European Mouflon on Vegetation

Subjects: Ecology
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The mouflon (*Ovis gmelini musimon*) is an introduced ungulate in continental Europe. It has adapted well to its occupied habitats over the last 150 years. Its growing population has drawn increasing attention to its impact on autochthonous species, especially in endangered ecosystems. Its allochthonous character, habitat selection, and feeding led scientists to question the raison d'etre of mouflons. The mouflon's space use and foraging strategies highlighted some pressure elements it exerts on those habitats. Mouflon trampling damage may be behind the degradation of rare, endangered grasslands.

mouflon invasive species rock grassland

1. Introduction

The taxonomic classification and scientific designation of mouflons have caused much debate among scientists [1]. There is a consensus that the mouflon of the Mediterranean islands of Cyprus, Corsica, and Sardinia descended from the Asian mouflon (*Ovis gmelini*) living from Turkey and Armenia to Iran [2]. They appeared in the Mediterranean basin about 8500 years Before the Common Era (BCE) at the beginning of the first waves of human-mediated animal population dispersal in the Mediterranean [3][4]. Asian mouflons were introduced to the Mediterranean islands by Neolithic humans, probably following a pre-domestication phase between 4500 and 8500 years (BCE), as shown by evidence from Neolithic archaeological sites [3][5][6][7]. The domestication process is assumed to have been limited, without morphological selection, but with preference for better survival success against predatory pressure [3][8]. Therefore, contrary to previous opinions that have taxonomically described the mouflon introduced to the Mediterranean islands as domestic sheep (*Ovis aries musimon/ophion*) due to pre-domestication [9]—that were later abandoned and became feral—researchers consider the mouflon present in Corsica and Sardinia and later introduced into continental Europe as a subspecies of the Asian mouflon (*Ovis gmelini musimon*), following the lead of several authors [1][10][11][12][13][14][15].

The first recorded introduction to continental Europe was by Prince Eugen of Savoy, who introduced mouflons to the Belvedere Game Park near Vienna in Austria in 1729–1731 [16]. The first successful introduction of mouflon into the wild was in the territory of the Austro-Hungarian Monarchy, in Ghymes, Nyitra County, where 80–100 mouflons, previously introduced into a hunting reserve in 1868–69, were released in 1883 on the estate of Count Károly Forgách to increase the variety of species for hunting purposes [17]. These mouflons came from Corsica and Sardinia via the Frankfurt am Main and Brussels zoos [18].

Although introductions to the European continent began in the 18th century, the population grew rapidly just after World War II. Haltenorth and Trense [19] estimated the European population at 14,000 individuals in 1955; Uloth [20] at 22,000 in 1968; Lochman [21] at 53,000 in 1978; Tomiczek and Türcke [22] at 84,000 in 1992; Weller [23] at 111–117,000 in 2001; and Apollonio et al. [24] at around 140,000 individuals in 2005, of which at least 23,000 are annually harvested. It is now a widespread species on the European continent, present in 24 countries from the Mediterranean to Scandinavia and from Spain to Ukraine [1][23].

There is a debate about whether the mouflon of Mediterranean islands can be called an autochthonous subspecies. In the case of the Cypriot mouflon, it cannot be excluded that wild mouflons arrived in Cyprus on their own during the last ice age when the Mediterranean Sea was 125 m below the current sea level [25], in which case it could be considered an autochthonous subspecies. Considering the presence of the mouflon in the Mediterranean islands for thousands of years, Satta et al. [26] declared the Sardinian population to be autochthonous. However, following Ferretti and Lovari [27], researchers consider those species or subspecies as an “alien” (allochthonous, non-native, non-indigenous, exotic) taxon that occurs outside its natural range (past or present) and dispersal potential (i.e., outside the range it occupies naturally), as a result of intentional or accidental introduction by man [28][29]. According to this definition, the Sardinian (and Corsican) mouflons cannot be considered autochthonous, and this is also true for the mouflons introduced from these islands to continental Europe [30][31][32][33][34]. However, as the mouflon population has been expanding and increasing in density over the decades raising conservation concerns due to the damage mouflons cause by trampling and grazing on rocky grasslands, in Hungary, they have been listed as an allochthonous species and an invasive subspecies as well [32].

