | 40 | 1.5 | 41 | 0.9 | 4 | 205 | 47 | 40 | | 37 | |
| Metacarpus | 12 | 172 | 43 | 37 | 0.5 | 35 | 0.7 | 4 | 163 | 40 | 32.5 | | 31 | |
| Femur | 11 | 276 | 54 | 71.5 | 1.5 | 65 | 2.3 | 4 | 257 | 81 | 53.4 | 1.43 | 58.5 | 0.71 |
| Tibia | 16 | 315 | 103 | 43.3 | 1.2 | 64 | 1.9 | 8 | 294 | 86 | 40.7 | 1.49 | 62 | 1.83 |
| Metatarsus | 13 | 201 | 71 | 37 | 0.7 | 33 | 1.2 | 5 | 192 | 21 | 35.5 | 1.05 | 31.1 | 1.46 |

often described as mountain deer, with a supposedly stocky build and short legs (Geist, 1998; Vila et al., 2010). This appearance, however, is influenced by the thick coat and a particular stance that individuals often assume in the presence of a threat, whereby the hooves of front and back legs are shifted close to each other to form a triangle with the abdomen, resulting in a hunched “horseshoe” posture (Fig. 34.4) (Flueck & Smith-Flueck, 2011a). Although short legs have been explained as an adaptation to rugged mountainous terrain for ungulates such as mountain goats (*Oreamnos americanus*), this explanation was recently invalidated for the huemul, and instead, huemul leg morphology was shown to fall well within the range of other cervids (Flueck & Smith-Flueck, 2011a).

Glands: *H. bisulcus* possesses tarsal, metatarsal, hind foot and forefoot interdigital (pedal) glands, and a pre-orbital gland located inside a relatively large lacrimal pit when compared to other *Odocoileus*. From museum huemul specimens, Hershkovitz (1958) found the glandular area of the metatarsals to sometimes be defined and the hair tuft to sometimes be developed, although this tuft alone did not necessarily signify existence of a functioning metatarsal gland; he found glands situated on lower half of huemul’s metatarsus, whereas, in taruca, glands were situated on the upper half. For the interdigital glands of the forefeet, the sacculles are minute for *Hippocamelus* spp., distinguishing them

from all other Neotropical deer. In *Odocoileus*, *Mazama*, and *Pudu*, the sacculles are well developed, whereas in the other genera (*Blastocerus* and *Ozotoceros*) they are absent altogether (Hershkovitz, 1958; Geist, 1998).

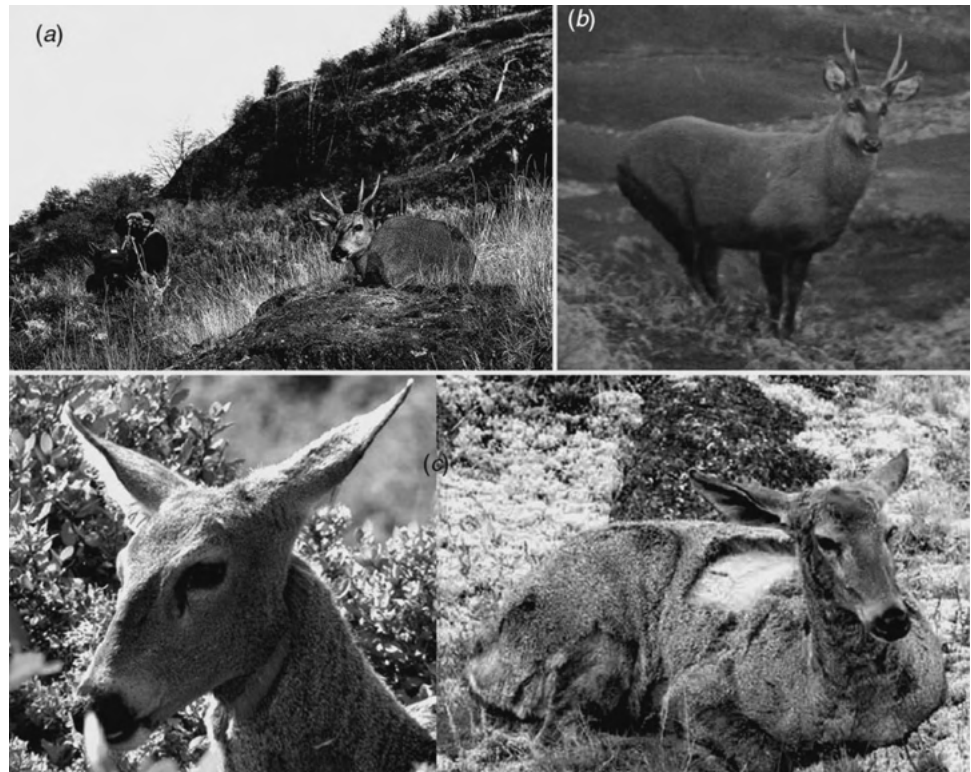
Habitat

Huemul occur today mainly in remote areas of the southern Andes mountains, from close to sea level up to 3000 m elevation. Their current latitudinal distribution falls predominantly within the *Nothofagus pumilio* lenga forest distribution, where they occur mainly within and at the edge of the forest (Jimenez et al., 2008). They are found in a variety of habitats: from coastal fjords and valley flats to steep mountain slopes above tree line and from open steppe grasslands to closed shrubby or forested habitats.

The Andean slopes, where they predominantly occur today, are often referred to as suitable habitat. Yet, being remnant populations, their current range may not be indicative of what constitutes prime habitat, which must be considered when identifying conservation priorities, for instance when modeling species distributions (Loiselle et al., 2003).

Habitat selection for each region will differ, depending on the availability of habitat types and the degree and type of

Fig. 34.4 (a) Huemul unaccustomed to humans frequently have very short flight distances (photo by J. Smith-Flueck); (b) The aggressive stance of huemul at close range, known as the horseshoe posture; and (c) The 7–9-cm-thick hair coat is best appreciated when being shed (courtesy of G. Garay). Note in the left photo that the diameter of the upper neck is substantially less than further down in the unshed portion



disturbances throughout the habitat, with huemul displaying high plasticity (Smith-Flueck, 2000; Vila et al., 2010). While the highly disturbed subpopulations of central Chile primarily inhabit steep north-facing slopes of 30–40° with rough terrain (Povilitis, 1998), huemul facing minimal human interactions are more frequently below tree line on gentler slopes. Huemul at Argentina's Shoonem Protected Park (PP), for instance, frequently uses the lake shore and adjacent lenga forest with slopes <25° (Smith-Flueck, 2003). When human disturbance was low at coastal periglacial sites, huemul concentrated in open valley bottoms (Frid, 1994, 2001; Van Winden, 2006), using the grasslands 49% of the time; males were exclusively there (Frid, 1994). After cattle were introduced at this study site, habitat use shifted to the old-growth forest (Frid, 2001). Habitat selection at three southern Chilean sites revealed a preference for lenga forest and rocky cliffs, and avoidance of grassland and steppe (Saucedo & Gill, 2004). Over a ten-year study, Guineo et al. (2008) observed huemul predominantly using the open grassland habitat, but after tourism and cattle activity increased in the area (approximately the past 5 years), they moved up to steeper forested slopes (Garay and Barrientos pers. comm.)

