



# Mouflon *Ovis gmelini* Blyth, 1841

# 21

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## Common Names

English	Mouflon
German	Mufflon
French	Mouflon
Spanish	Muflón
Italian	Muflone
Russian	Муфлón

In Cyprus, the Greek name for this species of sheep is Αγρινό.

## Taxonomy and Systematics

The genus *Ovis* constitutes one of the most complex mammalian genera owing to its evolution and systematic. During the last centuries, wild

sheep taxonomy was revised many times based on different criteria (morphologic, genetic, and biogeographic, e.g., Valdez 1982; Festa-Bianchet 2000; Hiendleder et al. 2002; Rezaei et al. 2010). Wild sheep taxonomy has been complicated by the fact that the different species of the genus *Ovis* can crossbreed and produce fertile offspring (Valdez et al. 1978; e.g., in the Asiatic mouflon/Urial *Ovis vignei* hybrid zone; Fig. 2), leading some authorities to consider, for instance, Asiatic mouflon and Urial as the same species (*Ovis orientalis*). A basic difference among classifications lies in the number of species recognized. No definitive consensus was achieved, but most classifications distinguish at least three morphological types (Bunch et al. 2006) and six wild species: Pachyceriforms of Siberia and North America, *Ovis canadensis* (bighorn sheep,  $2n = 54$ ), *Ovis*

*dalli* (Dall sheep,  $2n = 54$ ), and *Ovis nivicola* (snow sheep,  $2n = 52$ ); Argaliforms of Central Asia, *Ovis ammon* (Argali,  $2n = 56$ ); Moufloniforms of Eurasia, *Ovis vignei* (Urial,  $2n = 58$ ), and *Ovis gmelini* (Asiatic mouflon,  $2n = 54$ ). Note that the name *Ovis orientalis* has often been used/recommended for Asiatic mouflon (Shackleton and IUCN/SSC Caprinae Specialist Group 1997), but as it seems to refer to a hybrid of Alborz red sheep (Valdez 1982), the name is unusable and may enter into homonymy (Groves and Grubb 2011; Hadjisterkotis and Lovari 2016).

The scientific denomination of mouflon present in Mediterranean islands (Cyprus, Corsica, and Sardinia), and subsequently introduced into continental Europe during the eighteenth century (Weller 2001; Fig. 1), is probably among the most controversial (e.g., Cugnasse 1994; Gentry et al. 2004; Rezaei et al. 2010; Guerrini et al. 2015). However, archaeological (Poplin 1979; Vigne 1992; Groves 1989) and genetic evidence (e.g., Chessa et al. 2009; Rezaei et al. 2010; Demirci et al. 2013; Guerrini et al. 2015; Mereu et al. 2019; Portanier et al. 2022) that has now accumulated gives strong support for ranking them as subspecies of Asiatic mouflon *O. gmelini* (see also subsection “Phylogeny and Phylogeography”). Most recent genetic advances, based on microsatellite and mitochondrial DNA, separate into two independent subspecies the Corsican/Sardinian *O. g. musimon* and the Cyprus populations *O. g. ophion* which had a separate evolutionary history (Chessa et al. 2009; Guerrini et al. 2015, 2021; Sanna et al.

2015; Satta et al. 2021; Portanier et al. 2022). It can also be mentioned that Cugnasse (1994) suggested to differentiate Corsican and Sardinian mouflon by using *O. g. musimon* var. *corsicana* and *O. g. musimon* var. *musimon*, respectively, to account for the demographic disconnection occurring since Neolithic between the two island populations.

## Paleontology

The oldest fossil of mouflon *Ovis shantungensis* was found in central Asia (China, Nihowan) and would be dated  $>2$  mya (Teilhard de Chardin and Piveteau 1930). During the Pleistocene, the genus *Ovis* has evolved from this ancestral area, through successive speciation events, in at least six wild species (see section “Taxonomy and Systematics”), while spreading along two major migration routes: the first passing through northeastern Asia and Bering Strait toward North America, the second one going toward Eurasia and western Europe. Nowadays, the genus *Ovis* is largely distributed over palearctic and nearctic regions (Valdez 1982).

Mouflon present in Europe originated from Asiatic mouflon that arrived about 8500 years before the common era (BCE hereafter), at the onset of the very first waves of human-mediated dispersal of livestock across the Mediterranean Basin (Zeder 2008; Vigne et al. 2014). Relics of these very first migrations include the historically genetically and morphologically preserved mouflon populations



**Fig. 1** A male (left), a female and a lamb (right) of Mediterranean mouflon (photographs © Daniel Maillard – [www.danielmaillard.com](http://www.danielmaillard.com))

presently restricted to the islands of Cyprus, Corsica, and Sardinia (Chessa et al. 2009; Rezaei et al. 2010; Guerrini et al. 2015, 2021; Sanna et al. 2015; Mereu et al. 2019; Satta et al. 2021; Portanier et al. 2022). In these islands, Asiatic mouflon would have been introduced by Neolithic people, probably after a predomestication phase, between 4500 and 8500 years BCE as suggested by archaeological evidences in Neolithic sites (Poplin 1979; Groves 1989; Vigne 1992; Zeder 2008; Vigne et al. 2012, 2014). The domestication process is assumed to have remained primitive, likely limited to protection against predators with few interactions with humans and no morphological selection (Rezaei 2007; Zeder 2008). In addition, by returning to a feral state in mountainous areas of these scarcely populated islands, these primitive breeds survived, contrary to mainland populations, to the second migration of improved breeds (with productive traits such as wool, milk, and meat) occurring 5000–6000 years later from southwest Asia (Zeder 2008; Chessa et al. 2009; Barbato et al. 2017; Ciani et al. 2020).

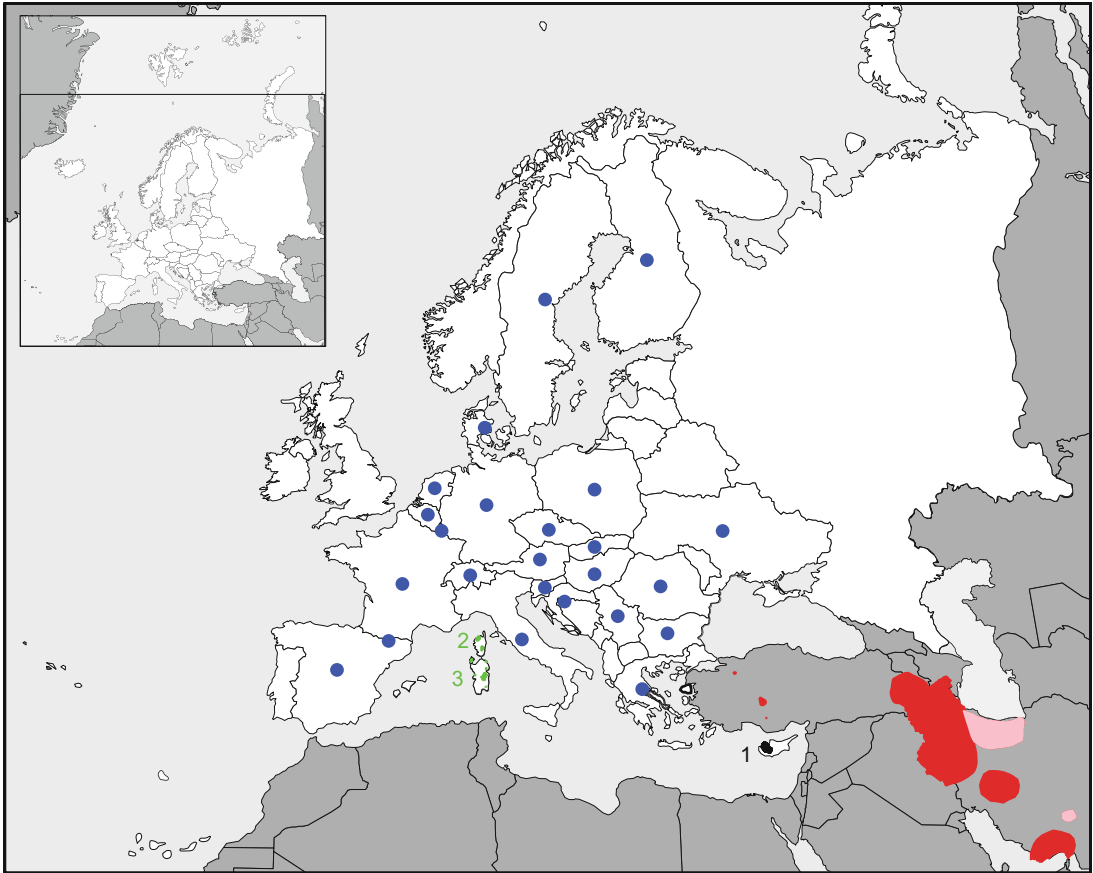
## Current Distribution

The native range of Asiatic mouflon includes 4 subspecies (Festa-Bianchet 2000) and extends from eastern Turkey, Armenia, southern Azerbaijan (including Nakhchivan Autonomous Republic), and northern Iraq to western Iran (Zagros mountains, southern Caucasus) for the Armenian mouflon *Ovis gmelini gmelini*, with isolated populations in central Iran for the Isfahan mouflon *Ovis gmelini isphahanica* and southern Iran for the Laristan mouflon *Ovis gmelini laristanica* (Fig. 2). It also includes an area where mouflon crossbreed with Urial *Ovis vignei* sp. The population of Anatolian mouflon *Ovis gmelini anatolica* in south-central Turkey (Konya-Bozdag area), previously isolated, is highly protected with most individuals being enclosed since 1989. Two populations (Karaman-Karadag and Ankara-Sariyar) have been created from reintroductions between 2004 and 2007 with individuals from the Konya-Bozdag area (60 and 120 founder individuals, respectively; Özüt 2009). The last population estimates were around

700 Anatolian mouflon in the Konya-Bozdag-enclosed population (after 200 individuals were removed for reintroductions), and 50–100 individuals outside the fences (Özüt 2009).

Populations created from feral individuals after the very first domestication attempts of Asiatic mouflon between the Neolithic and the Upper Paleolithic are restricted to the Mediterranean islands of Cyprus, Corsica, and Sardinia (see sections “Paleontology” and “Phylogeny and Phylogeography”; Fig. 2). In Corsica, there are two populations: one in the massif of Monte Cinto (Northwest, >900 individuals), and one in the massif of Bavella (Southeast, >200 individuals; Benedetti et al. 2019; Portanier et al. 2022). In Sardinia, the current distribution is limited to the eastern part of the island (Ogliastra, Gennargentu, Supramonte, and Albo; ~6000 individuals), Montiferru in the West, and a few managed/protected areas where the species has been introduced (Pabarile, Capo Figari, and Asinara; Apollonio et al. 2010; Puddu and Maiorano 2016; Satta et al. 2021). The Cyprus mouflon is present in the Paphos forest (North-West of the island; ~3000 individuals; Hadjisterkotis 2001) and recently extended its range toward Troodos mountains (Nicolaou et al. 2016).