The EU uses the term invasive alien species (IAS) to classify species whose introduction or spread threatens or negatively impacts biodiversity and ecosystem services [35]. Although only a small percentage of introduced species become invasive, their negative impacts may become substantial over time [36]. The invasive alien character definition has three criteria: the spatial scale, the temporal scale, and the threat to biodiversity [37][38]. By displacing native plants and animals, invasive species change the former ecological conditions and transform the human environment, causing unpredictable harm [39]. Studies [40] and survey results [41] about invasive species identified habitat loss and fragmentation as the top risk in Europe, while invasive species ranked second. Unlike the regulations of some EU member states such as Hungary—e.g., [42][43]—the EU IAS regulations [35][44] or the updated EU list [45] does not list mouflon as a concern of the Union. However, in Hungary, the survey [41] posited a contrary result by placing invasive species at the top of the threat-to-biodiversity list, ranking the mouflon as the fourth most harmful invader of ecosystems.

Scientific studies consider the mouflon invasive and claim a negative impact on ecosystems [46][47] due to its (1) trampling and degradation of grasslands [47][48], (2) invasiveness by displacing native species [40][41][47][49], and (3) foraging strategies. Therefore, the research included the mouflons’ morphophysiology, habitat selection, and food preference with their impacts, against the backdrop of the ecological and legislative debate on invasiveness and its European regulation.

At the same time, Ricciardi and Cohen [50] quantified the rate of spread and impact of invaders on native species. Their results showed that the correlation is weak or does not exist between the mechanisms of invasion and its impact. Invasiveness is purely a potential of a species to spread fast on a new territory. In their view "*the term "invasive" should not be used to connote negative environmental impact*" [50] (p. 309). They argue that introduced species reaching high densities can quickly attain higher establishment success levels and dominate native communities. A widely spread introduced species will likely affect multiple native species *"over large fractions of their respective ranges and drive"* [50] (p.310). However, success of invasion and ecological impacts highly depend on dispersal opportunity and anthropogenic factors. Their argumentation emphasizes a link between invasiveness and impact, if exists any, is significantly determined by human activity [50].

2. Habitat Use, Diet, and Feeding Strategy of Mouflons

Rock grasslands and meadows are the preferred habitat types [51] for the mouflon in its home range because they resemble the south-exposed, warm, and dry surfaces found in its original Mediterranean habitats. Cransac and Hewison [52] argue that the mouflon spends 80% of its time in non-forested ranges regardless of the season. Náhlik and Dremmel [53] defined the mouflon's habitat use, with most occurring in range parts covered by oak, beech, broadleaved woods, or meadows and clear-cut fields. The habitat preference analysis found positive responses for younger beech, 50+-year-old oak woods, meadows, and clear-cut areas. The findings suggest that mouflon habitat use may cause browsing damage [53], primarily to forest regeneration seedlings [51][54][55] and in open habitats created by human activity [48].

Large-herbivore-induced ecosystem or economic damage is often associated with large groups [56][57][58]. Concerning the degradation risk, mouflon herds are a factor because they maintain the large social group form throughout the year. The mouflon group size depends on habitat coverage, population density, disturbance level (including predation and hunting), and forage concentration [59][60][61][62].

According to their foraging strategies, ruminants are classified into three categories: grazers, browsers, and intermediate feeders [63][64][65]. Each type leads to differing resource exploitation and vegetation impact. Gordon [65] argued that the difference between ruminants is behavioral rather than morphological, while the food supply determines the difference between grazers and browsers. Ecological studies on foraging focus on the immediate intake rate and diet selection, while animal scientists evaluate diet selection as per nutritional value. The relationship between morphology and physiology still requires more understanding because browsers and grazers have distinct perspectives on resource distribution. This perception drives their distribution and shifts around the resources [65].