Movements and Home Range

Studies of marked and known individuals indicate that huemul have a relatively stable home range, with both sexes having ranges of a similar size. Although information on

movements is still somewhat limited, it is clear that huemul show considerable flexibility in movement behavior. There is significant variation in range size between populations, seasonal shifts in elevation, and variation in intensity of use of the different parts of the home range.

For undisturbed animals, reported average home range sizes vary from 159 ha in Chubut (Flueck et al., 2022) to 309 ha in Torres del Paine, (Garay et al., 2016b) and 444 ha in Aysen (Gill et al., 2008). Most activities, however, focus on a relatively small portion of the home range. In Aysen, mean range size calculated for a core area, including 50% of observations, was just 13.5% (57 ha) of the area that included 95% of observations (Gill et al., 2008). The mean distance moved in 24 h was 706 m, suggesting that normal daily movements focused in or around a core area. Disturbance can however force huemul to undertake substantial temporary movements, for example movement of up to 4 km to apparently avoid tourist activities and approximately 8 km to temporarily avoid logging operations have been observed (Drouilly, 1983; Gill et al., 2008; Smith Flueck et al., 2018a).

Before reaching maturity, sub-adult huemul are known to move away from their natal home range to settle permanently in a new area. Fawn marking studies in Torres del Paine have so far indicated that this movement is quite short and not even undertaken at all by some individuals: of 16 tagged fawns, four were known to be dispersed up to 3 km and three remained near their natal area. The distance moved and fate of the remaining nine animals were unknown (Garay et al., 2016a). In Aysen, one sub-adult female was observed to

move approximately 8 km before permanently settling in a new area (AN8370 Gill et al., 2008).

In some areas, huemul have been found to undertake a short seasonal shift in home range, moving between higher elevations in summer and lower elevations in winter. However, these movements are only evident at sites where huemul were using higher elevations and are relatively limited in extent, with average distances between summer and winter ranges of only 500 m and just 200 m in elevation (Gill et al., 2008), respectively.

Past anthropogenic activity, mainly in the shape of over-hunting, effectively excluded huemul from extensive areas of low-elevation terrain. Historical accounts reveal that huemul once undertook long-distance seasonal migrations, similar to other deer species in mountainous regions. They exist today as a refugee species, stuck year-round in their summer range, having lost the learned tradition—passed down from mother to young—to migrate to lower elevations to avoid adverse winter conditions (Flueck et al., 2022, 2023; see Video 34.1, I in Supplement). Huemul is the only cervid known to use mountain summer ranges year-round in reaction to anthropogenic activities.

Activity Patterns

From a study on activity patterns during daylight hours (Guineo et al., 2008), it appears huemul are crepuscular, with inactivity (resting and ruminating) between active feeding bouts. Comparison of the four seasons shows there to be three active feeding bouts during the day from late winter (August) to end of summer. By fall this reduced to two and then further reduced to only one long daylight-feeding session in winter. Time spent feeding during the day changed from 70% to slightly under 50% for the winter and summer, respectively. Males spent more time resting than females, though females rested more in spring. When a group moved from one place to another, a female would lead the group, often making slow progress with frequent stops, attentive to her surroundings. Sometimes the lead doe might stand for 2 h in one spot without moving, not even her head, while the male was feeding or bedded.

Feeding Ecology

The huemul is a mixed feeder and an intermediate concentrate selector. Several diet studies from various habitat types along the species' distributional range have been published using either histological analysis of fecal pellets or direct feeding observations (reviewed in Smith-Flueck, 2000, 2003; Vila et al., 2010). When we compare the available histological diet studies ($n = 9$), the huemul mainly consumed

browse and forbs, and in six of these studies, browse (i.e., ligneous) species made up > 50% of the diet. Forbs surpassed browse species only at the Chillan study site (central Chile) and Los Glaciares NP (see supplementary Table 34.1). Grass was always the least consumed, though at most it comprised 16% of the total diet at Tamango NR (Flueck & Smith-Flueck, 2012a). In comparison, the closely related taruka have had grass comprise as much as 57% of their diet (Gazzolo, 2006). Moreover, the diet of huemul could not be differentiated from steppe guanaco on the basis of ^{13}C collagen values (Barberena et al., 2011).

