conservation

S2: Compendium: Review of Consequences for Ungulates when losing Migratory Traditions

Content:

Implications of having lost migratory traditions

Humans have achieved a very sophisticated and temporarily privileged status among mammals. Their capacity to domesticate wild animals for providing them with food, materials, labor, and hedonistic enjoyment, has produced a sustained growth of this forced symbiosis until reaching, as a whole, 97% of the current biomass of mammals in the world (Berger et al., 2020). On a planet with finite resources, this expansive anthropic artifact results in a consequence of the phenomenon, namely the numerical decrease of wild species, their habitats, the loss of culturally transmitted knowledge, and the retraction of animal spatial distributions towards refuge environments.

1. Nutritional ecology and seasonal migrations

As early as 1925 the naturalist von Colditz considered the commonly found simple forked antlers in huemul as a sign of some sort of degeneration, since older samples reached up to 5 tines per side. Additionally, huemul being prevented from accessing winter areas was suggested to affect huemul health by resulting in malnutrition (Liebermann, 1962). Similarly, in historical times the related *Odocoileus* spp. were largely extirpated from the mesquite savannas range of north-central Texas, where specimens had much superior antler development when compared to remaining extant animals in timbered areas, attributed to a combination of the favorable foraging conditions on historical ranges and low population densities (Wells and Stangl, 2003). As luxury tissue, antler development clearly serves to indicate the nutritional conditions experienced by the male (Bubenik and Bubenik, 1990). Similarly, Liebermann (1962) considered the areas that the huemul were forced to use in winter as inhospitable high elevations and stated that huemul "were pushed there and fatally lost their biological capital before they could adapt". This was corroborated more recently with at least 88% of dead (n=34, Flueck and Smith-Flueck, unpubl.) and 86% of live huemul affected with skeletal pathologies, antler asymmetry, and spread over a large geographical region (Flueck and Smith-Flueck, 2008, 2017; Flueck, 2020). All these samples were collected from individuals living year round at high elevations coinciding with old-growth lenga forest habitats (*Nothofagus pumilio*), and representing summer range habitat. These unusual pathological conditions together with the altered spatiotemporal use of habitats further qualify huemul as a refugee species (Flueck and Smith-Flueck, 2006, 2011; Kerley et al., 2012).

The underlying cause of the extant disease pattern relates to the commonly described effect of topography and precipitation on micronutrients, such as leaching occurring on ridge land while adjacent valley soils maintain or increase concentrations (Ren et al., 1987). Extensive areas thus exhibit lower concentrations of minerals in plants at high rather than low altitude (reviewed in Flueck and Smith-Flueck, 2011), as shown in mountain goats (*Oreamnos americanus*) living at higher altitudes having lower levels of essential selenium than elk and deer remaining in lower areas (Fielder, 1986). This was

corroborated in areas with extant huemul where soils from those higher sites had deficient selenium levels, whereas soil levels in low valley bottoms were adequate (Flueck et al., 2014). Areas used by huemul during summer (and also during winter), are generally considered to represent summer ranges based on winter conditions and fertility, such that all livestock producers in these areas remove their animals before winter and move them to winter areas (Gonzalez and Tapia, 2017; Massara Paletto and Buono, 2020). Notably, since colonial times, past and current livestock producers move their animals out of the Protected Park Shoonem before winter, as is the practice in other similar watersheds both in Argentina and Chile, to move them to areas considered appropriate winter ranges (Ladio and Lozada, 2004). Similarly, red deer (*Cervus elaphus*) introduced to former huemul areas remained as residents for several decades before adopting migratory behavior, when they always returned to winter ranges in that season (Flueck and Smith-Flueck, 2011). Congruently, huemul reported in the accompanying paper to be year-round residents in a summer range were deficient in several essential micronutrients based on hair analysis (Flueck, 2020), which explains the prevalent bone disease and low average live span (Flueck, 2015; Flueck and Smith-Flueck, 2008, 2017). The high frequency of asymmetry of antlers and their deformed development in many subpopulations also indicate nutritional problems (Geist, 1998). Besides causing a rare bone disease in huemul, selenium deficiency also affects metabolic and immune systems, such that the unusual reactions reported to caseous lymphadenitis and putative parapoxvirus pathogens may relate to such deficiencies (Flueck, 2020). Bighorn sheep (*Ovis canadensis*) were also shown to have lost traditional seasonal movements by overhunting that resulted in many herds having associated seasonal nutritional deficiencies, and which was considered the ultimate cause of declining herds (Honess and Frost, 1942; Packard, 1946; Leopold et al., 1963; Risenhoover et al., 1988). Moreover, reviewing a global database of large migratory mammalian herbivores, Teitelbaum et al. (2015) found that animals living in resource-poor environments travel farthest to fulfil their resource needs, and also had increased home range sizes. However, this trait only works for certain resources, mainly levels of protein, energy, fibers, and salt. Low phosphorous and/or calcium also is noted and results in chewing of bones. Importantly however, deficiency of many essential trace minerals are not perceived by ruminants, for example copper or selenium deficiencies. Thus, while migratory ungulates may leave a summer range temporarily to access a salt lick on the winter range, trace mineral deficiencies do not elicit a response. Instructively, although many wild ungulate exhibit substantial plasticity regarding to migrate versus to remain resident, or changing migratory paths and localities (Spitz et al., 2018), huemul was the only example of having changed to become residents in typical summer ranges (Xu et al., 2021).