Marchand [66] promoted ruminant classification by considering the digestive system morphology and diet composition. Rumen morphophysiology is very diverse per the ability to graze or browse [66][67]. It constrains the animal's diet selection, thus can influence the species' impact on vegetation. To highlight the morphophysiological differences of the rumen, Clauss et al. [67] proposed the distinction of ruminants as either moose type or cattle type, arguing that Hofmann's [63] triad classification should be used for diet composition only. Clauss et al.'s [67] principle defines ranges of >75% or >90% grass consumption for grazers. Placing species on the scale shows that there are fewer obligate grazers than browsers. Variation analysis of the diet composition is forward-looking when assessing new threats on vegetation and land use arising from climate-warming-led changes that alter large herbivore foraging.

Both diet composition and morphophysiology place the mouflon into the grazer category [54][68][69][70][71]. Accordingly, in mountainous habitats and Central European forests, the mouflon's summer diet comprises a high proportion of grass and grass-like species. In the autumn and winter, the mouflon shifts to seeds, fruits, and woody components (also due to snow cover) [54][72][73]. The seasonal variation was found to be smaller in Mediterranean ranges, i.e., environmental seasonality has a great influence on the mouflon's diet composition [66].

The mouflon's rumen structure is an important morphological element. The mouflon's rumen is less viscous and more stratified [67], ensuring a longer retention time, and it can digest low-quality food well. Marchand's [66] data showed a higher proportion of shrubs and trees in the diet composition; thus, the grazers' grass proportion threshold of 75%–90% was not reached. Therefore, they consider the mouflon as a variable grazer (consuming a low but significant portion of dicots) and not an obligate grazer. Mouflons can occupy habitats where grass is scarce, which draws into question the extent to which cattle-type species can include forage other than grass in their diet [66]. The mouflons' ability to live and still maintain their population where grass is scarce makes specific locations attractive because they limit competition from native herbivores [74]. Marchand's [66] study stated that mouflons can show unusual feeding strategies even with 73% up to 83% forbs and below 20% graminoid intake. Despite Bertolino et al. [74] and Dremmel [72] describing the mouflon's diet variation as the most stable throughout the year compared to red deer and chamois, the mouflon adapts to changing environmental conditions and food availability by changing its diet habits. Seasonal availability of feeding species also causes a shift [54][72][73][74] in its diet, leading to a plant taxon proportion change. This confirms the mouflon's opportunistic foraging strategy; therefore, analyzing the mouflon's diet composition helps to understand its impact on those ecosystems and its competition with native ungulates [66][72].

Based on different mouflon diet composition analyses, habitat preference is of greater significance than food preference [51]. The species commits to its habitats even if they deteriorate, thereby narrowing its diet or forcing it to intake a higher proportion of fibrous forage. However, as Derioz et al. [75] found in France, significant habitat change can force the mouflon to alter home ranges. The data did not prove severe grazing damage to the ecosystems because the rare or protected plants were in similar abundance to other plant species. Instead, seasonal weather conditions caused high diversity [51]. With the seasonal variety noted above, rumen content examinations in Central European areas showed high levels of graminoid species, forest mushrooms, some dicots or fruits, and nuts. These results support the hypothesis that herbivore foraging is much more diversified than that of domesticated or bred-in-captivity wild species [76].

Baráth et al. [48] referred to earlier micro-histopathological examinations of mouflon feces. Their results determined an 80% proportion of monocotyledons, while woody plants accounted for only up to 7.8%. Rumen content analyses in the Czech Republic also showed the dominance of herbaceous plants over the whole year, with woody species being included during wintertime. Studying an overlap of three ungulate species' (wild goat (*Capra aegagrus*), roe deer (*Capreolus capreolus*), and mouflon) foraging strategies, Heroldová's [73] results stated that the mouflon is a typical grazer, combining its diet composition with shoots and seeds in colder periods. She found a high similarity between goat and mouflon diets and the least overlap between the diets of roe deer and mouflons. In winter months, the three species showed high competition for broadleaved sprouts, which caused high levels of vegetation damage. Within this context, the mouflon should still display an advantage compared to other large herbivores because it is a non-selective, generalist feeder that can consume lower-quality food that other species do not because of its ability to digest fibrous forage. A higher proportion of grass in its diet predicts lower forest damage, but with overlapping diet niches in wintertime, it is comparable to the diet of red deer [73][75]. Slovak and Hungarian studies also confirmed woody plants in the mouflon's winter diets, comprising up to 35% and 32%, respectively [72][77][78].