Since the eighteenth century (see subsection “Phylogeny and Phylogeography”), mouflon have been introduced as a new game species in 24 European countries: Andorra, Austria, Belgium, Bulgaria, Croatia, the Czech Republic, Denmark, Finland, France, Germany, Greece, Hungary, Italy, Luxembourg, Netherlands, Poland, Romania, Serbia, Slovakia, Slovenia, Spain (including Canary islands, i.e., Tenerife, La Palma, and La Gomera), Sweden, Switzerland, and Ukraine (Fig. 2; Weller 2001; Linnell and Zachos 2011; Cassinello 2018). Mouflon were also introduced in Argentina, Chile, and the USA (California, Texas, and Hawaii; Weller 2001) and are also present in fenced areas or hunting estates in numerous countries. It has to be noted that the population from Kerguelen islands (French Southern and Antarctic Territories), of conservation concerns with endemic plants, has been eradicated in the 2010s (Terres Australes et Antarctiques Françaises 2013).



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**Fig. 2** Current distribution of mouflon in Europe. Native populations are represented in red (*Ovis gmelini gmelini*, *Ovis gmelini anatolica*, *Ovis gmelini isphahanica*, and *Ovis gmelini laristanica*; data from the International Union for Conservation of Nature, <http://maps.iucnredlist.org/map.html?id=15739>) or pink (area where *Ovis gmelini gmelini* and *Ovis gmelini laristanica* cross-bred with Urial *Ovis vignei* sp.). Although some of these subspecies are referenced as *orientalis* on the IUCN red list, we used *gmelini* here in accordance with the section

“Taxonomy and Systematics” and, e.g., Festa-Bianchet (2000). The mouflon populations on Mediterranean islands are represented in black ([1] Cyprus *Ovis gmelini ophion*) and green ([2] Corsica and [3] Sardinia *Ovis gmelini musimon*; data from Hadjisterkotis 2001; Corti et al. 2011; Puddu and Maiorano 2016). The European countries where mouflon persist after being introduced are noted with a blue point. Note that the countries where mouflon are present only in captivity are not reported on this map  
Map template: © Copyright Getty Images/iStockphoto

## Description

### Size and Morphology

The complex genetic and demographic history of island populations and of introduced populations of mouflon (see sections “Paleontology” and “Phylogeny and Phylogeography”) has contributed, through genetic founding effects and/or high variability in environmental conditions encountered, to

generate large inter-population variation in body and horn development. This is well illustrated by population-specific horn growth patterns (e.g., Hoefs 1982; Hoefs and Hadjisterkotis 1998; Figs. 3.5 and 7.2 in Garel et al. 2006b). To account for these inter-population differences, we summarized in Table 1 >3500 adult morphological and body mass measurements collected from known-age animals in 9 French populations spanning a large range of environments (ranging from 180 to

**Table 1** Adult morphological and body mass measurements (95% prediction interval) in 9 French continental and island populations of mouflon. Data were collected both during spring-summer (capture) and autumn-winter (capture and hunting). We reported values taken at

$\geq 7$  years and  $\geq 4$  years old for males and females, respectively, i.e., when asymptotic body growth has been reached for most of the measurements (Hoefs and Hadjisterkotis 1998; Lincoln 1998; Garel et al. 2005d; Hamel et al. 2016)

Metrics	Males	Females	Sample sizes (males–females)	Populations <sup>a</sup>
Tail length	Bony, very short (<10 cm)		–	–
Body length (cm)	124.5–145.6	102.7–133.8	95–201	1, 2
Hind foot length (cm)	30.7–35.3	28.8–33.5	155–598	1, 3, 6
Shoulder height (cm)	70.6–86.8	61.4–80.4	97–200	1, 2
Neck circumference (cm)	30.1–48.8	20.8–33.6	99–294	1, 3
Horn length (cm)	48.6–90.3	0.5–19.1	295–121	1, 2, 3, 4, 6, 7, 8
Body mass <sup>b</sup> (kg)	26.1–61.8	18.8–37.7	268–1078	1, 2, 3, 5, 6, 7, 8, 9

<sup>a</sup>Populations: 1 – Caroux-Espinouse massif (43.63 °N, 2.97 °E); 2 – Gap-Chaudun massif (44.63 °N, 5.98 °E); 3 – Cinto massif (42.38 °N, 8.90 °E); 4 – Chartreuse massif (45.33 °N, 5.79 °E); 5 – West Vercors massif (44.86 °N, 5.26 °E); 6 – Bauges massif (45.69 °N, 6.24 °E); 7 – Queyras massif (44.76 °N, 6.88 °E); 8 – Briançonnais massif (44.97 °N, 6.61 °E); and 9 – North-East Vercors massif (45.11 °N, 5.56 °E)

<sup>b</sup>Combining live body masses and eviscerated body masses converted into live body masses using the allometric equation:  $\text{live} = e^{0.4131} \times \text{eviscerated}^{0.9687}$  calibrated on 88 animals for which we had both measurements

2966 m a.s.l., from 2.97 to 8.90 °E, from 42.38 to 45.69 °N, and from Mediterranean/island areas up to mountain ranges) and genetic origin (e.g., Garel et al. 2005a; Portanier et al. 2017). Newborn (<1 week) body mass ranges between 1.6 and 3.4 kg (Mottl 1960; Pfeffer 1967; Briedermann 1989; Hadjisterkotis 1996b). It has to be noted that island populations might have undergone island dwarfism during their evolutionary history (e.g., shoulder height in Cyprus: males = 68.0 cm, females = 61.4 cm,  $n = 13$  versus continental populations in Table 1; Pfeffer 1967; Hadjisterkotis 1993, 1996b).

Mouflon are among the smallest wild *Ovis* in the world (Valdez 1982) with a marked sexual dimorphism both in terms of size and body mass (up to ~64% during autumn), horn and coat (Table 1; see subsections “Pelage” and “Growth”). While males have large horns, females may or may not have short horns (Hoefs and Hadjisterkotis 1998; Garel et al. 2007). When present, the horns of females are thin, often asymmetric with a circular shape. In males, horns are thick, with a triangular basis and a circumference that decreases from the base to the tip (Fig. 1). They are also symmetric and show three sides with a marked fronto-nuchal edge and the fronto-orbital edge almost completely rounded off. Differences in skull design between males and females have been revealed and

hypothesized to play a role in the mitigation of the considerable forces that exert on the horns and skulls of mouflon during head-to-head horn clashes (Schaffer 1968; Schaffer and Reed 1972; Jaslow 1989).

The high diversity in origin of populations and in the environments that they inhabit has also contributed to large inter-population variation in phenotypic characteristics of this species. For instance, marked differences in the proportion of horned females among populations have been documented: from 43% in the Corsican population of Bavella (only 13% in the other Corsican population of Cinto; Sanchis 2018) to values close or equal to 0%, both in island populations (Sardinia, Pfeffer 1967; S. Ciuti, pers. comm.; Cyprus, Maisels 1988; Hadjisterkotis 1993) and in most of the introduced populations (Pfeffer and Genest 1969; McClelland 1991). The fact that hornless females is the rule in most introduced populations would originate from a much larger contribution of animals coming from Sardinia than Corsica during the early phases of introduction of mouflon in continental Europe (Pfeffer and Genest 1969; Apollonio et al. 2010). Similarly, large variation in the form of horns occurs in males that can partly result, in some populations, from artificial selections against desirable or undesirable trophy characteristics (Garel et al. 2007; Schröder et al.

2016). Horns in males can be heteronymous (left horn first twists clockwise and then anticlockwise) or perverted (growth in the same plane with sickle-shaped horns), curving back behind the head toward the anterior-posterior axis of the body, with tips directed above the neck (supracervical) or at the sides of the neck (cervical; Fig. 1; Pfeffer 1967; Groves and Grubb 2011). In both cases, the basic growth pattern is converging with a relatively narrow tip-to-tip spread when compared to greatest spread as animals aged. With the notable exceptions of Cyprus and Armenian mouflon, the supracervical horn growth is rare in wild sheep (Hoefs and Hadjisterkotis 1998; Groves and Grubb 2011; Hadjisterkotis et al. 2016). At the opposite, distinct homonymous horn curl configuration also exists (left horn twists clockwise), where the tip-to-tip spread equals the widest spread with horn tips pointing outward the anterior-posterior axis of the body as animals get older. Intermediate types exist, with, for instance, horns angling more vertically, with a more parallel horn growth pattern with the tips turning inward toward the neck/face in a tight circle (Pfeffer 1967; Groves and Grubb 2011).

## Pelage

The typical pelage coloration exhibited by females varies from light tan to dark brown (Valdez 1982). The dorsal patch is absent or indistinct. Lambs are similar in appearance to ewes. In males, short, coarse, and thick hair forms the outer coat (Frisina and Frisina 2000). The general color of the coat on mature rams is rufous brown or foxy red shading into chocolate brown on the head and face. A black coat is found on sides of the neck, throat, and chest with a band on the flanks and down the withers, on the outer front surfaces of the forelegs above the knees, and on the front and outer sides of the hind limbs above the hocks (Valdez 1982; Frisina and Frisina 2000). Ears are grayish with the margins and part of their interior that are white. White/grayish coat is also found as a broad band on the rear border of the saddle patch and on muzzle and chin shading into grayish rufous in the middle of the black area on the

throat. Similarly, the buttocks and all under parts are white, except for a narrow black streak down the forelegs. Limbs also exhibit a streak of white on their back surface above the knees and hocks. In winter coat, the general color of the upper parts deepens and becomes more of a chestnut brown. The saddle patch on each side of body (not systematically present in some populations) lightens until in many older rams it becomes nearly white (Frisina and Frisina 2000). Both males and females display a white facial mask which shows a great inter-individual variability in size (Garel et al. 2005d, 2006a; see also subsection “Age Determination”).

## Age Determination

Excepted in lambs (when less than 6 months old) for which error in age determination is very unlikely (Garel et al. 2006a), horn annulus technique in males (Geist 1966; Hemming 1969) and tooth eruption and replacement of the lower incisors in both sexes (Rieck 1975; Piegert and Uloth 2005) are the only reliable criteria used to estimate age when handling animals. Tooth eruption pattern allows a reliable estimation of age until 3.5 years in autumn-winter (the hunting season for ungulates in most countries; e.g., Milner et al. 2006) during which five stages of tooth eruption can be described: no permanent incisor for lambs, two permanent incisors for yearlings, four permanent incisors for 2.5 years old, six permanent incisors for 2.5–3.5 years old, and eight permanent incisors for  $\geq 3.5$  years old. In males, the horn annulus technique (Geist 1966; Hemming 1969), which is based on counts of horn growth annuli, provides an index of age to the nearest year. Horn growth annuli correspond to drastic reduction of horn growth which mainly results from hormone-induced factors related to the reproductive cycle and from photoperiod (see subsection “Horn Growth and Reproductive Activity”). This index becomes less accurate as the animal aged and the first horn annulus is worn away.