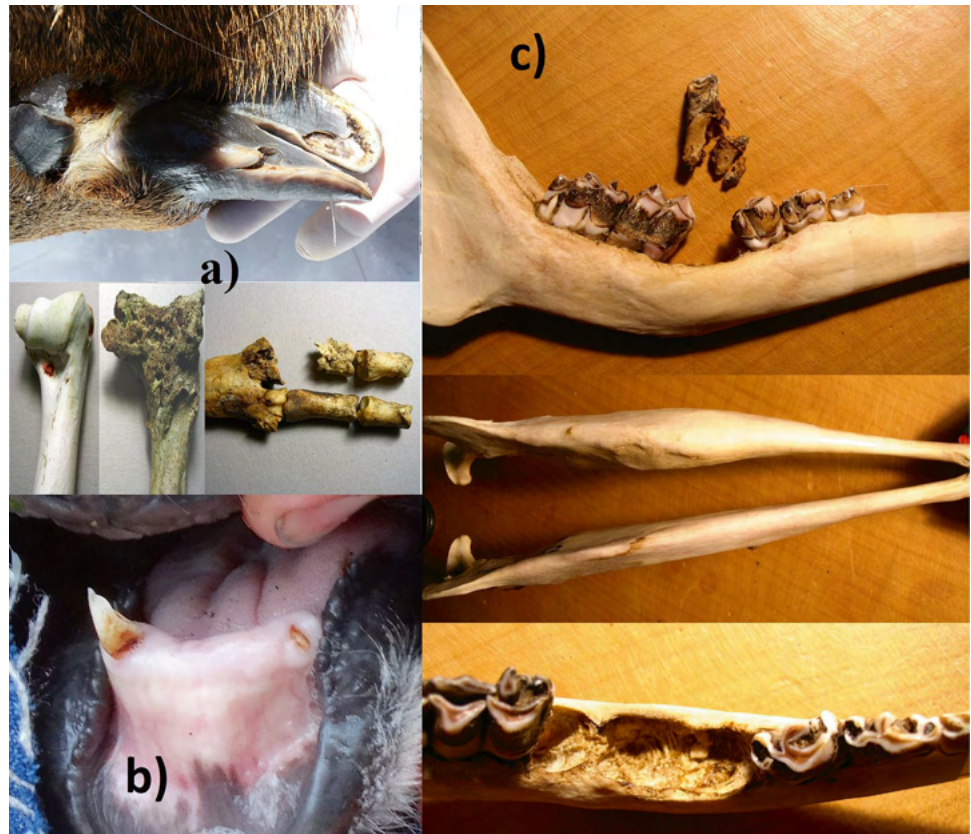
Extant remnant populations show a diverse diet totaling at least 191 different plants consumed (Flueck & Smith-Flueck, 2012b), yet diets at the local level are generally narrow. A few extreme examples from very different habitats are provided here. For the periglacial coastal habitat at Témpano Fiord, deer concentrated on the shrub *Fuchsia magellanica*, making up 75% of the adult females' feeding time (Van Winden, 2006), while at the neighboring Bernado Fiord, where *F. magellanica* is not present, they were observed consuming the herb *Gunnera magellanica* 82% of the time (Frid, 1994; Van Winden, 2006). Meanwhile, for the Andean Lake La Plata subpopulation (≥ 920 m.a.s.l.), the predominant plant in the autumn diet was the shrub *Maytenus disticha* at 70% of the total diet (Smith-Flueck, 2003).

Despite the extreme importance of *G. magellanica* in the diet of the periglacial subpopulation, this species was never detected in the La Plata study, though was catalogued as part of the plant community (Smith-Flueck, 2003). Two decades later, however, it was important in the diet of a radio-collared male in this same subpopulation (Smith-Flueck et al., 2018b) that lacked all but one incisor, had facial abscesses causing mandibular bone deformation, and died malnourished (Fig. 34.5). This difference in diet between these two subpopulations and the sick male's selection demonstrates the plasticity of the species to accommodate a wide variety of plant species.

When we compare the winter diet of one study population 2 years apart (Vila et al., 2009a, 2009b; Supplement Table 34.1), we find extremely different diet compositions, suggesting either high plasticity in response to some varied environmental condition or discrepancies in the sampling and/or analysis techniques. The total species counted in the diet doubled from 16 to 33 species between the two winters and trees composed 21% of the diet in the former study versus 5% in the latter. Percent frequency of several plants also varied: *Embothrium coccineum*, which was one of four predominant plants in the first study making up 15% of the winter diet, never was observed the second winter.

The huemul's diet varies substantially from one population to another and likely reflects food availability, demonstrating high intraspecific variation regarding food preference, similar to other cervids (Putman & Flueck,

Fig. 34.5 (a) Extensive rip on the abaxial side of the left hoof wall, and partially detached and missing subunguinus (sole), and examples of articular lesions on humerus and foot bones; (b) 4–5 year-old male with only one front tooth remaining (photos by W. Flueck and M. Escobar); and (c: top to bottom) molars broken into several pieces and misaligned, deformation of the mandibular, and disappearance of several teeth alveoli (photos by W. Flueck)



2011). Moreover, even when only two plant species made up 69% of the diet, the huemul's trophic niche was 1.19 ± 0.06 , which compares with 1.05 ± 0.09 of mule deer, *Odocoileus hemionus* (Smith-Flueck, 2003).

In an old-growth Andean *Nothofagus pumilio* forest, the top four genera, which comprised 67.7% of the total huemul diet, were the same top four of an allopatric red deer population and a Kulczynski similarity index showed a diet overlap of up to 62% for the two deer species (Smith-Flueck, 2003). Though this suggests potential competition when the two become sympatric in this habitat, the adequate niche breadth determined for this huemul population's diet indicates behavioral plasticity and ample room for diet compensation and is relevant only if it reduces the population growth rate of huemul to <1 (discussed in Flueck & Smith-Flueck, 2012b). In comparison, low diet overlaps for a sympatric population of huemul and cattle in an Argentine national park, showed cattle do not appear to compete directly for food (Vila et al., 2009b). More important is that cattle can be indirect competitors through reducing shrub density; encouraging predators (Wittmer et al., 2010); carrying diseases to which huemul are susceptible; and perhaps most detrimental are dogs of livestock herders that frequently kill huemul. In some areas, such as Bernardo O'Higgins National Park, herders themselves kill huemul for sustenance (Berger et al., 2020).

Reproduction and Growth

Huemul bucks, like other *Odocoileinae*, demonstrate serial polygyny (Povilitis, 1983; Smith-Flueck, 2000). Their breeding period varies between subpopulations, falling anywhere from mid-February to May (Smith-Flueck, 2000). One doe at the Rio Claro Nature Reserve (NR) underwent estrus twice in 1982 (20 March, 12–13 April) and once in 1983 (15 March); she was accompanied and mated by various bucks during these two mating seasons (Povilitis, 1985). Similarly, at Torres del Paine National Park (NP), successful copulations were recorded from end of March to early April over the 10-year study period (Guineo et al., 2008; Garay et al., 2016b). The latest recorded birth, a fawn born on March 14, 2024, at Shoonem Breeding Center in Argentina, indicates a conception date somewhere between August 7 and 27 (Smith-Flueck unpublished data).