2. Carrying capacity in migratory ungulates using summer and winter ranges

Conventionally, habitat carrying capacity for ruminants is based on forage supplies of energy and protein (Van Soest, 1982). In this respect, such type of nutritional constraints for current low-density huemul appear improbable, considering equivalent habitats support high densities of exotic herbivores such as red deer, although the latter also access typical winter ranges (Flueck and Smith-Flueck, 2006). Today, ecotonal ranges formerly used by huemul produce 3000-5000 kg/km^2 of exotic ruminant biomass, equivalent to 40-60 huemul/km^2 if they would forage similarly, as would be expected from mixed feeders (Flueck, 2010). Currently no huemul exist anymore in extra-Andean Argentine Patagonia which supported up to 25 million sheep, 4 million cattle and 0.5 million horses (von Thüngen and Lanari, 2010). Krieg (1940) also suggested that forage, which supported a large quantity of exotic herbivores with superb body development, could not explain the few or absent huemul. However, an evaluation of habitat should be restricted to the limiting nutrients (Van Soest, 1982), which frequently are specific macro- and micronutrients, rather than protein and energy supplies. As Liebermann (1962) al-

ready observed: "everybody familiar with mountains knows that summer and winter ranges are different and separated vertically; with snow fall, huemul must descend, however, it was exactly the lower hill sides and fertile valleys which were settled by men and his livestock. If huemul find lower areas occupied by livestock and people, they need to remain in higher places, where they will suffer from malnutrition with consequences to their offspring, and being weakened they are more prone to disease and easier prey to natural predators".

3. Fundamentals of migratory traditions

In seasonal mountain areas, winter ranges naturally contain year-round residents besides the migratory members that utilize upper elevation summer ranges (Adams, 1982; Peters et al., 2017; Gogan et al., 2019; Koprowski and Krausman, 2019; Xu et al., 2021). Ungulates dispersing or being translocated to winter ranges tend to remain as residents initially (Haller, 2002; Flueck and Smith-Flueck, 2011), and it can take 90 years, or 12 to 13 generations, for half of the descendants of translocated animals to become migratory (Festa-Bianchet, 2018). Moreover, eventually established migratory traditions are rigid enough such that deer may ignore excellent areas (Gogan et al., 2019), traverse them to spend the summer in much inferior habitat at 110 km from their winter range (Flueck, 1989). They may also disregard elevated predation risks besides signals of habitat quality (Sawyer et al., 2019; Flueck and Smith-Flueck, 2011), as shown by traversing several mountain ranges in order to use their traditional winter and summer ranges (Moser, 1962).

Migratory behavior (altitudinal and horizontal) takes generations to evolve and is passed down culturally (Putman and Flueck, 2011; Festa-Bianchet, 2018; Jesmer et al., 2018; Gogan et al., 2019). A seasonally migrating female commonly gives birth to the young in the summer range, and in autumn the young follows the mother to migrate to the winter range, and back to the summer range the following spring, with the animals exhibiting very high fidelity to migratory routes and seasonal ranges (Jakopak et al., 2019; Morrison et al., 2021). Instructively, if a mother dies on the winter range, the young most often remains there accompanying other resident animals (Flueck, 1989; Thirgood, 1995; Via et al., 1995; Avital and Jablonka, 2000; McClure et al., 2005). A winter range rarely is inhabitable during summer such that all animals migrate away, but it occurs on ranges with wet/dry seasons.

The process leading to such partially migratory populations was also evidenced with European red deer introduced to winter ranges formerly used by huemul, where initially they remained all year as residents (Flueck and Smith-Flueck, 2011). After several decades, however, migratory behavior was adopted by some deer, and marked red deer migrated 24 linear kilometers (Flueck, 2005). This was also shown to have occurred with red deer recolonizing the Swiss National Park (Haller, 2002). Instructively, two occasions of reintroductions of huemul corroborate this basic pattern of recolonization behavior among cervids. Huemul were reintroduced to Torres del Paine National Park (Chile) between 1977-1980, with resident groups remaining in valley bottoms, and a subsequent expansion reached into grassland areas where they overlap with guanaco (Rau 2003, Guineo et al. 2008). Similarly, huemul reintroduced in the Los Rios region (Chile) became all-year residents in valley bottoms together with guanaco (F. Vidal unpubl. data).