From observations in the field, different morphological criteria have been used to estimate the

age categories of mouflon (Türcke and Schmincke 1965; Pfeffer 1967; Tomiczek 1989; Boussès and Réale 1994). In males, observers have principally relied on the position of the horn tip relative to the base of the neck and eyes (the so-called circular arc theory; Piegert and Uloth 2005). In females, the size of the white facial mask, which corresponds to a whitening of the hair of the face, was considered to progress from the nostril toward the face as animal aged. From these criteria, field studies (e.g., Le Pendu et al. 1995; Ciucci et al. 1998; Cransac et al. 1998; Réale et al. 1999) generally distinguished between lambs, yearlings (1 year), and 2–3 wider age categories as animals get older and inter-individual variation in age criteria increases (e.g., 2–3, 4–6, and >6 years old; Bourgoïn et al. 2018). However, except in lambs, errors in age determination are common (>20% in adult males and >50% in adult females; Boussès and Réale 1994; Garel et al. 2005d, 2006a).

## Physiology

### Thermoregulation

Mouflon, as all other homeothermic animals, regulate their own body temperature through internal metabolic processes. Heat stress affects significantly the heat balance, and the main thermoregulatory mechanisms are the reduction in heat production, the increase in heat loss (Johnson et al. 2003), and the molting of the pelage (Lincoln 1990). Seasonal changes in annual and daily prolactin secretion and their relationships with melatonin secretion, metabolism, and thermoregulation have been reported in mouflon. Seasonal changes have been shown to be associated with changes in day length, with highest and lowest concentrations of prolactin occurring during summer (long days) and winter (short days), respectively (Lincoln 1990; Santiago-Moreno et al. 2004). Spring molt is timely associated with rising plasma prolactin concentrations, and hair growth, that takes place between the summer and winter solstices, coincides with low-plasma concentrations of prolactin (Santiago-Moreno et al. 2004).

In addition, an endogenous circannual rhythm of molting has been demonstrated in this species (Allain et al. 1994). Lastly, it has also been suggested that horns core might contribute to the heat exchanges in mouflon and play as such a thermoregulatory role in this species (Hoefs 2000).

### Horn Growth and Reproductive Activity

The body mass is the prevailing factor determining horn growth throughout the first year of age (Santiago-Moreno et al. 2006). Thus, young mouflon rams, aged up to 18 months, exhibit a regular and nonseasonal development of horns through the year under captive regimen (Santiago-Moreno et al. 2000b). Afterward, in subadult (2 years old), adult ( $\geq 3$  years old), and old ages (>10 years old), the rate of horn growth shows a seasonal pattern modulated by day length (Lincoln 1998) with largest monthly growth occurring in spring and summer (Santiago-Moreno et al. 2005a). The greatest growth in length occurs within the first 2–3 years of life and subsequently decreases year by year (e.g., Garel et al. 2005d).

The annual cycles of reproductive activity and horn growth follow opposite trends (Lincoln 1990), although both are mainly regulated by circulating testosterone levels and photoperiod (Toledano-Diaz et al. 2007). The onset of horn growth arrest in the mouflon coincides with maximum testosterone secretion in the pre-mating season. The horn growth is at a minimum during the period of optimum sperm production and maximum testis and accessory sex gland activity (autumn). The rate of horn growth before the mating season may be related to springtime testosterone levels (Toledano-Diaz et al. 2007; Santiago-Moreno et al. 2012). The greater horn growth in spring involves an appreciable use of energy resources. The decrease of photoperiod in autumn appears to act as a signal to stop horn growth, allowing energy resources to be diverted toward combat and the production of better quality semen. Interestingly, the improvement of sperm quality in mouflon occurs between September and December, coinciding with the



preparing and mating seasons in this species. Normal sperm cell morphology is closely linked to the correct progress of spermatogenesis and is essential for optimum sperm function and fertilization capacity (Martínez-Fresneda et al. 2019). The resurgence of horn growth in spring is positively correlated with the percentage of spermatozoa with morphological abnormalities (Santiago-Moreno et al. 2003).

## Reproductive Physiology

As reported in many species of large ungulates (Gaillard et al. 2000), body mass, more than age, appears to be the main factor controlling sexual maturity and reproductive performance in mouflon ewes and rams (Lincoln 1989; Santiago-Moreno et al. 2001b; Garel et al. 2005a). In females, onset of puberty is thus found to depend on a body mass threshold corresponding to ~80% of the adult body mass (Santiago-Moreno et al. 2000a, 2001b; similar threshold has also been found in other ungulates: Hewison 1996; Sand 1996) that can be reached in ewes during the first or second year of life (Mottl 1960; Lincoln 1998; Santiago-Moreno et al. 2001b). Similarly, males may initiate full spermatogenesis (male puberty) during their first year of life (Lincoln 1998). However, in males, physical maturity is also necessary for successful matings, and only rams 3 years old or more have been observed in rutting activities (Bon et al. 1992, 1995; Lincoln 1998).

During the reproductive period, ovulatory activity, assessed by measuring the plasma progesterone concentration in blood samples, reveals a mean duration of the oestrus cycle of 17 days. Ovulations are expected to be highly synchronized (Santiago-Moreno et al. 2001b) leading to highly synchronized births (80% of births may have occurred in 3–6 weeks; Bon et al. 1993a; Hadjisterkotis and Bider 1993; Garel et al. 2005a). Photoperiod is generally accepted as the primary environmental cue influencing seasonal breeding pattern, mediated via the pineal gland and melatonin secretion (Santiago-Moreno et al. 2000c). Other environmental variables, such as climate-

related seasonal variation in resource availability, are also expected to shape the timing and synchrony of reproduction in large herbivores (Bunnell 1982; Rutberg 1987). Geographical variation in these factors probably contributes to explain the inter-population differences in the timing and synchrony of breeding activities reported in the literature (Pfeffer 1967; Lincoln 1989; Bon et al. 1993a; Santiago-Moreno et al. 2001b; Garel et al. 2005a). However, as a genetic basis for photoresponsiveness has also been found in both sheep (*Ovis aries*) and wild ruminants (Santiago-Moreno et al. 2001b), the genetic history of populations (see sections “Paleontology” and “Phylogeny and Phylogeography”) could also contribute to the regional differences reported. In females, the existence of an endogenous rhythm of reproduction is synchronized through the circadian rhythm of melatonin secretion (Gómez-Brunet et al. 2008). Uterine regression and resumption of ovulatory activity after parturition is about 25 days, although ovulatory activity in the early postpartum period is not always associated with successful conception and pregnancy (Santiago-Moreno et al. 2001a).

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## Genetics

### Chromosomes

$2n = 54$  (Nadler et al. 1973)

### Phylogeny and Phylogeography

The Armenian mouflon *Ovis gmelini gmelini*, from western Iran and easternmost Turkey, and the Anatolian mouflon *O. g. anatolica*, endemic to central Anatolia (Fig. 2), are considered to be the most likely ancestors of all breed of domestic sheep (DNA analyses: Hiendleder et al. 2002; Bruford and Townsend 2006; Demirci et al. 2013; Sanna et al. 2015; chromosome number: Nadler et al. 1973; Valdez et al. 1978; type of hemoglobin A: Bunch et al. 1978). It is also widely acknowledged that mouflon present in Europe are the feral descendants of the very first

domesticated Asiatic mouflon introduced by Neolithic people during the first waves of sheep domestication across the Mediterranean Basin (see section “[Paleontology](#)”).

Some authors have initially considered mouflon present in Mediterranean islands and subsequently introduced into continental Europe (see section “[Current Distribution](#)”) as belonging to a full species *O. musimon* (Nadler et al. 1973). The most recent classifications considered them either as subspecies of Asiatic mouflon *O. gmelini musimon/ophion* (e.g., Cugnasse 1994; Shackleton and IUCN/SSC Caprinae Specialist Group 1997; Festa-Bianchet 2000; Hadjisterkotis and Lovari 2016; see section “[Taxonomy and Systematics](#)”) or of domestic sheep *O. aries musimon/ophion* due to the predomestication phase that they have undergone (e.g., Wilson and Reeder 2005; International Commission on Zoological Nomenclature; Bern Convention, Table 2). However, while sheep domestication occurred ~9000 years BCE (Zeder 2008), divergence times up to 110–171 kya between sheep and mouflon haplotypes have, for instance, been reported in mitochondrial phylogeny of Sardinian and Cyprus populations (Sanna et al. 2015; Mereu et al. 2019). These populations thus did not originate from domestic sheep but have evolved separately. The same is expected for the Corsican mouflon which share a large part of their history with those from Sardinia (Satta et al. 2021; Portanier et al. 2022). This gives support for considering mouflon on Mediterranean islands as wild taxon rather than as domestic subspecies (Guerrini et al. 2015; Portanier et al. 2022). They should thus be unvaryingly referred to as *Ovis gmelini musimon/ophion*, i.e. as subspecies of the Asiatic mouflon. This taxonomic designation should help protecting the rare gene pools of these populations (Chessa et al. 2009; Guerrini et al. 2015; Hadjisterkotis and Lovari 2016; Mereu et al. 2019; Portanier et al. 2022) which have been preserved in their historical ranges from genetic introgression from domestic breeds (see subsection “[Hybridization](#)”).

Cyprus mouflon occupies a place apart in the history of sheep domestication being at the start of the migration routes toward western regions which

were reached by human expansion a few hundreds of years later after the first archeological evidences of domestication in the fertile crescent (Zeder 2008; Mereu et al. 2016). Mouflon were introduced 2500–4000 years later in Corsica and Sardinia (Poplin 1979; Vigne 1992; Portanier et al. 2022). This history has contributed to the genetic isolation among islands that persists since Neolithic times and the likely existence of many historical events to the present-day genetic differentiation among Cyprus and western populations (Chessa et al. 2009; Guerrini et al. 2015, 2021). In addition, it cannot be completely discarded that wild mouflon would have arrived by their own on Cyprus during the last ice age when the Mediterranean sea level was 125 m below the current sea level (Hadjisterkotis 2012). Cyprus is geographically close to the native populations (Fig. 2), and Cyprus mouflon was found to be phenotypically and genetically closely related to Anatolian individuals carrying the rare haplotype X at the D-loop region (Demirci et al. 2013; Sanna et al. 2015; Guerrini et al. 2021).