Females give birth once a year to a single fawn under prime conditions (Povilitis, 1979; Montecinos, 1995; Smith-Flueck, 2000). The gestation period is assumed to be 200–220 days. During the first month, the fawns, lacking agility, spend much of their time bedded and hiding and frequently change their bedding site, similar to other cervid fawns (Garay et al., 2016a). Weaning has been assumed to occur around the fourth month of age (Aldridge, 1988), yet 5-month-old fawns have been observed nursing (Montecinos,

1995, Smith-Flueck unpublished data). At one year of age, the yearling stands the same height as the mother, and its youth is distinguished by its facial features and shorter neck (Guineo et al., 2008). In the central Chilean population, fawn recruitment was 0.50 in the late 1970s but on later surveys drastically decreased (Povilitis, 1998). In Tamango NR, fawn recruitment averaged 0.37 (range of 0.20–0.59 between 1986 and 1997) (Smith-Flueck, 2000). For female fertility, Corti et al. (2010) calculated an average of 0.72 (2005–2007). Observations from Rio Claro NR suggest some females bear young only in alternate years. One female monitored there from 1980 to 1986 raised only three fawns, one of which died within 6 months. She became pregnant for at least five of those years (Aldridge, 1988). Little is known about female fecundity in huemuls but if too low could be a major cause of population decline. One factor that affects fecundity is the age of the doe when giving birth for the first time. Texera (1974) documented a female huemul that bred at 6 months of age and as a yearling had a successful birth. When environmental conditions are met, this is observed in various *Odocoileinae* species (Robinette et al., 1955). In Torres del Paine NP, two marked females had fawns at 2 years of age (Guineo et al., 2008; Garay et al., 2016b), while one female in Rio Claro did not reproduce until her fourth year (Povilitis, 1998). Corti et al. (2010) assumed a primiparous age of 3 years old when modeling the Tomango NR subpopulation. Yet the potential to miss fawns that died soon after birth might have also influenced the assumed age of primiparity as any of those females ≥ 3 years at primiparity could have given birth before. Variation in age of primiparity is important for population dynamics and wildlife management because it can affect population growth (Rice et al., 2021). The variation observed in primiparity in huemul suggests that environmental factors might be influencing later primiparity in some locations, such as nutrient deficiencies. For instance, puberty has been shown to be associated with the attainment of a critical weight above which individuals have an increasing probability of ovulation and conceiving (Albon et al., 1983). Information on fertility ratios and primiparity can signal habitat constraints on optimal body condition even when pathological clinical symptoms are not apparent, and thus can be a useful tool for adaptive conservation management.

Behavior

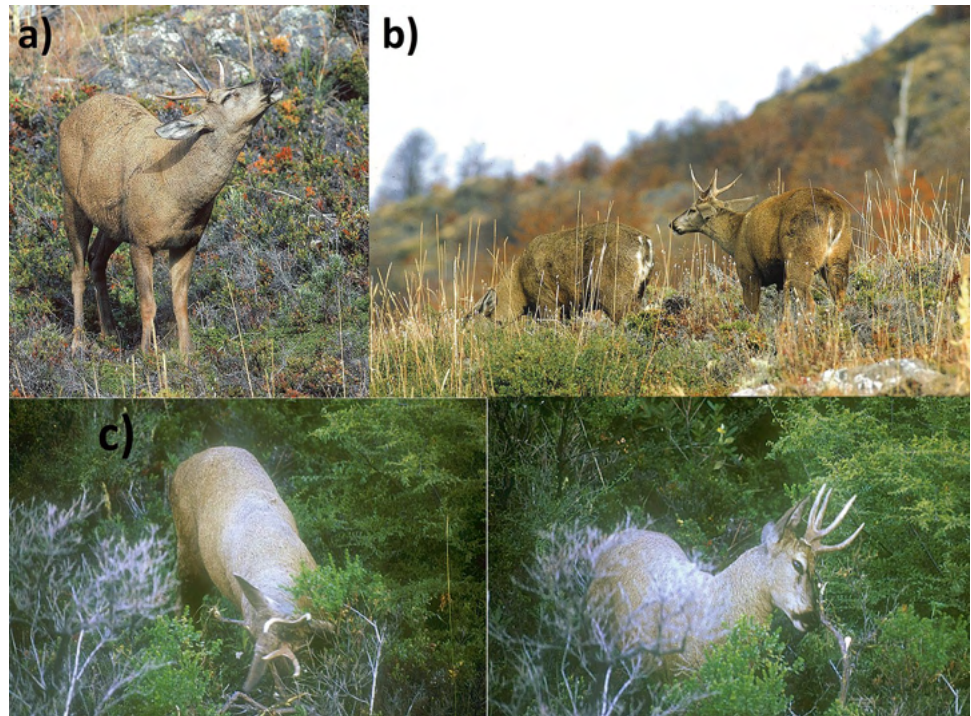
The huemul's social behavior is unmistakably New World in origin (Geist, 1998); huemul bucks, for instance, appear to be sexually opportunistic (Povilitis, 1983, 1985), like those of *Odocoileus*, though monogamy may replace serial polygyny where densities are low (Povilitis, 1985). Mating behavior has been well described (Povilitis, 1985; Garay et al.

2016b; Geist, 1998; Guineo et al. 2008; Vidal, 2010) (Fig. 34.6). Fights between bucks have been described as normally “friendly” sparring between two males of different status (Povilitis, 1985; Geist, 1998; Garay et al., 2016b); however, vigorous chases have been observed, resulting in fatality of one of the contesting males in a semi-captive center (E. Arias, pers. comm. 2003). Rutting bucks produce various vocalizations unique to this species, while females snort when chased by bucks (Povilitis, 1985; Geist, 1998; Smith-Flueck, 2000; Garay et al., 2016b). As with other cervids, bucks urine-test to determine the does' estrous state and display the common flehmen or lip-curling posture (Fig. 34.6).

Group sizes are commonly stated as solitary or one to five (Redford & Eisenberg, 1992; Povilitis, 1983; Frid, 1999; Wensing, 2005; Vila et al., 2010; Corti et al., 2010; Guineo et al., 2008; Briceño et al., 2013). Gross (1949) recorded groups of ten in summer, while wintering groups of 100 or more were observed during Prichard's (1902) study. In current times, up to eight have been recorded in open habitat (Frid, 1999; Wensing, 2005; Guineo et al., 2008) and 11 individuals in autumn in a closed deciduous forest habitat (Smith-Flueck, 2000). When observing radio-collared individuals in Aysen, Chile, group size ranged from 1 to 10 (mean 2.1; $n = 776$) (Gill unpublished data). Guineo et al. (2008) noted only larger group sizes in autumn. Winter conditions can also play a role—for example, in one study, a subpopulation of huemul congregated at the lakeshore to avoid the snowpack (Smith-Flueck et al., 2018a). Briceño et al. (2013) found that the study site with higher densities also had a higher mean group size than the lower density site, 2.43 individuals versus 1.48, respectively (though not a significant value). Intraspecific variation of groups size in white-tailed deer was shown to relate to differences in cover density: open environments correlated with larger group sizes than closed ones (Hirth, 1977; Lagory, 1986), potentially an adaptive antipredator strategy, which is also the case with roe, fallow, and red deer and muntjac (Carranza & Valencia, 1992; Thirgood, 1996; Hewison et al., 2001; Bhattarai & Kindlmann, 2018).