When studying the crop damage extent of the mouflons, the Czech research compared the proportion and quality of agricultural crops versus natural forest species and showed red deer, roe deer, and mouflons ingesting all agricultural plants grown next to a forest. However, the proportions of agricultural food consumed varied with the seasons for all these three herbivores. The comparison proved that agricultural plants were of lesser importance despite the lower nutritional value of the natural forage [79].

A diet niche comparison study for red deer, roe deer, chamois, and mouflons conducted in an Alpine environment confirmed similar results. The mouflons demonstrated the lowest diet variability with very high graminoid consumption [74]. The obligate grazer level of over 75% grass-like species' ingestion was not reached in these habitats either [67]. Dicot species consumption reached its highest level in summer, comprising 22% of the annual diet.

Groups of these species were stable in Alpine environments, and the mouflon did not switch to woody species and conifers despite the findings of Heroldová et al. [77] and Homolka [54], who demonstrated that the species did switch in Central European low-, mid-, and highlands. Redjadj et al. [80] also emphasized the diet overlap between chamois and mouflons, classifying chamois' grass ingestion as obligate grazing, while other studies [74] found the grass intake ratio to be in the lower range with seasonal differences. In contrast, mouflons—and sheep [81]—showed a stable grass consumption proportion with no seasonality. Loison et al. [82] discussed interspecific competition among ibex, chamois, and mouflon. Referring to the impact of body size difference between red deer and mouflons [83][84][85], with red deer displacing mouflons, the same impact is described in relation to mouflons and chamois. Habitat partition occurs as the chamois moves to safer, higher places because of the presence of mouflons [31]. The same displacement behavior was reported in the Pyrenees [74]. Habitat selection and home range use preference are crucial to understanding species interactions and resource sharing. Individuals can exploit abundant resources, but when resources are constrained, the high diet niche overlap leads to competition [74]. Homolka's [54] and Heroldová's [73] high diet overlap analysis result between red deer and mouflons in Central Europe was confirmed by Dremmel [72] in Hungary and by Bertolino et al. [74] in Alpine regions as well. They proved that these two herbivores share similar resources and, at the same time, also confirmed the low diet overlap with roe deer. These results also prove the limitations of exclusion experiments, which underscores the necessity for a complex view of mouflon-caused trampling and browsing damages when it shares ranges with red deer. It also draws the invasive character of the mouflon into question.

Climate warming poses new problems in terms of the effects of habitat selection, use, and consequently feeding. As climate change accelerates, experiment results gained in France's Caroux Massif provide forward-looking insights into mouflon population management and the conservation of temperate, protected areas. Mammal thermoregulation is either behavioral or autonomic (involuntary, e.g., sweating). Behavioral thermoregulation lasts longer at a lower cost versus autonomic reactions [64] and stands as a primary response to thermal conditions crossing the critical threshold. Past this limit, large herbivores adapt by changing their thermogenic foraging strategies and their habitat preference for higher thermal coverage, i.e., moving to the woods from moorland [64]. Marchand et al. [64] measured a sex- and scale-dependent response to hot periods. Females selected better foraging opportunities over thermal cover for lambing and avoided unsafe plateaus. Older males preferred selected forests on the plateau with thermal cover. On the hottest days, both sexes preferred forests, and rams leveraged the moorlands' food and thermal cover until twilight, while females exchanged food and cover for shelter. Within seasonal and diurnal shifts, thermal conditions play an increasingly vital role in habitat use and preference in winter (snow coverage) and summer. Nature conservationists and wildlife managers should consider this.

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