Mouflon from Corsica and Sardinia were later introduced into continental Europe (Uloth 1972; see also section “[Current Distribution](#)”). The first recorded introduction would date of 1729–1731 (Uloth 1972; Tomiczek 1989; Weller 2001) by Prince Eugen of Savoy in the game pasture of Belvedere, near Vienna, Austria. The origin of continental mouflon populations is often uncertain, and some evidences of crossbred with other domestic sheep, feral, or wild mouflon have been reported, raising caution on the genetic integrity of these populations (but see subsection “[Hybridization](#)”). Related to this uncertainty in the level of hybridization within introduced populations, Cugnasse (1994) suggested referring to them by adding the suffix “× *Ovis* sp.” to the Latin name. This author also suggested referring to Mediterranean mouflon rather than European mouflon to keep track of the geographical origin of the founding populations.

## Genetic Diversity

Ancestral populations seem to exhibit depleted levels of allelic richness and/or heterozygosity

(e.g., Anatolian, Corsican, Sardinian and particularly Cyprus populations, Özüt 2001; Guerrini et al. 2015; Barbato et al. 2017; Satta et al. 2021; Portanier et al. 2022). In some of these populations, strong demographic bottlenecks have been reported (e.g., Pfeffer 1967; Özüt 2001; Kaya et al. 2004; Satta et al. 2021), possibly explaining this limited genetic diversity, although genetic bottlenecks have not been detected in Cyprus and Anatolian populations (Özüt 2001; Guerrini et al. 2015). On the other hand, introduced populations have been evidenced to have a higher than expected heterozygosity (Kaeuffer et al. 2007; Portanier et al. 2017) that may have contributed to their persistence despite a very low number of founder individuals (e.g., one male and one female in Kerguelen Archipelago).

Genetic diversity is an important element in conservation purposes since it can be linked to individual phenotypes and fitness (e.g., twinning rate, Kaeuffer et al. 2008; parasite resistance, Portanier et al. 2019) and thus to the adaptive potential of populations (Hedrick 2011). Several populations benefit from conservation measures such as a reintroduction programs (Corsica, Sardinia, Cyprus, and Turkey; Hadjisterkotis and Bider 1993; Özüt 2001; Berlinguer et al. 2005; Rieu 2007) to increase population sizes, favor population expansion, and enrich the genetic diversity (see section “[Management](#)”). Cloning and assisted reproductive technologies have even been considered as conservation measures (Loi et al. 2001; Hosseini et al. 2009; Hajian et al. 2011).

## Hybridization

Introgression of domestic or non-native genetic material, which may occur due to hybridization between the different *Ovis* species, might be considered as a threat since it can cause phenotypic modifications (e.g., be larger, Hess et al. 2006), with possible negative effects on fitness (e.g., loss of local adaptations, Burke and Arnold 2001) and, when really high, raise questions about the definition and the delimitation of a species. Several Iranian populations have been shown to

hybridize with Urial (Valdez et al. 1978; Fig. 2). Across Europe, hybridization occurs with domestic sheep, either because of contact zones between domestic and wild sheep (e.g., in Armenian and Sardinian mouflon, Bleyhl et al. 2018; Satta et al. 2021), or due to deliberate crossbreeding with primitive domestic breeds to improve fecundity or body/trophy growth (Türcke and Schmincke 1965; Uloth 1972; Lorenzini et al. 2011; Ciani et al. 2014; Schröder et al. 2016; Barbato et al. 2017). However, recent investigations in several continental and island populations show that introgression of domestic sheep into mouflon is not systematic and most often negligible, especially in historical mouflon range of island populations where populations appear overall pure (Schröder et al. 2016; Barbato et al. 2017; Iacolina et al. 2019; Mereu et al. 2019; Ciani et al. 2020). In harvested continental populations, the removal of animals with undesirable characteristics might have contributed to explain the low level of introgression detected (Schröder et al. 2016; Iacolina et al. 2019). In island populations, by occupying remote/mountainous areas, resident populations were less prone to genetic introgression from domestic sheep, and such introgressions from not locally adapted breeds were most likely counterselected by natural and sexual selection.

## Population Genetics and Structuring

Genetic differentiation between mouflon populations has been shown to be relatively high (e.g., Corsica versus mainland France, Portanier 2018). Within populations, a marked sex-specific genetic structure can also be expected (e.g., in Sardinia, Satta et al. 2016, 2021, in Corsica, Portanier et al. 2022 but see Barbanera et al. 2012 in Cyprus) due to the sex-specific space-use (Marchand et al. 2015a, b, 2017) and the strong spatial segregation between sexes (e.g., Bourgoin et al. 2018). In a French-introduced population, this socio-spatial behavior has been found to reduce gene flow among females socio-spatial units (Petit et al. 1997; Portanier et al. 2017, 2018) and to contribute to the persistence

of a historical genetic footprint more than 14 generations after mouflon introduction (Portanier et al. 2017). The socio-spatial behavior of ewes relies on a strong philopatry (Dubois et al. 1992, 1994; Martins et al. 2002) and a preponderant role of habitat characteristics on female movements and habitat selection (Marchand et al. 2015a, 2017; see section “**Habitat and Diet**”). Among habitat characteristics, both natural and anthropogenic linear landscape features, and, to a lower extent, habitats avoided during the rutting period (i.e., habitat perceived as unsafe or offering low quantity and quality resources), have been found to be resistant to gene flow (Portanier et al. 2018). Conversely, habitats selected during the rutting period (i.e., perceived as safe or offering resources) would be much more permeable. This is the case for steep slopes (used as refuge against predators) that appear to be an important determinant of landscape genetic resistance in mouflon (Portanier et al. 2018) as reported for several other wild sheep species (see Epps et al. 2007; Roffler et al. 2016).

Rams are expected to insure most of the gene flow in mouflon (Portanier et al. 2017) due to their relaxed spatial behavior (Dubois et al. 1993, 1996) and reproductive dispersal, i.e., excursions outside their home ranges during the rutting period (Martins et al. 2002; Malagnino et al. 2021), as well as the limited impacts of linear landscape features on their movements (Marchand et al. 2017). This contributes to a much lower genetic structuring in males than in females (Portanier et al. 2017).

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## Life History

### Growth

Few studies have reported information on the prenatal growth pattern of mouflon. Santiago-Moreno et al. (2005b) found 12 body size metrics studied by transrectal ultrasonographic measurements on captive ewes to be closely related to gestational age by simple linear or allometric models. The postnatal growth pattern of mouflon has been better investigated (e.g., Hoefs 1982;

Garel et al. 2007), but more in males than in females for which no reliable age criteria exist above 4 years-old (see subsection “**Age Determination**”). In males, growth patterns were often based upon hunting records, i.e., transversal data that may bias age-related patterns (Cam et al. 2002), or from the longitudinal monitoring of a restricted number of known-age animals experiencing captive conditions with a supplementary feeding (e.g., Lincoln 1998; Santiago-Moreno et al. 2005a). To overcome these limits, we analyzed data from free-ranging mouflon of known-age trapped during spring (before summer drought) in the Caroux-Espinouse population (for more details on the population and study site, see Garel et al. 2005a, 2007; Marchand et al. 2014a, 2015a). Mouflon show typical monomolecular patterns of growth (Gaillard et al. 1997) with males being larger and experiencing active growth in body mass ( $n = 662$ ) and hind foot length ( $n = 392$ ) for a longer period than females ( $n = 521$  and  $360$ , respectively). Sexual dimorphism was marked from 6 months of age onward with adult males that weighed in average 44.2% more than adult females and that had skeletal size in average 7.1% longer (see also Table 1 for data collected all over the year). Males reached their asymptotic body size and mass at 3 and 7 years-old, i.e., approximately 1 and 3 years later than females, respectively. As already mentioned for phenotypic characteristics (see subsection “**Size and Morphology**”), postnatal growth shows large inter-population variation in this species (e.g., Figs. 3.5 and 7.2 in Garel et al. 2006b).

### Reproduction

An early onset of reproduction (~6–10 months-old) has been reported in some populations (Land 1978; Briedermann 1992; Garel et al. 2005a; Sanchis 2018) with up to 50% of female lambs pregnant (see also subsection “**Reproductive Physiology**”). However, in most mouflon populations, the first reproductive attempt of females is considered to arise at the second breeding season when females have benefited of two seasons of growth (age at first reproduction: 1.5 years-old; TÜRCKE and

Schmincke 1965; Valdez 1976; Hadjisterkotis and Bider 1993; Boussès and Réale 1998; Garel et al. 2005a). High-pregnancy rates can be reached and have been found both in wild and captive populations (from six populations: median [range]: 90.6% [83.3–99%],  $n$  [range] = 106 [27–396]; Briedermann 1992; Garel et al. 2005a; Nahlik 2001) and both in primiparous yearling females (93%; Cugnasse et al. 1985) and adult multiparous ones (Garel et al. 2005a).