Huemul have been considered unique among cervids in that the sexes aggregate all year—except for a brief period during the fawning period (Frid, 1999). Mixed-sex groups occurred in all seasons in the Aysen radio-telemetry study (Gill unpublished data). Wensing (2005), however, observed at one of two study sites that sexual segregation was not due to fawning alone, as the sexes remained separate up to the beginning of fall. Huemul are not alone as Hirth (1977) observed white-tailed deer in mixed male–female groups at all seasons in open habitat. For taruca, huemul's closest relative, mixed-sexed groups were also common year-round (Barrio, 2013; Merkt, 1985). This begs the question: Why do *Hippocamelus* species form mixed male–female aggrega-

Fig. 34.6 Rut behaviour: (a) flehman to determine estrous cycle of female; (b) male pursuing female in estrus (photos by J. Smith-Flueck); and (c) thrashing some bushes and apparent scent-marking the damaged bush with forehead (photos by R. Gill)



tions year-round in some situations? Is this an adaptive response to low population densities or rather a remnant behavior from their past in the steppe landscape? This remains to be studied. Possibly with more behavioral studies, we will validate intraspecific variation in huemul group structure and will be able to explain underlying ecological factors.

Huemul groups have been described as fluid (Povilitis, 1983; Frid, 1999; Wensing, 2005), with members coming and going, similar to other *Odocoileus* species (Smith, 1989; Lingle, 2003); Garay et al. (2016b) also observed transient behavior, but group structure was more often stable. Time of year, landscape, group size, antipredator strategies, and densities can play a role in the amount of group cohesiveness (Lingle, 2003) and need further study with huemul.

One striking behavior of huemul is their lack of wariness and curiosity toward humans (Fig. 34.4; see Video 34.2, II in Supplement; Grosse, 1949; Wensing, 2005). Even young fawns not familiar with *Homo sapiens* allow strangers to come within a few meters (See Video 34.3, III in Supplement; Smith-Flueck, 2003). Historical accounts tell of indigenous people killing huemul at close range using rocks and knives (Tonko, 2008). However, huemul groups faced with some constant threat of human disturbance will display longer flight distances (Smith-Flueck, 2000). Frid (1994) found huemul readily habituated to the behavioral researchers and could be approached to within 5 m, yet 5 years later at this same site, following an illegal introduction of cattle, the flight distance had increased to 200 m (Frid, 1999).

Disease

In recent years, there has been a rise in detection of clinical disease signs, likely due to an increase in public awareness of the species' decline. The impact of these diseases on huemul population dynamics, however, has not been determined. *Corynebacterium pseudotuberculosis* was detected only recently in huemul (Morales et al., 2017) despite its common presence in both Chile and Argentina since the early 1900s (Flueck & Smith-Flueck, 2020), and in Bernard O'Higgins NP (BONP), Vila et al. (2019) assumed parapoxvirus to explain the debilitating foot disease. Deficient nutrition has been proposed as a root cause behind the apparent weak resistance of huemul to disease (Flueck & Smith-Flueck, 2011b). Severe bone lesions (Fig. 34.5) occur in subpopulations spread along ca.1000 km of the Andean mountains (Flueck, 2015; Flueck & Smith-Flueck, 2020). In three Argentine subpopulations, 57% of carcasses ($n = 35$) had serious osteopathologies (Flueck & Smith-Flueck, 2008), while in Shoonem Protected Park, 4 of 6 young adults evaluated at capture were missing teeth (Tooth-Loss Syndrome described by Smith-Flueck et al., 2018b). Nutritional ecology is the most parsimonious explanation behind this phenomenon (Flueck & Smith-Flueck, 2011b; Flueck et al., 2014a; Flueck, 2015; Smith-Flueck & Flueck, 2017). Preliminary studies show the same huemul with bone disease to be deficient in key micro-nutrients [selenium (Se), copper (Cu), manganese (Mn) (Flueck, Smith-Flueck and Winkel unpublished data)], which is substantiated by preliminary

soil analysis (Flueck et al., 2014b). A Chilean subpopulation deficient in Se (Flueck et al., 2014a) and Cu (Chihuailaf et al., 2014) also exhibited similar osteopathic conditions (Flueck, 2015). Se deficiency, for one, has myriad negative implications for wild herbivores (reviewed in Flueck et al., 2012). For instance, reproductive success was shown to significantly improve in Se-deficient black-tailed deer supplemented with Se (Flueck, 1994). The most overt malady associated with Se deficiency is white muscle disease (nutritional muscular dystrophy), which typically occurs in newborn fawns (Flueck et al., 2012). Deficiencies also affect the reproductive performance of both sexes, affect the age of first breeding, litter size, conception rate, birth weight, and neonatal mortality, and cause retention of the placenta; during gestation, maternal Se nutrition affects the efficiency of growth in offspring irrespective of postnatal management (Flueck et al., 2012). Furthermore, Se deficiency impairs bone metabolism, causing osteoarthritis, periodontitis, mandibular thickening, and premature tooth shedding, and also reduces immune function and resistance to infectious disease and affects iodine metabolism (Flueck et al., 2012). Iodine is also likely deficient in huemul (Flueck & Smith-Flueck, 2011b, 2017); the only blood sample analyzed for iodine levels showed severe iodine deficiency in a male at Shoonem PP (Flueck unpublished data). Furthermore, skulls from a Chilean population revealed thin bones, particularly those that form the walls of the cranial cavity, suggesting chronic metabolic imbalances as a response to mineral deficiency (Nunez-Cook et al., 2022).

In summary, etiological factors limiting huemul recovery include nutritional deficiencies, as described above, and associated immunosuppression. Why mineral deficiencies in soil did not surface as a problem in the historical past can be explained by the current year-round use of what historically was only summer range. Huemul no longer migrate to the lowlands to obtain sufficient trace minerals, essentially stuck as refugees in their current home (Flueck et al., 2022, 2023).