Among cervids, using summer ranges and also accomplishing short visits during summer to access mineral licks on winter ranges (Brandborg, 1955; Mincher et al., 2008) are cultural migratory behaviors which are transmitted vertically (Adams, 1982; Nelson and Mech, 1999; Festa-Bianchet, 2018; Jesmer et al., 2018). These cultural traits in ungulates can go back 5000 to 6000 years ago (Andersen, 1991; Berger et al., 2006; Lyman, 2006), and are highly immutable (Sawyer et al., 2019). Preserving such cultural traits are considered important, especially for endangered species (Ryan, 2006; Jesmer et al., 2018).

Individuals of various ungulate species have been observed to briefly leave their summer range to make large excursions to winter ranges solely to use a mineral lick for a few hours to a few days, despite the increased risk from predation (reviewed in Flueck and Smith-Flueck, 2011). Many remaining huemul populations are tied year round to refuge areas on summer ranges because the residents on original winter ranges are extinct, and the few extant dispersers getting there are consistently being eliminated (Flueck and Smith-Flueck, 2011). Although a few recent sightings of huemul in ecotonal areas show that some do occasionally disperse from summer-range refuges, they do not establish reproductive populations as they can not survive in valleys settled by humans, inevitably being hunted, or killed by dogs or road traffic (Flueck, 2018). While migration and summer jaunts to mineral licks are learnt behaviors, dispersal is innate, being an emigration of individuals by random diffusion that is predetermined genetically and is not in response to environmental conditions (Howard, 1960). Odocoilines had little or no plasticity in terms of whether or where they migrate: resident deer remained residents, and migrant deer remained migrants, regardless of age, reproductive status or number of years monitored (Gogan et al., 2019; Sawyer et al., 2019). However, some individual plasticity does occur which explains the development of new movement patterns including recolonizations (van de Kerk et al., 2021; Xu et al., 2021).

The spacial capacity of migration among Odocoilines has been shown to reach distances up to 104 km (Gogan et al. 2019), up to 264 km (Sawyer et al. 2016), and even up to 410 km (Kauffman et al. 2020). This implies that huemul also can migrate substantial distances, and it corroborates the historical accounts referring to migrating huemul.

Therefore, the resident behavior reported for huemul that takes place on a summer range, not a winter range as is the norm for cervids, is an artefact of anthropogenic elimination of the migratory tradition resulting in the extirpation of all huemul in historical winter ranges.

4. Relevant case: a fossil deer suffering from bone pathology

The study of bones from a fossil deer endemic to Crete island revealed many pathological lesions (Lyras et al., 2019), equivalent to those described in huemul (Flueck and Smith-Flueck 2008, 2011, 2017). Lyras et al. (2019) concluded that the fossil deer on this island were affected by severe metabolic bone disease from soil mineral deficiencies and possible overgrazing of the habitat. Similarly, many huemul populations have been described as persisting in artificial "islands" with concomitant bone pathology (Flueck and Smith-Flueck 2011).

5. Implications for conservation

To base management strategies on the extant distribution, when it is an artefact, is erroneous as was shown for bighorn sheep in North America (Honess and Frost, 1942), and ibex (*Capra ibex*) and chamois (*Rupicapra rupicapra*) in Europe (Yockney and Hickling, 2000; Phoca-Cosmetatou, 2004; Baumann et al., 2005). The name "alpine chamois" resulted from historic overhunting which nearly exterminated chamois in low lands, but which survived in Alpine refuges. However, modern translocations resulted in its recovery such that it expanded to forested areas even far from the Alps, such that now it is also recognized as "forest chamois" in areas clearly corroborated by archaeozoology (Baumann et al., 2005). Huemul is another species which has been limited to suboptimal habitat for many decades if not centuries. If in such cases the currently used habitats are identified as the conservation priority areas for the species in question (e.g. Riquelme et al., 2018), without recognizing that these represent a suboptimal portion, this then might present one of the largest risks for such refugee species (Kerley et al., 2012; Faurby and Araujo, 2018; Nüchel et al., 2018). Sedentariness in artificial settings is considered one of the largest problems challenging long-term persistence of bighorn sheep populations

(Risenhoover et al., 1988), and acknowledging historical species ranges is thus important for recovering endangered species (Laliberte and Ripple, 2004; Phoca-Cosmetatou, 2004; Cromsigt et al., 2012; Kerley et al., 2012; Lea et al., 2016; Faurby and Araujo, 2018). Yet, although little knowledge exists about natural movement patterns of South American deer, this is likely to be fundamentally important to maintain viable populations (Grotta-Neto and Duarte, 2019). Whereas natural sink areas are the norm to be surrounding well-performing populations in source areas, there is the need to differentiate the former from an artificial ecological trap, since the latter will drive a local population to extinction (Battin, 2004). Moreover, it is essential that the shifting baseline syndrome be overcome (Soga and Gaston, 2017): repeating old, unfounded and outdated interpretations, like huemul being a "mountain deer", being short-legged, non-migratory, etc. As shown with published fake information, these get cited many times, over long periods, and even with causing impact on human health (Bar-Ilan and Halevi, 2021).

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