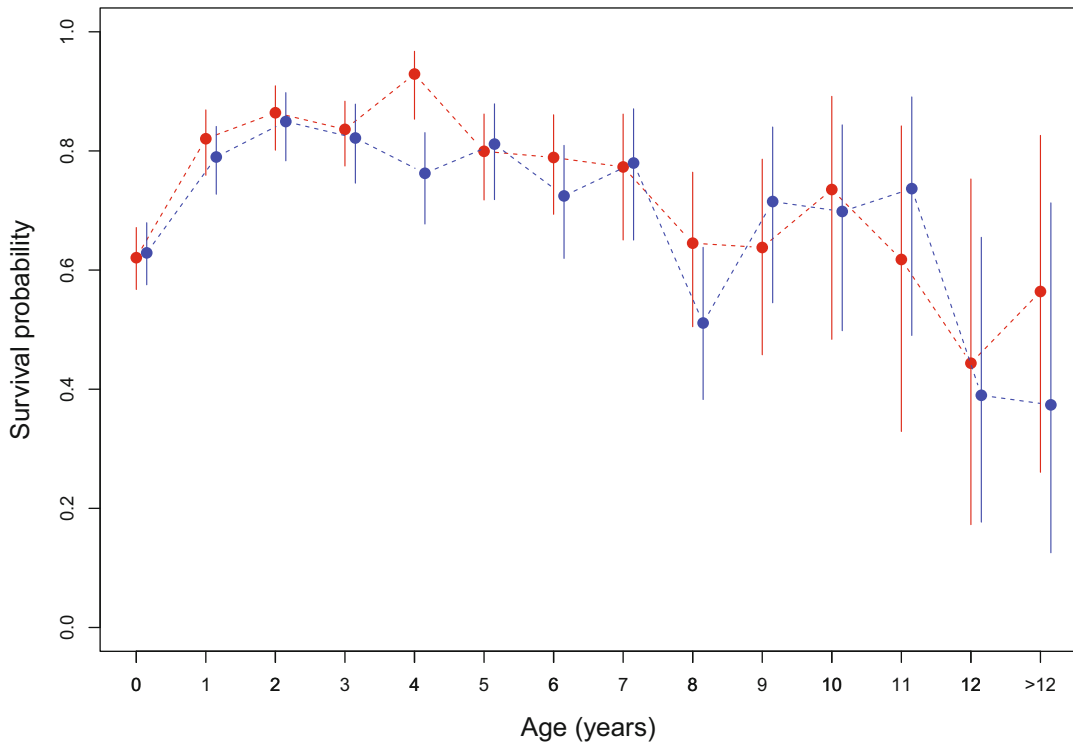
From studies conducted at latitudes of 34–56 °N, rutting season extends from mid-October to December in most populations (e.g., Pfeffer 1967; Bon et al. 1993a; Hadjisterkotis and Bider 1993; Garel et al. 2005a). Females give birth to lamb (s) after *c.* 148–159 days of gestation (Mottl 1960; Türke and Schmincke 1965; Briedermann 1992), i.e., from late March to late May. Although females are commonly considered as monotocous (Türcke and Schmincke 1965; Boussès and Réale 1998; Garel et al. 2005a), twins have been observed (mostly from postmortem examination) in enclosed populations (Briedermann 1992), in free-living populations given supplemental feed (Nahlik 2001; Sanchis 2018), and in wild populations (Briedermann 1992; Hadjisterkotis and Bider 1993; Boussès and Réale 1998; Garel et al. 2005a). High twinning rates have even been reported in the wild population of the Kerguelen Archipelago (in adult females: 36.4%; Boussès and Réale 1998). In this population, the probability of twinning increased with decreasing level of heterozygosity in ewes, but this correlation could result from local genetic effects rather than general inbreeding level (Kaeuffer et al. 2008). Some authors have also posited that in such populations, females would have partly inherited their reproductive ability (e.g., of twinning) from wild ancestors crossbred with domestic sheep (Pfeffer 1967; Boussès and Réale 1998; Garel et al. 2005a) in which domestication processes had meat production and greater prolificity as an initial aim (Chessa et al. 2009). None of the primiparous females autopsied in the previous studies had twins, and the sex ratio of fetuses was statistically balanced between males and females (Garel et al. 2005a).

To our knowledge, no data have been published on the age-related reproductive success in males

which require access to hardly reachable data such as the genetically reconstructed pedigree (see Coltman et al. 2002 in bighorn sheep). However, reproductive effort of many different species of ungulates is consistently higher in prime-aged than in younger males and very old age classes (Mysterud et al. 2004). We may thus expect the same marked age-structured pattern of reproductive success in mouflon rams. In females, for which the presence/absence of a lamb provides more tractable data on their breeding success, observations from ewes marked in the Caroux-Espinouse population would suggest an increase in breeding probability in very old age classes (Richard 2016), rather than the commonly expected lower and more variable reproductive performance as animals get older (Martín and Festa-Bianchet 2011). This finding would provide some support to the terminal investment hypothesis in female mouflon, i.e., when survival prospects are low (see Fig. 3), and residual reproductive value approaches zero, individuals should invest all available resources in their terminal breeding attempt (Williams 1966; Pianka and Parker 1975; Clutton-Brock 1984).

Ewes may thus express a high reproductive potential: with a breeding attempt the first year of life in some populations, high reproductive rates over their lifetime and a litter size that may sometimes exceed 1. This reproductive output can be modulated by environmental conditions encountered as suggested by the linear decrease in female productivity from continental rich environments (lamb-ewes ratios >0.8) to Mediterranean islands where resource shortage is common (lamb-ewes ratios <0.5; Ciuti et al. 2009). For instance, the wild population of Corsican mouflon in Bavella experiences among the lowest lamb-ewes ratio ever reported (0.22; Sanchis 2018); while in captivity with a supplementary feeding, >90% of adult females reproduce (G. Comiti, pers. comm.). However, whether these low lamb-ewes ratios are only a matter of low fecundity in females and/or of low survival in lambs has still been little investigated.

Surprisingly, high-reproductive investment has also been reported in some populations facing limiting conditions. In the population on Kerguelen archipelago and in Soay sheep (*Ovis aries*) on



**Fig. 3** Sex and age-specific survival probabilities (vertical lines indicate 95% confidence interval) of known-age mouflon (red:  $n = 730$  females; blue:  $n = 816$  males; 1986–2018 period) monitored by Capture-Mark-Resighting in the Caroux-Espinouse massif, France (see Garel et al. 2004). These results are an update of previous published survival analyses performed in this population

during a restricted period (1986–1995) of nonlimiting conditions (Cransac et al. 1997; Dupuis et al. 2002; King and Brooks 2003). This update allows to account for density-dependent conditions encountered by this population after 1995 (Garel et al. 2007) and provides a comprehensive analysis along a gradient of density-dependent resource limitation

St Kilda archipelago (a closely related species, Chessa et al. 2009, with the same generation time, Hamel et al. 2016), females may give birth as 1 year and/or may produce twins, even under severe environmental conditions, and even at a cost of survival (Clutton-Brock et al. 1991, 1996; Boussès and Réale 1998; Tavecchia et al. 2005). Similarly, most of females in the Caroux-Espinouse population did not postpone their first breeding attempt in 40 years of monitoring, despite marked environmental changes in resources availability (Cugnasse et al. 1985; Garel et al. 2005b; Richard 2016), whereas age at primiparity is usually the first vital rate to be impacted by density-dependent food limitation in ungulates species (Bonenfant et al. 2009). Female mouflon could thus adopt in some populations a less conservative strategy than usually reported in

ungulate females (Festa-Bianchet and Jorgenson 1998; Gaillard and Yoccoz 2003; Toïgo et al. 2007; Loison et al. 1999), by investing more energy in producing young and less in surviving long (Richard 2016; see subsection “Survival”).

## Survival

Studies of marked individuals throughout their lifespan are also the only way to get reliable information on demographic parameters (survival and breeding probabilities) in free-ranging populations (Festa-Bianchet et al. 2017). In mouflon, very few long-term (>10 years) monitorings by capture-mark-recapture/resighting have been performed. We thus relied again on the analysis of data available from the French population of

mouflon inhabiting the Caroux-Espinouse massif to illustrate age and sex-specific patterns in demographic parameters. In this population, mouflon survival of both sexes fits to the marked age-structured patterns classically reported in ungulate species with a survival improving in early life, reaching a plateau in prime age (2–7 years old), and then declining from 8 years onward (Loison et al. 1999; Gaillard et al. 2000; Fig. 3). Survival also becomes more variable as animals get older. This increase of mortality rate with age (actuarial senescence) most likely results from the decline in physiological functions with aging and is expected in any age-structured population (Hamilton 1966; Gaillard et al. 2000; Gaillard and Yoccoz 2003).

Another general rule is that the male survival should be lower and more variable than female survival (Toïgo and Gaillard 2003) in large iteroparous and highly dimorphic ungulates (sexual size dimorphism SSD  $\geq 20\%$ ; Ruckstuhl and Neuhaus 2002). This is due to contrasted life-history tactics between sexes (e.g., Clutton-Brock et al. 1982; Jorgenson et al. 1997) which lead males to be more sensitive to food limitation than females (Toïgo and Gaillard 2003). Mouflon with their marked SSD (e.g., Table 1), and the limiting resources conditions experienced by the Caroux-Espinouse population (Garel et al. 2007), confirm this pattern (sex-specific survivals over all age classes are 0.751 [0.733; 0.769]<sub>95%</sub> in males and 0.785 [0.768; 0.801]<sub>95%</sub> in females) and illustrates possible costs caused by sexual selection in males. Although this gender difference is expected to increase with age, there is no such evidence here (Fig. 3). In accordance with this sex-specific survival pattern, maximal longevity reported for this population is lower in males (14 years) than in females (17 years). More generally, for both sexes, very few (<1%) known-age animals have been resighted or recaptured beyond 13 years-old.

## Habitat and Diet

In its Caucasian original range, mouflon occupy plains, hills, lowland steppes, plateau slopes, mountain grasslands, and shrublands on dry and

open slopes, with a preference for slightly rugged terrain where antipredator strategy for survival mostly relies on a high visibility (Baskin and Danell 2003; Bleyhl et al. 2018). However, as a result of its long history of introduction (see section “Current Distribution”) and of an important behavioral plasticity, mouflon have been able to persist and can now be found in highly variable habitats, i.e., from coastal areas (e.g., Hawaii’s Big Island) to high mountains (e.g., Alps), from flat terrains to rugged habitats, and from open areas to dense forests (e.g., pampa in Argentina versus continental forests from Eastern Europe).

## Spatial Movements and Home Range

Depending on gender (males generally use larger areas as a result of reproductive dispersal during the rutting period; Dubois et al. 1993, 1996; Malagnino et al. 2021) and on habitats, the annual home range of mouflon ranges from a few hundred to a few thousands of hectares (e.g., 200–350 ha in females-males from the Caroux-Espinouse population, 950–1700 ha in females-males from the Cinto population [Corsica, France]; Marchand 2013). This space use pattern and its variation between populations are generally related to the existence of seasonal or altitudinal migration imposed by variation in resources availability and by the presence of snow cover in winter (due to the absence of interdigital membrane between digits, deep snow strongly impedes movements in mouflon). Both anthropogenic (roads, tracks, and trails) and natural (ridges, talwegs, and forest edges) linear features that mouflon can easily cross can constitute behavioral barriers for movements, delineating individual home ranges and influencing intrapopulation gene flow (Marchand et al. 2017; Portanier et al. 2018). As a result of females’ philopatry and poor dispersal abilities in mouflon, a strong socio-spatial segregation is often reported within populations (Martins et al. 2002; Bourgoïn et al. 2018), with the existence of several population units that use specific ranges and have little contacts and exchanges of individuals with each other (Darmon et al. 2007; Portanier et al. 2017).

## Habitat Selection and Activity Pattern

Habitat selection and activity pattern of mouflon mostly depend on the trade-off between foraging resources, cover from risks imposed by potential predators (including humans, either in hunted populations or as a result of the “ghosts of predator past”; Byers 1997), and cover from adverse climatic conditions (food/cover trade-off; Lima and Dill 1990). Generally crepuscular and bimodal, the activity of mouflon can be largely modulated depending on seasonal and individual constraints (Bourgoin et al. 2008; Pipia et al. 2008). Likewise, habitat selection is characterized at the daily scale by an alternation between foraging areas used during active periods and refuge areas used during ruminating/resting periods. Once again, this pattern can be modulated depending on seasonal and/or individual constraints (Marchand et al. 2015a).