Status in the Wild

The huemul, along with the guanaco, are the only large native herbivores to inhabit sub-Antarctic Patagonia. They were first classified as endangered by the IUCN in 1982 (Black-Decima et al., 2016). Their endangered status, based on the IUCN Red List criteria B2ab(i,ii,iii,iv,v); C2a(i) (IUCN, 2012), was derived from the 2008 assessment (Jimenez et al., 2008), using the criteria that the area of occupancy was estimated to be less than 500 km², that subpopulations all contain <250 individuals and are severely fragmented, and that the overall population, which must be <2500 individuals to fit this criteria, continues to decline.

They are also classified as endangered in both countries' red books (Glade, 1993; Ojeda et al., 2012). They are one of four animals classified as a Natural Monument (Law 2646/93) in Argentina; they hold a dignified position on the Chilean coat of arms alongside the Condor, and they have been listed in Appendix I of CITES and the Convention on Migratory Species (CMS) since 1974 and 1997, respectively. Argentina and Chile ratified their first conservation national plans for the huemul in 2002 and 2001, respectively, and a binational conservation plan in 2012.

Huemul subpopulations vary in size from <10 individuals to approximately 100 (Serret, 2001; Vila et al., 2006) with total population estimates between 1048 and 1500 individuals (Povilitis, 1983; López et al., 1998; Díaz, 2000). Densities of 0.02–8.6 Huemul/km² have been reported (Table 34.2).

Along a 2000 km stretch, 101 subpopulations were identified (Vila et al., 2006). A few subpopulations of huemul that are at higher densities but with current stability unknown include, for Chile, Tamango and Cerro Castillo NRs and Torres del Paine NP, and for Argentina, Shoonem PP and Glacier and Perito Moreno NPs. Those declining include the most northern population in central Chile (Povilitis, 1998) due to human population growth (Povilitis, pers. comm.); in southern Chile, the BONP population for unknown causes (Pack et al. 2022); the Los Alerces NP population from fluorosis due to toxic volcanic ash (Izquierdo et al., 2018); and the Nirihua subpopulation in Nahuel Huapi NP, which is likely to already be extinct. The usurpation of this area by people claiming indigenous rights has jeopardized this subpopulation, which had an estimated five animals at that time (Pastore & Vila, 2003). While once providing the strictest protection afforded by the national government—the area inhabited had been designated earlier as “zona intangible” or untouchable zone—these huemul no longer fall under protection, nor will the indigenous leaders allow further monitoring to be conducted. Trends for most other subpopulations are unknown.

Huemul populations continue to decline due to natural and anthropogenic threats (Smith-Flueck & Flueck, 1995, 2001a, 2001b; Smith-Flueck, 2000; Saucedo & Gill, 2004; Flueck & Smith-Flueck, 2006; Smith-Flueck et al., 2011; Zuliani & Monjeau, 2022; Zuliani et al., 2023), which include habitat loss and modification (i.e., increasing encroachment by tourism, particularly adventure tourism), hunting, poaching, predation (i.e., puma, dogs and foxes: Corti et al., 2010; Smith-Flueck et al., 2011), auto collisions, disease, deficiency of essential trace minerals (discussed in disease section), and toxic volcanic emissions. Flueck and Smith-Flueck (2013a and b) reported on the first case of fluorosis in wild ungulates from a volcanic eruption, which caused a die-off of a red deer population and affected livestock. Loss of genetic diversity is also a concern, with one

Table 34.2 Densities of various huemul subpopulations

| Location | Density # huemul/km ² | Total area km ² | References |
|--|-------------------------------------|----------------------------|--|
| Lago Largo, CL | 0.2 | 25 | Colomés Gonzalez (1978) |
| Río Chillán, CL | 0.02 | 50 | Colomés Gonzalez (1978) |
| Río Claro, CL | 1.2 | 10 | Colomés Gonzalez (1978) |
| Nevados de Chillán, CL | 0.05 | 1000 | Povilitis (1979) |
| Nevados de Chillán, CL | 0.02 survey 1997 | 3000 | Povilitis (1998) |
| Bernardo O'Higgins NP, CL-V Tempango | 2.07 | 10.6 | Frid (1994) |
| Bernardo O'Higgins NP, CL-V Tempango | 1.32 | 10.6 | Wensing (2005) |
| Bernardo O'Higgins NP, CL-V Bernardo | 5.66 includes 2 fawns | 10.6 | Frid (1999) |
| Bernardo O'Higgins NP, CL-V Bernardo | 8.52 | 8.8 | Wensing (2005) |
| Bernardo O'Higgins NP, CL | 4.59 both valleys combined | 19.4 | Wensing (2005) |
| Bernardo O'Higgins NP, CL- V Bernardo | 7.78 mean for surveys 2004–2008 | | Briceño et al. (2013) |
| Bernardo O'Higgins NP, CL-V Huemules | 1.62 mean for surveys 2004–2008 | | Briceño et al. (2013) |
| Bernardo O'Higgins NP, Katraska Valley | 4.17 mean for surveys 2004–2008 | | Briceño et al. (2013) |
| Bernardo O'Higgins NP, Bernardo Valley | 3.48 excluded fawns | | Pack et al. (2022) |
| Bernardo O'Higgins NP, Huemul Valley | 0.52 | | Pack et al. (2022) |
| Tomango NR, CL | 5.45 survey 1995; includes 8 fawns | 11 | López (1997) |
| Tomango NR, CL | 3.32 survey 1996; with 12 fawns | 19.9 | Velásques (1997), Smith-Flueck (2000) ^a |
| Tamango NR, CL | 1.79 mean 2005–2007, adults only | 19.9 | Corti et al. (2010) |
| Cerro Ventisquero, AR | 1.0 | 11 | Smith-Flueck and Flueck (1997) |
| Cerro Pirque provincial reserve, AR | 0.5 | 20 | Smith-Flueck (2003) |
| Penins. Huemul, Lago La Plata, AR | 1.6 (minimum density) | 20 | Smith-Flueck (2003) |
| Perito Moreno NP, AR | 0.35 | 17 | Serret (1988) |
| Perito Moreno NP, AR | 0.5 | 12 | Serret (1989) |
| Perito Moreno NP, AR | 0.73 | 30 | Serret (1990) |
| Perito Moreno NP, AR | 0.68 | 37 | Serret (1991) |
| Perito Moreno NP, AR | 1.2 | 17 | Serret and Borghiani (1998) |
| Los Glaciares NP, AR | 0.45 | 40 | Serret and Merino (1995) Merino (1995) |
| Los Glaciares NP, AR | 0.67 | 21 | Serret and Borghiani (1996) |
| Los Glaciares NP, AR | 0.8 | 20 | Serret and Borghiani (1997) |
| Torres del Paine, NP, CL | 0.82 | 62 | Garay (2013) |
| Torres del Paine, NP, CL | 1.11 | 62 | Garay (2014) |
| Cerro Risco, Los Alerces NP, AR | 0.7 | Not available | Vila and Pastore (2003) |
| Cerro Risco, Los Alerces NP, AR | 0.3 | 46.5 | Vila et al. (2009b) |
| Nirihua, Nahuel Huapi NP, AR | 0.06 (4 males and 1 unknown adult) | 80 | Pastore and Vila (2003) ^b |