During the first months of lamb's life in spring, reproductive females generally use habitats offering both security and abundant resources, maximizing their own survival and survival of their lamb(s) while providing enough food resources to cover the increased energetic needs imposed by lactation (Hadjisterkotis and Bider 1993; Bourgoin et al. 2008; Ciuti et al. 2008, 2009; Pipia et al. 2008). During this period of abundant resources, males and nonreproductive females are highly active and focus on favorable foraging areas (Bourgoin et al. 2008; Pipia et al. 2008; Marchand et al. 2015a).

During summer, in areas where temperatures are high, mouflon are generally less active during daytime, when they select thermal refuges, and more active at nighttime when they focus on foraging areas (Bourgoin et al. 2011; Marchand et al. 2015b). Both males and females movements are thus preferentially directed toward habitats offering thermal cover when diurnal temperature overruns a given threshold (~15–17 °C in Marchand et al. 2015b; see also Sanchis 2018). In males, this selection persists during nighttime. In females, a concomitant increase in nocturnal activity rate has been reported to compensate for the drastic reduction in activity level during the hottest period of the day. This activity shift may contribute in

limiting thermoregulatory costs (Bourgoin et al. 2011). Thermal cover also influences habitat preferences of males at a broader spatial scale (home range) exemplifying the importance of this factor for male fitness (Rettie and Messier 2000). Conversely, females often trade-off food and thermal cover with refuges and better conditions for lamb survival, especially at the home range scale (Marchand et al. 2015a), and their behavioral responses to hot summer conditions were thus restricted to the hottest period of the day only and by temporally shifting their feeding activity to the night. Similar results were reported in Corsica, where a site occupancy approach was used over 30,000 ha to investigate habitat selection by mouflon during summer (Sanchis 2018). Detection probability also strongly decreased with increasing temperatures and could be divided by up to 2 from 10 °C to 30 °C (Garel et al. 2005c; Cazau et al. 2011; Sanchis 2018).

During autumn and winter, foraging resources become scarce and mouflon spend most of their time foraging. In some areas, food supply is provided and seems important for successful overwintering (Heroldova et al. 2007). In areas where snow cover persists and where winters are harsh, mouflon often move to lower altitudes and use distinct areas than those used in summer (Baskin and Danell 2003; Darmon et al. 2014). Altitudinal migration, or even long-distance migration, have been consequently reported in several mountainous populations (Pfeffer and Settimo 1973; Rigaud 1985; Dubois et al. 1993; Talibov et al. 2009), but little is known on the determinants, on the proportion of individuals concerned, and on the ecological and biological consequences for mouflon populations. Collective migratory movements have been observed in Corsica (P. Benedetti, pers. comm.).

Whatever the season, these behavioral patterns can also be modulated depending on the level of human activities in natural areas (lethal, i.e., hunting, or nonlethal, such as recreational activities). For instance, human disturbance generally results in a temporal shift of activities toward nighttime and an exacerbated selection of refuge areas during daytime (Benoist et al. 2013; Marchand et al. 2014b; Sanchis 2018). However, the long-term



consequences of this spatio-temporal shift related to human activities, e.g., on energetic balance, reproduction, and/or survival, remain unknown.

## Feeding

Among large herbivores, mouflon have been classified as a “grazer” species based on the relative consumption of grasses and browse and on the morphology and physiology of their digestive system (Hofmann 1989). Indeed, its diet is mostly composed with grasses and forbs when these plants are available in sufficient quantity (Marchand et al. 2013). Besides, its rumen morphophysiology is particularly suitable for grass digestion and contains specific bacteria able to provide energy from cellulosis contained in grasses (Clauss et al. 2009, 2010). However, when grasses are temporally/seasonally and/or locally scarce, mouflon can feed on dicots, i.e., forbs, shrubs, fruit, and even trees (Marchand et al. 2013). As a result, >100 plant species have been reported in mouflon diet. Likewise, mouflon have been able to persist and spread in areas where grasses are uncommon (e.g., Kerguelen archipelago), calling into question the classification of mouflon as a grazer (see Clauss et al. 2010; Marchand et al. 2013). However, a strong decrease in body mass has been observed in a population facing an important loss of open (i.e., grass-rich) areas and between individuals with decreasing levels of open areas in their home ranges (Garel et al. 2007; Marchand et al. 2014b). This suggested that this mismatch between the digestive features of mouflon and their actual diets in most areas where it persists has to be interpreted owing to the introduction history of the species.

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## Behavior

### Social Behavior

Mouflon is a gregarious species in which group size and composition are unstable (fission-fusion dynamics; Bon et al. 1990, 1993b). As a result of a strong sexual size dimorphism (Table 1) and

sex-specific needs, adult males and females live in segregated groups out of the rutting season and can use different habitats depending on sex-specific seasonal needs and constraints (sexual segregation with both social and spatial components; Bourgoïn et al. 2018). Sexual segregation between young males and females increases with the age of males, resulting in young males often found either in groups of females or in groups of adult males. The social component appears to be important not only for sexual segregation between the sexes but also between age groups among males (Cransac et al. 1998; Bourgoïn et al. 2018).

Reproductive females generally isolate from other individuals during a few hours-days for lambing (Hadjisterkotis 1993; Marchand et al. 2021). As soon as their lamb is able to follow their mother (follower type *sensu* Lent 1974), they form groups of females and lambs that use specific habitats offering both security and abundant resources until weaning; which progressively occurs around 3 months after births.

### Mating Behavior

During the rutting season, two reproductive tactics have been reported in mouflon rams, depending mostly on their age (Bon et al. 1992). Dominant old males generally tend receptive females by following them and by impeding attempts to mate of other males (tending tactic). By contrast, young subordinate males rather court females, attempting to breach the defense of dominant males (courting tactic). Whatever their age, reproductive dispersal is often observed in males during the rutting season, i.e., important movements of males out of the home range they use the rest of the year (Malagnino et al. 2021), with consequences on gene flow (Portanier et al. 2018).

Inter- or intrasexual interactions consist in repeated behavioral postures (McClelland 1991). Interactions between males involve low-intensity agonistic displays such as foreleg kicks and twists (an animal closely approaches another one and rotates its head approximately 90° with the horn directed away from the recipient’s body). Head

butting (in both sexes) and clashes (in males) predominate in intrasexual agonistic interactions, and the former behavior is regularly used to initiate the interaction in both sexes. Male-female interactions show more variation in the behaviors which initiate the encounter, but usually begin by males performing twist, flehmen (male tightly retracting its upper lip until it curls completely away from its toothless upper jaw), or low stretch (male stretches its head and neck as forward as possible). Much more behavior components are exhibited during male-male interactions as compared to female-female encounters which are often very brief.

## Parasites and Diseases

Several studies on diseases of mouflon were performed not only on island and introduced populations across Europe, but also in Chile and in the sub-Antarctic Kerguelen archipelago, stressing the high diversity of both internal and external parasites mouflon may host (see Hille 2003 for a review).

### Ectoparasites

Among the external parasites, some infestations by acarid and insects are sporadically reported in mouflon, including the sarcoptic mange caused by *Sarcoptes scabiei* (Bornstein et al. 2001; Poglayen et al. 2018), hypodermosis caused by larvae of the warble fly *Hypoderma diana* (Colwell 2001), and oestrosis caused by larvae of the sheep nasal bot fly *Oestrus ovis* (Moreno et al. 1999, 2015; Poglayen et al. 2018).

The most prevalent ectoparasites are the ticks belonging to the *Ixodida* order. The tick *Ixodes ricinus* was observed in most of the study areas within Europe and was often the only species observed in northern and high-elevation areas (e.g., Germany, Netherland, Poland, Czechoslovakia, Austria, and French Alps). In southern parts of Europe (Cyprus: Ioannou et al. 2011; south of France and Corsica: Grech-Angelini et al. 2016; Mercier 2016; Italia: Poglayen et al. 2018) and

Ukraine (see Hille 2003 for a review), a higher diversity of tick species was observed with five to eight species per country, belonging to the genera *Haemaphysalis*, *Hyalomma*, *Rhipicephalus*, and *Dermacentor*. In the Caroux-Espinouse population, the infestation of mouflon by ticks in spring was positively correlated with the body mass of mouflon and with the level of rainfall, but negatively correlated with the mean ambient temperature (Bourgoin et al. 2014).

Ticks are of main concern as they can transmit several pathogens of veterinary and zoonotic importance. Mouflon have been shown to have direct or indirect signs (high antibody titers) of contamination with pathogens such as *Anaplasma phagocytophilum* (anaplasmosis; Stefanidesova et al. 2008; Silaghi et al. 2011; Kauffmann et al. 2017; Hornok et al. 2018), *A. ovis* (Ioannou et al. 2011), *Borrelia burgdorferi* s.l. (Lyme borreliosis; Trávnicek et al. 1999; Zeman and Januška 1999; Juřicová et al. 2000; Trávnicek et al. 2003; Štefančíková et al. 2008), *Babesia* spp. (babesiosis; Ferrer et al. 1998; Kauffmann et al. 2017), *Coxiella burnetii* (Q fever; e.g., Martinov et al. 1989; Hubalek et al. 1993; López-Olvera et al. 2009; Candela et al. 2017), and *Rickettsia* sp. (Ioannou et al. 2011; Hornok et al. 2018). Tick-borne encephalitis virus (Zeman and Januška 1999; Bagó et al. 2002) and tick paralysis (Konjevic et al. 2007) were also reported in mouflon.

### Endoparasites

Necropsies of mouflon from France and Germany revealed the presence of 42 and 34 different species/morphotypes of helminths in their digestive and respiratory tracts, respectively (Gauthier et al. 2001; Hille 2003). The prevalence of lungworm infections by Protostrongylidae, belonging mostly to the *Muellerius*, *Cystocaulus*, *Neostrongylus*, and *Protostrongylus* genera, is generally high (Gauthier et al. 2001; Hille 2003; Panayotova-Pencheva 2006; Poglayen et al. 2018). The life cycle of these parasites requires a gastropod as an intermediate host, while the less prevalent *Dictyocaulus* sp., located in the trachea and the large bronchi at the adult stage, has a direct life cycle.