^a These citations include densities for various years at Tamango NR, with 1996 being the peak year. ^b This population is assumed extinct

isolated population shown to have low diversity (Corti et al., 2011). Many of these direct and indirect threats are likely to be synergies amongst them. For example, introduced animals (e.g., livestock and hares) as alternative prey will change the natural predator-prey balance and can lead to increased huemul kills. Wittmer et al. (2010) found removal of sheep led to more predation on huemul. If we then include potential inbreeding and nutritional deficiencies with concomitant weakened immune systems, disease may be further exacerbated, making the individuals even more susceptible to predation.

Competition with introduced ungulates (mainly cattle and exotic red deer) is frequently implicated as one of the main

current causes behind the decline, yet no evidence exists to back this. More importantly, livestock practice played a major role in the decline of this species in the twentieth century due to associated poaching, predation by ranch dogs, and effects of habitat loss. Though disease transmission through livestock has not been well documented, its potential impact is of concern. For instance, *Corynebacterium pseudotuberculosis* (CLA) in the Cerro Castillo NR subpopulation was likely transmitted from sheep, with approximately 33% of observed individuals having CLA-compatible lesions (Morales et al., 2017). Notably, the geographic relationship between the wild and domestic species started more than 100 years ago, yet this disease had not previously been

reported. As for red deer's impact, sympatry of the two species accounts for less than 2% of the current 60 subpopulations. Instead, several huemul populations have died out without red deer being present or if present at extremely low densities (Smith-Flueck, 2003).

Status in Captivity

The subject of breeding huemul in captivity has been a very sensitive issue for many Argentines and Chileans due to past failed attempts. Given the low numbers, high fragmentation, and the nutritional deficiencies found throughout the distribution range, conservation centers can serve to research and develop dietary supplementation protocols, with the long-term aim to boost in situ numbers by reintroducing animals to former more productive range in the lower elevations, backed by community involvement. Recovery strategies must include repopulating historical distribution sites (Flueck et al., 2022, 2023). Various publications present the history of ex situ huemul, while promoting captive breeding as a conservation tool and outline benefits, precautions, and protocols toward achieving success (Smith-Flueck, 2000; Smith-Flueck et al., 2004; Vidal, 2010; Vidal et al., 2011; Escobar Ruíz et al., 2017, 2020). One can derive valuable data from captive programs on veterinary care, longevity, gestation, diet, reproductive cycles, and behavior (Eisenberg, 2000). There were several early success stories, and one of the more fascinating ones—with tales of the animals' immediate adaptation to living in captivity aided by their innate tameness—occurred on Victoria Island inside Nahuel Huapi NP (Smith-Flueck, 2000). These early attempts provide sound lessons for modern-day programs. A center established in 2005 at Huilo Huilo Reserve, Chile, had provided by 2016 the first successful reintroductions into the wild. A second semi-captive center (Shoonem Breeding Center, Argentina), approved by the Chubut province Fauna Division in late 2018, brought in five unhealthy adults in the late winters of 2022 and 2023 for rehabilitation, and already can claim four successful births. By providing winter supplementation of deficient minerals, all three adult females had healthy fawns in 2024, all sired by a male at the center (Flueck unpublished data). Times have changed, including safer, more humane, protocols for capture operations (Smith-Flueck et al., 2018a), such that, for example, dogs are no longer used to capture huemul. Providing for the animal's welfare by using the best available techniques is key to modern success. For future centers, F. Vidal (pers. comm.) recommends that isolation and sanitary management of the premises be of vital importance and that centers be free of visitors and any possible external contagion vectors. Centers are undoubtedly an excellent tool to repopulate former huemul range.

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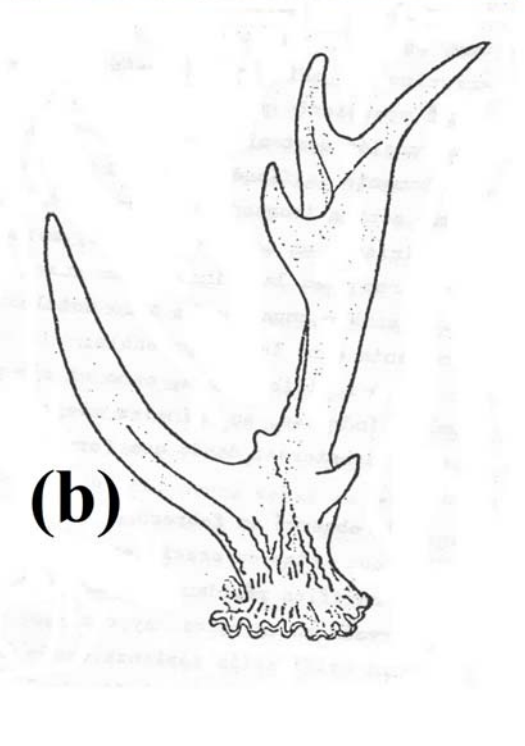
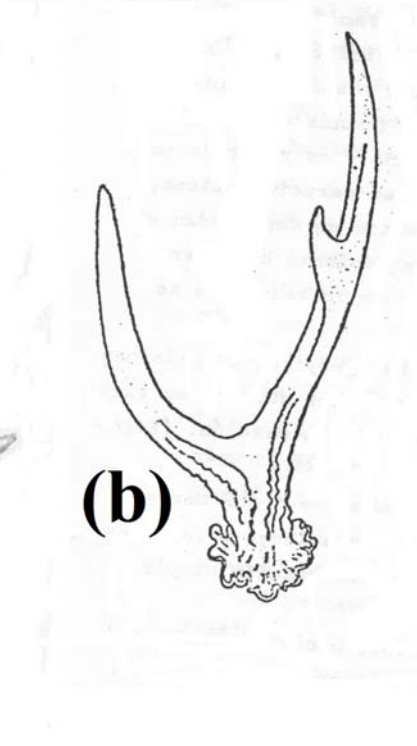
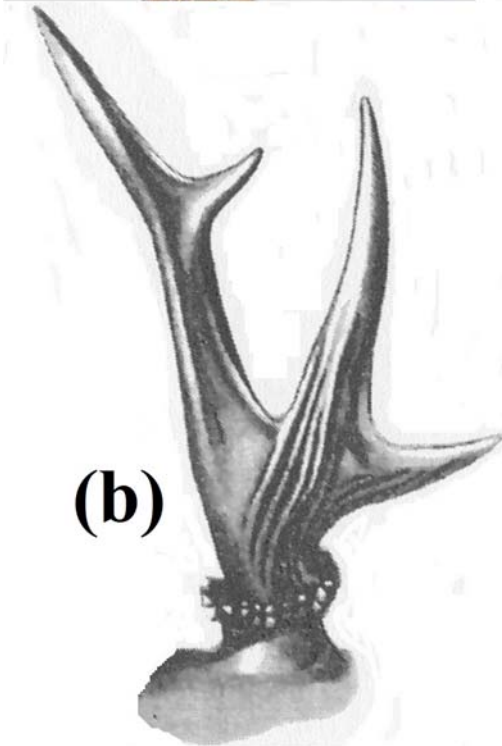
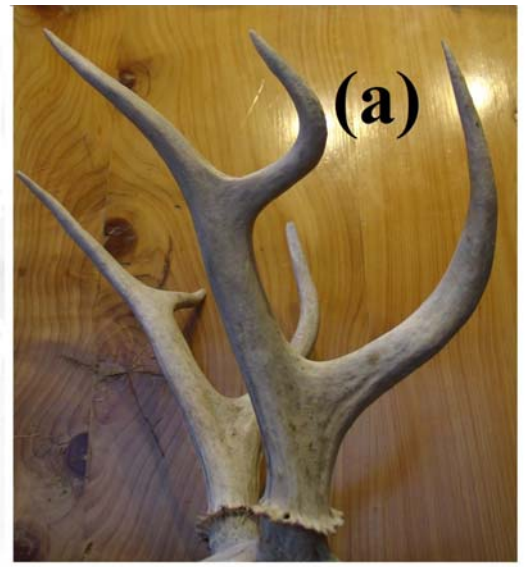
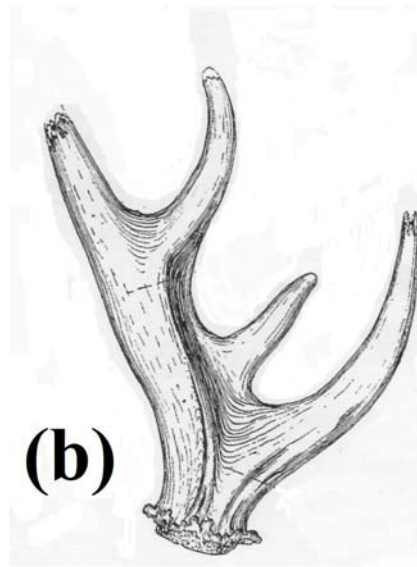
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Supplementary Figure 34.1. Huemul antlers still commonly have three tines, and had up to five in the past. (a) Extant and (b) historical specimens from Patagonia (Flueck and Smith-Flueck 2012b).

The chapter is also online

https://doi.org/10.1007/978-3-031-17756-9_34

where there are three (3) videos

Supplement Table 34.1. Summary of diet studies (expanded from Vila et al. 2010).

| Study area | Seasons | Method* | Herbs % | Grasses % | Shrubs % | Trees % | Total Browse % | Citation |
|--|-------------|---------|-------------------------|--------------------|----------------------------------|---------|----------------|---------------------|
| Chillan | All | MF | 46 | 0.17 | 29 | 4 | 33 | Colomes 1978 |
| Los Huemules del Niblinto | Sp-S-F | MF;DO | 46.2 | 4.3 | 42.3 | 11.5 | 53.8 | López et al 2000 |
| Chillan | Sp-S-F | MF;DO | 64 | | 25 | 9.5 | 34.5 | López et al 2001 |
| PN Nahuel Huapi | All | MF | 9.3 | 9.2 | 58.6 | 19.5 | 78.1 | Galende et al 2005 |
| PN Los Alerces | All 2001 | MF | 5.7 | 2.1 | 64.4 | 27.4 | 92.8 | Vila et al 2009a |
| PN Los Alerces w | Winter 2001 | MF | 4.8 | 4 | 70.0 | 21.2 | 91.2 | Vila et al 2009a |
| PN Los Alerces (Table 1**) | Winter 2003 | MF | 17.65 | 1.39 | 65.61 | 4.98 | 70.59 | Vila et al 2009b |
| PN Los Alerces (Fig 2) | Winter 2003 | MF | 45 | 1 | 49 | 5 | 54 | Vila et al 2009b |
| PN Los Alerces (n=1) | Summer 2009 | MF | 43.09 | 0.83 | - | - | 56.08 | Borrelli et al 2016 |
| PN Los Alerces (n=1) | Summer 2009 | MR | 44.18 | 0.51 | - | - | 55.32 | Borrelli et al 2016 |
| Lago La Plata | Sp-S-F | MF | 27.3 | 0.4 | - | - | 72 | Smith 2003 |
| RN Tomango | Sp-S | MF | 22.91 | 15.56 | - | - | 61.52 | Sierralta 2003 |
| PN Glaciares | Summer | MF | 50 | 11.8 | 29.4 | 8.5 | 37.9 | Merino 1995 |
| PN Glaciares (Los Vueltas) | Late Summer | MF | 23.8 | 8.82 | 36.84 | 30.55 | 67.39 | Vila et al 2011 |
| PN O'Higgins Fiordo Témpano Fig. 17 Females | S-F | DO | 18 | 1 (herbs or grass) | 79 | 2 | 81 | Van Winden 2006 |
| PN O'Higgins Fiordo Témpano Fig. 18 males | S-F | DO | 55 | 0 | 45 | - | 45 | Van Winden 2006 |
| PN O'Higgins Fiordo Bernardo Fig. 21 male & female | F | DO | 99 (82% is one species) | 1 | small % of herbs could be shrubs | - | - | Van Winden 2006 |

* MF and MR = microhistological analysis of fecal and rumen samples, respectively; DO = direct observations.

** The plant categories total only 89.63% (not 100%) as only key plant species were included in Vila et al (2011).