Regarding the parasitism of the digestive tract, the prevalence and diversity of helminth species are significant, especially for nematodes inhabiting the abomasum and the small intestine of mouflon (Gauthier et al. 2001; Hille 2003; Maerten 2014; Poglayen et al. 2018). Most of these nematodes belong to the order Strongylida, and some species have a well-recognized pathogenicity and are shared with domestic small ruminants, such as *Haemonchus contortus* (Cerutti et al. 2010). Isolation and counts of adult strongyles from mouflon hunted during autumn-winter showed an increase of the infestation with age and a negative relationship with body condition (Hille 2003; Maerten 2014). In spring, the number of eggs shed in feces is higher in young individuals, reproductive females, and individuals in poor body condition (Portanier et al. 2019; Bourgoïn et al. 2021). Both candidate gene (MHC DRB1 exon 2) and neutral genetic diversity (16 microsatellites) have been found to be associated with resistance to gastrointestinal nematodes (Portanier et al. 2019).

Other helminths observed in the digestive tract of mouflon include trematodes and cestodes. The small liver fluke *Dicrocoelium dendriticum* is the most common fluke and was reported in all the European countries where parasitological studies were conducted, while the pathogenic common liver fluke *Fasciola hepatica* and the rumen fluke *Paramphistomum/Calicophoron* spp. are more rarely detected in mouflon (Gauthier et al. 2001; Hille 2003; Poglayen et al. 2018; Bourgoïn et al. 2021). *Moniezia expansa* and *M. benedeni* are the main adult cestodes developing in the small intestine of mouflon, especially in lambs and young individuals (Hille 2003).

Intestinal infestations by the protozoan *Eimeria* sp. are highly prevalent, and often multi-infections with different species of *Eimeria* occur. The intensity of fecal oocyst excretion is generally the highest in mouflon in poor body condition and in young mouflon (Hille 2003; Bourgoïn et al. 2021). More rarely described in free-ranging mouflon, infestations by *Giardia duodenalis* can be observed, especially in lambs and young individuals (Cockenpot 2013).

Mouflon can play the role of the intermediate host for different parasites. It includes *Sarcocystis*

sp., with cysts located in muscles (Goldova et al. 2008; Coelho et al. 2014; Poglayen et al. 2018) and the zoonotic protozoan *Toxoplasma gondii*, with potential consequences on the reproductive success of ewes, and also risks for people consuming game meat (Gauss et al. 2006; Aubert et al. 2010; Bartova and Sedlak 2012; Gotteland et al. 2014; Verma et al. 2015; Heddergott et al. 2018; Almería et al. 2018). Larvae of cestodes can be detected during a carcass examination of mouflon such as the metacestode larval stage of *Taenia hydatigena* (*Cysticercus tenuicollis*) attached to the peritoneum in the abdominal cavity, or the hydatid cysts of *Echinococcus granulosus* in the liver and/or lungs (Hadjisterkotis 1997). The metacestode larval stage of *Taenia multiceps* (*Coenurus cerebralis*) is located in the brain or the spinal cord of the host and may cause nervous or behavioral disorders (Hille 2003; Poglayen et al. 2018).

## Infectious Diseases

The infectious keratoconjunctivitis, caused by *Mycoplasma conjunctivae*, has been reported in mouflon in France (Cransac et al. 1997; Cugnasse 1997) and in the Spanish Pyrenees (Marco et al. 2009). Following epizootics, marked decreases in abundance (Garel et al. 2005c) and survival probabilities (Cransac et al. 1997) have been detected, with a constant decline for males in all age class (~–20%) and age-specific variation for females (with survival probabilities declining by up to –30–60% among lamb and young ewes).

Antibodies against other pathogens of veterinary and zoonotic importance have also been detected in mouflon, such as *Salmonella abortusovis* (abortive salmonellosis; Martín-Atance et al. 2012), *Chlamydia abortus* (chlamydiosis; López-Olvera et al. 2009), *Mycobacterium avium* ssp. *paratuberculosis* (paratuberculosis; López-Olvera et al. 2009), caprine arthritis-encephalitis virus (Guiguen et al. 2000), bluetongue virus (Rossi et al. 2014), and Schmallenberg virus (Rossi et al. 2017).

Other diseases have been searched for in a limited number of individuals (*Leptospira* sp.,

*Mycoplasma agalactiae*, and *Neospora caninum*): None of the individuals tested were infected; however, this does not preclude the possibility of low prevalence of these diseases. Mouflon are also expected to be susceptible to diseases affecting ruminants in general, such as brucellosis and tuberculosis. However, the exact epidemiological role of mouflon populations in the transmission of all these infections remains to be determined.

Additional sanitary issues have been reported in some mouflon populations. For instance, the Cyprus population suffers from a large range of bone problems similar to those of domestic animals (Hadjisterkotis 1996c). The most important defects are degenerative changes and spondylosis (a.k.a. spondylosis deformans or ankylosing spondylosis). At the articular processes and facets, degenerative arthropathy is present and the reaction of the osteophytes produces ankylosis of the articulations between vertebral bodies (intervertebral parts) and between the costal facets and the head of the ribs (costovertebral parts). Disk damage with osteophytosis and sometimes degenerative changes of the vertebral body and a greater spinal curvature were also observed mainly in males throughout the thoracic vertebra, which could result from the greater strain their spinal cords endure, as in fights during the rutting season. Affections of the hoofs have also been reported in mouflon, among which the most common is the contagious foot rot disease, caused by *Dichelobacter nodosus* in association with *Fusobacterium necrophorum* (Belloy et al. 2007; Bennett et al. 2009). It is usually passed on from domestic sheep to mouflon on shared pastures. An inflammation and necrosis of the interdigital tissue among feet is observed. The animals produce a hyperplastic foot horn, show lameness, and often feed in a recumbent position (Volmer et al. 2008).

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## Population Ecology

### Population Dynamics

In line with its fast living strategies (at least in females; see subsection “[Reproduction](#)”), mouflon have a short generation time (4.21 years;

Hamel et al. 2016), may reach in some populations a very high population growth rate ( $\lambda = 1.34$  in Kaeuffer et al. 2009), and show a temporal variability in prime age survival similar to that of breeding probability (Richard 2016). This suggests a lower canalization of adult survival than usually reported in other ungulates species (Gaillard and Yoccoz 2003). Variability in environmental conditions encountered during early life probably contributes to this temporal variability in demographic rates (Lindström 1999) and has been found to generate sex-specific cohort effects on phenotypic traits such as body mass (Garel et al. 2007; Hamel et al. 2016). Typically, female body mass shows less phenotypic variability among cohorts and stronger compensatory/catch-up growth than males, whereas males show more progressive changes throughout life. This supports that stronger selective pressures for rapid growth in this dimorphic species make males more vulnerable to poor environmental conditions early in life and less able to recover rapidly after a poor start.

As in any other ungulate species, population dynamics of mouflon results from complex interactions between per capita food resources (Kaeuffer et al. 2009; in Soay sheep Catchpole et al. 2000; Coulson et al. 2001), climatic conditions (Hadjisterkotis 2002; Garel et al. 2004), disease (Cransac and Hewison 1997), and, when present, predation (either natural or from hunting; Espuno 2004; Garel et al. 2005c). Age structure is also expected to shape the response of demographic rates to density and environmental stochasticity (Sæther 1997; Gaillard et al. 2000; Coulson et al. 2001). In absence of predation/hunting, mouflon populations could grow close to their maximum growth rate over a wide range of population densities (Bonenfant et al. 2009; Kaeuffer et al. 2009) and, when resources are not limiting (e.g. in populations released to a new environment), should display a typical “irruptive dynamics” (see Kaeuffer et al. 2009 in the mouflon population of the Kerguelen archipelago). In such a situation, the mouflon population quickly reaches, and may exceed, the carrying capacity of its environment, before collapsing and entering in a second phase of successive

irruptions. This pattern has also been documented in Soay sheep (Clutton-Brock et al. 1991). In both species, it has been related to the high-reproductive potential of ewes (see subsection “[Reproduction](#)”) in association with delayed density-dependent processes on demographic rates during the irruptive phases.

Phenotypic traits, such as body mass and trophy size, have also been found to be density-dependent and related to intraspecific competition for resources (Garel et al. 2007; in Soay sheep see Forchhammer et al. 2001). Yearly monitoring of phenotypic measurements, such as lamb body mass, could thus be used as an early warning sign of food limitation in this species, providing a quantitative basis when setting hunting quotas (Morellet et al. 2007).

### Competition with Other Ungulates

Numerous populations of mouflon also share habitats with other wild or domestic ungulate species (e.g., red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and axis deer *Axis axis*, Pyrenean *Rupicapra pyrenaica pyrenaica* and Alpine chamois *Rupicapra rupicapra rupicapra*, Iberian wild goat *Capra pyrenaica* and Alpine ibex *Capra ibex*, aoudad *Ammotragus lervia*, wild boar *Sus scrofa*, sheep, goat, and cow), resulting in a high potential for competition, particularly between similar-sized species (Pfeffer and Settimo 1973; Gonzales 1986; Hadjisterkotis 1993; Heroldova 1996; Bertolino et al. 2009; Darmon et al. 2012; Miranda et al. 2012; Chirichella et al. 2013; Redjadj et al. 2014; Centore et al. 2018). Although important spatial and/or diet overlaps have been reported with other species in some areas where mouflon have been introduced, contrasted results have been observed in terms of competition for native species. Species-specific adaptations to local environmental conditions (e.g., differences in activity patterns or habitat selection; Darmon et al. 2012, 2014) may contribute to coexistence without negative impacts from mouflon in most cases. However, spatial adjustments, diet overlap, and activity shifts in native species related to the presence of mouflon were also reported and interpreted as evidence for interspecific

competition (Bertolino et al. 2009; Chirichella et al. 2013; Centore et al. 2018). However, to our knowledge, no study has evidenced so far a negative impact of mouflon on body mass, growth, reproduction, or survival of other ungulate species. By contrast, competition with livestock, and particularly with domestic sheep, is a key concern for mouflon (see section “[Management](#)”).

### Effects of Climate Change

Thermal conditions during summer have been identified as a major driver of spatial and temporal behaviors in mouflon populations inhabiting Mediterranean areas (Pipia et al. 2008; Bourgoïn et al. 2011; Marchand et al. 2015b; see subsection “[Habitat Selection and Activity Pattern](#)”). However, behavioral adjustments identified did not prevent females from losing up to 15% of activity time over a 24-h period during hot summer days (Bourgoïn et al. 2011). In addition, as daily temperature increases, ambient temperatures experienced by mouflon never stopped increasing despite shift in habitat selection (Marchand et al. 2015b). This suggested that this shift might be insufficient to maintain ambient temperatures around the threshold controlling thermoregulation (~15–17 °C). In line with these findings, fitness-related traits, such as body mass, and fitness components, such as lamb survival and female productivity, have been found to be impacted by summer heatwaves and droughts (Garel et al. 2004) or to be correlated with temperature-related parameters (e.g., latitude; Ciuti et al. 2009). As an example, a high lamb mortality was recorded during the 4-month period around the severe 2003 drought in the Caroux-Espinouse population (Garel et al. 2004). Adults harvested during the hunting season following this severe drought were on average  $3.4 \pm 0.8$  kg lighter than those harvested in the three previous hunting seasons, representing a >11% and >17% mass loss in adult males and females, respectively. In Cyprus, the higher mortality in fall/early winter has also been partly associated with the low resources quality and quantity experienced by animals some months

earlier during the long hot and dry Cypriot summers (Hadjisterkotis 2002). These first insights raise concerns on the long-term consequences of global warming in Mediterranean areas where mouflon populations will face in a near future more intense and more frequent heatwaves (Paeth and Hense 2005).

## Conservation Status

The conservation status of mouflon is summarized in Table 2.

## Management

This species remains a paradox for conservation and management (Garzón-Machado et al. 2012). On the one hand, several native populations (Özütlü 2009; Hajian et al. 2011) and mouflon on Mediterranean islands are of conservation concern (Cassola 1985; Shackleton and IUCN/SSC Caprinae Specialist Group 1997; Hadjisterkotis and Lovari 2016; Portanier et al. 2022) and often benefit locally of a protection status (e.g., for

Cyprus: “The Protection and Development of Game and Wild Birds Law of 1974 (39/1974), article 9,” for Corsica: “Ministerial order of 1st March 2019, NOR: TREL1824291A”; see also Apollonio et al. 2010). Though not always assessed, several threats have been identified in these areas: poaching, hunting (nontarget species) and associated disturbance, habitat loss (e.g., forest encroachment), hybridization with sheep and more generally loss of genetic diversity related to population isolation, competition and sharing of pathogens with domestic herds, and development of recreational activities in natural areas (Hadjisterkotis 2001; Rieu 2007; Khorozyan et al. 2009; Talibov et al. 2009; Bleyhl et al. 2018; Satta et al. 2021; Brivio et al. 2022). In its Caucasian original range, competition with herds of several hundreds of domestic sheep, usually accompanied by several shepherds and 1–4 dogs/100 sheep, is a key issue since it might have pushed mouflon into marginal habitats (Khorozyan et al. 2009; Talibov et al. 2009; Bleyhl et al. 2018; Brivio et al. 2022).

These numerous threats justified important efforts to improve the conservation status in its

**Table 2** Summary of mouflon status in international agreements for conservation of animal and plant species

List	Taxon	Status	Date	Notes
IUCN red list	<i>O. gmelini</i>	Near Threatened A2cde ver 3.1 (global)	2020-03-18	Current population trend unknown. Four subspecies included: Anatolian and Armenian mouflon lumped into <i>O. g. gmelini</i> , Isfahan mouflon <i>O. g. isphahanica</i> , Laristan mouflon <i>O. g. laristanica</i> and Cyprus mouflon <i>O. g. ophion</i>
Bern Convention	<i>O. aries (musimon, ammon)</i>	Appendix 3 <sup>a</sup>	1979	
CITES	<i>O. gmelini</i>	Appendix 1 <sup>b</sup>	2022-06-22	Only the population of Cyprus. No other population is included in the Appendices
Habitat directive	<i>O. gmelini musimon</i> (or <i>O. ammon musimon</i> ) <i>O. orientalis ophion</i> (or <i>O. gmelini ophion</i> )	Annex 2 <sup>c</sup> Annex 4 <sup>d</sup>	1992	Natural populations in Corsica and Sardinia

<sup>a</sup>Protected Fauna species

<sup>b</sup>Species threatened with extinction. Trade in specimens of these species is permitted only in exceptional circumstances (e.g., scientific research)

<sup>c</sup>Animal and plant species of community interest whose conservation requires the designation of special areas of conservation

<sup>d</sup>Animal and plant species of community interest in need of strict protection

native range and in Mediterranean islands during the two last decades. As examples, between 2004 and 2007, two reintroductions of Anatolian mouflon occurred in central Turkey (Karaman-Karadag and Ankara-Sariyar) using founder individuals from the Konya-Bozdag area (Özüt 2009). In Cyprus and Corsica, some individuals have been enclosed and reproduce in captivity for reintroduction (Hadjisterkotis and Bider 1993; Rieu 2007). However, the breeding program for the Cyprus mouflon was considered a failure due to the introduction of inbred animals with reduced viability (Hadjisterkotis and Lambrou 2001). Mouflon are also one of the first wild endangered species for which cloning and assisted reproductive technologies have been considered as conservation measures (Loi et al. 2001; Hosseini et al. 2009; Hajian et al. 2011). Managing habitats is another simpler lever for mouflon conservation (Khorozyan et al. 2009; Talibov et al. 2009; Bleyhl et al. 2018). As an example, increasing grass availability, e.g., by using prescribed burning or cutting when woody plants encroach (Cazau et al. 2011), or by limiting competition with domestic herds (Bleyhl et al. 2018; Brivio et al. 2022), may help increasing forage abundance for mouflon facing habitat loss. Likewise, food supply is provided and seems important for successful overwintering in some populations where snow cover persists during winter (Nahlik 2001; Heroldova et al. 2007).

On the other hand, mouflon has been introduced with success as a game species in numerous countries (see section “Current Distribution”), allowing the development of thriving businesses based on trophy hunting (Shackleton and IUCN/SSC Caprinae Specialist Group 1997; Hofer 2002). In some populations, this selective hunting may have had detrimental effects on individual phenotypic characteristics (Garel et al. 2007). Introduced mouflon have also sometimes raised management concerns when negative impacts on ecosystems are reported (Heroldova and Homolka 2001; Michaelidou and Decker 2002). Severe impacts on commercial forests or endemic plants have been recorded when mouflon have been introduced in forested areas and sites of high economical or environmental values (e.g., Hawaii, Kerguelen,

and Canary islands; Rodríguez et al. 1988; Rodríguez Luengo and Piñero 1991; Homolka and Heroldova 1992; Chapuis et al. 2001; Hess and Jacobi 2011). More generally, when grasses become scarce, mouflon can locally/seasonally cause damages on trees, artificial pastures, vineyards, orchards, and/or crop fields (e.g., in Cyprus see Hadjisterkotis and Vakanas 1997). As a result, mouflon have been classified as invasive in Hawaii and Canary islands and have been eradicated from Kerguelen archipelago during the 2010s (Giffin 1979; Garzón-Machado et al. 2012; Terres Australes et Antarctiques Françaises 2013).

Both native and introduced populations of mouflon may also play an important role in food webs and in the maintenance and/or recovery of carnivores and raptors (Pouille et al. 1997; Cugnasse and Golliot 2000; Andersen et al. 2006; Herzog 2018). Mouflon newborns and juveniles are indeed preys for the golden eagle *Aquila chrysaetos* and for the red fox *Vulpes vulpes*, but the impact of these predators on populations may be limited and may not concern adults (Hadjisterkotis 1996a; Cugnasse and Golliot 2000). More direct killings were reported by stray dogs than foxes, although foxes are also one of the major scavengers of dead mouflon (Constantinou and Hadjisterkotis 2016; Nasiadka et al. 2021). By contrast, predators such as lynx *Lynx lynx* and wolf *Canis lupus* can play a significant role on population size and persistence. In several areas where one of these predators recovered during the last decades, marked drops in mouflon populations were recorded (Pouille et al. 1997; Andersen et al. 2006; Möckel 2017; Herzog 2018). Mouflon seem particularly sensitive to predation by large carnivores during winter as movements are impeded by snow and as group size is at its highest in restricted winter ranges.

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## Future Challenges for Research and Management

Further research is needed to inform managers on the extent to which populations of mouflon can adapt to the fast ongoing global changes, in particular in its native range (where knowledge is

critically lacking) and more generally where populations are of conservation concerns.

Mouflon seem particularly sensitive to heat stress and droughts, with both behavioral and demographic side effects reported (Garel et al. 2004; Bourgoïn et al. 2009; Marchand et al. 2015b) and a strong dependence on water availability during the hottest period in the most arid/Mediterranean areas (Hadjisterkotis 2001). With rising temperatures and more frequent/intense droughts predicted (Paeth and Hense 2005), and numerous expected consequences on mouflon habitats, better understanding how the behavioral ecology, dynamics, and distribution of mouflon populations can be affected by global warming is an important research avenue.

Likewise, habitat loss and interactions with domestic livestock (competition, sharing of pathogens) have already been identified as major threats for numerous populations of mouflon, in particular in its native range (Hadjisterkotis 2001; Khorozyan et al. 2009; Talibov et al. 2009; Bleyhl et al. 2018; Brivio et al. 2022). Habitat fragmentation and loss of connectivity imposed by the development of human activities and associated infrastructures, the cessation of ancestral migration routes, and disturbance imposed by the development of recreational activities in natural areas may constitute other challenges for most populations of mouflon that are still to be evaluated (Marchand et al. 2014a, 2017; Bleyhl et al. 2018). As the size of domestic herds generally increases in mountainous areas (García-Martínez et al. 2009), so do the populations of other wild large herbivores that coexist with mouflon (in Europe; Apollonio et al. 2010); it is likely that questions of competition between wild and domestic species, of the impact of introduced mouflon on ecosystems, and of the sanitary issues resulting from increasing interspecific contacts will arise even more in many countries (Khorozyan et al. 2009; Talibov et al. 2009; Bleyhl et al. 2018).

**Acknowledgments** The authors thank Giuseppe Puddu, the Observatoire de la Grande Faune et de ses Habitats (OGFH) and Simone Ciuti for providing some of data presented in this chapter. They also warmly thank all the

professionals from the Office National de la Chasse et de la Faune Sauvage (now Office Français de la Biodiversité; Thibaut Amblard, Pierre Benedetti, Thierry Chevrier, François Couilloud, Dominique Dubray, Jeanne Duhayer, Philippe Gibert, Christian Itty, Jean-Michel Jullien, Daniel Maillard, Eric Marty, Frédéric Sanchis and SD 34) and the numerous trainees and partners (GIEC du Caroux-Espinouse, GIC des Bauges, ONF, PNR des Bauges et de Corse, OEC, DREAL Corse, LDAV73, LDA2B) involved in the long-term studies performed on the Caroux-Espinouse, Bauges, and Corsican study sites. Thanks to Sebastian Piegert for translating from German to English and Luca Corlatti, Simone Ciuti, and Nicolas Morellet for the useful comments that they provided. We would like also to thank the Minister of Agriculture, Rural Development and Environment of the Republic of Cyprus (Dr. Kostas Kadis), the Senior Officer of the Ministry of Agriculture Rural Development and Environment (Dr. Marina Michaelidou Kadi), and the Director of the Agricultural Research Institute (Dr. Dora Chimonidou) for their support. JSM is supported by grant AGL2017-85753-R (AEI/FEDER, UE).

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