New insights into the past and recent evolutionary history of the Corsican mouflon (Ovis gmelini musimon) to inform its conservation

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RESEARCH ARTICLE

New insights into the past and recent evolutionary history of the Corsican mouflon (*Ovis gmelini musimon*) to inform its conservation

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Abstract

Human-mediated species dispersal across the Mediterranean stretches back at least 10,000 years and has left an indelible stamp on present-day biodiversity. Believed to be a descendant of the Asiatic mouflon (*Ovis gmelini gmelinii*), the Corsican mouflon (*O. g. musimon*) was translocated during the Neolithic as ancestral livestock by humans migrating from the Fertile Crescent to the Western Mediterranean. Today, two geographically limited and disconnected populations can be found in Corsica. Whether they originated from distinct founders or one ancestral population that later split remains unknown, although such information is pivotal for the species' management on the island. We genotyped 109 and 176 individuals at the Cytochrome-*b* gene and 16 loci of the microsatellite DNA, respectively, to gain insights into the natural history of the Corsican mouflon. We found evidence confirming that the Asiatic was the ancestor of the Corsican mouflon, which should thus be unvaryingly referred to as *O. g. musimon*, i.e. as a subspecies of the Asiatic mouflon. Haplotype divergence dating and the investigation of genetic structure highlighted a strong and ancient genetic differentiation between the two Corsican populations. Approximate Bayesian Computation pointed to the introduction of a single group of founders as the most reliable scenario for the origin of the entire Corsican population. Later, this ancestral stock would have decreased in number, facing genetic bottlenecks and eventually resulting in two divergent demes. Splitting most likely occurred several hundred years ago. Their shared past notwithstanding, we discuss whether the two relic Corsican mouflon populations should be now considered as distinct management units.

Keywords Approximate Bayesian computation · Historic faunal relocation · Human-mediated introduction · Management units · Phylogeography · Ungulates

Introduction

The knowledge of the natural history and genetic characteristics (e.g. diversity, inbreeding) of a given population is highly important in evolutionary biology, zoological

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systematics and especially conservation management (Lande 1988; Fitzsimmons et al. 1995). Indeed, genetic diversity is strictly related to the adaptive potential of populations and thereby to the ability of species to cope with environmental changes (Frankham et al. 2004). Populations with small effective size and reduced genetic diversity may suffer from inbreeding depression (i.e. loss of individual fitness due to inbreeding; Coltman et al. 1999; Keller and Waller 2002; Taylor et al. 2017), with possible negative consequences for their dynamics and persistence (Bozzuto et al. 2019). In addition, when two populations experience contrasting environments, even if they stem from the same gene pool (e.g. a common origin of founder individuals in the event of introduced populations), allelic frequencies can diverge in response to natural selection, leading to genetic differentiation and local adaptations (Williams 1966). Nonetheless, divergence may also owe to either genetic drift in distinct population demes (Wright 1931) or different population histories, as occurs for instance when demes are founded by individuals of various origin (e.g. Biebach and Keller 2009; Portanier et al. 2017). Therefore, understanding both the genetic structure and the history of populations is crucial in order to offer cogent conservation management recommendations (e.g. genetic reinforcement, reintroductions). This knowledge can help to mitigate the loss of local adaptation (e.g. outbreeding depression; Edmands 2007), favour advantageous genetic diversity (e.g. introduction of adaptive alleles, Portanier et al. 2019; heterosis, Keller et al. 2014) and support the establishment of management units (MUs; Moritz 1994; Palsbøl et al. 2007).

Such knowledge is particularly relevant when considering wild insular populations. Indeed, wildlife faces higher extinction rates on islands than on mainland. Habitat loss due to sea-level rise is one of the most important threatening factors, the danger it poses to local biota being exacerbated by diminished or entirely lacking opportunities to move to alternative areas (Ricketts et al. 2005; Courchamp et al. 2014). On the one hand, island populations have usually evolved under a reduced level of competition due to both geographic and genetic isolation, with natural selection often resulting into a high level of endemism, with the occurrence of biodiversity hotspots and priority conservation areas (Myers et al. 2000; Whittaker and Fernández-Palacios 2007; Kier et al. 2008; Loso and Ricklefs 2009). On the other hand, the small size and naïve nature of most island populations render them particularly prone to extinction (Milberg and Tyrberg 1993).

The Mediterranean Basin is not only one of the most important biodiversity hotspots in the world but also one of the most threatened by climate change (Myers et al. 2000; Giorgi 2006; Ducrocq 2016). Numerous endemic species occur on Mediterranean islands (e.g. Grill et al. 2007; Jeanmonod et al. 2015; Escoriza and Hernandez 2019), with the mouflon (*Ovis gmelini* spp., Bovidae) being a flagship species deserving particular attention from conservation biologists (Garel et al. in press). The classification of populations currently occurring on Mediterranean islands (Cyprus, Corsica and Sardinia) has been repeatedly debated (Cugnasse 1994; Rezaei et al. 2010; Guerrini et al. 2015; Garel et al. in press), sometimes making their conservation challenging. However, it is now widely acknowledged that these populations originated from the Asiatic mouflon (*O. g. gmelinii*), which was translocated as ancestral livestock by humans migrating from the Fertile Crescent to the Western Mediterranean 11,000 years before present (BP hereafter) (Poplin 1979; Vigne 1992; Zeder 2008). The domestication process is assumed to have remained primitive, hence limited to protection against predators, with only few interactions between animals and humans and no artificial selection (Rezaei 2007; Zeder 2008). Accordingly, Mediterranean mouflons have been found to be genetically and morphologically close to their Asiatic conspecifics, providing weight for ranking them as a subspecies of their ancestor (Chessa et al. 2009; Rezaei et al. 2010; Guerrini et al. 2015; Sanna et al. 2015; Mereu et al. 2019). Being located at the start of the migration routes towards the western regions, the mouflon of the island of Cyprus differs from its Sardinian and Corsican conspecifics in many ways and is thus thought to be endemic to this island (Barbanera et al. 2012). The Cypriot mouflon would have been introduced by Neolithic people around 10,500 BP (Zeder 2008; Fig. 1A), reaching the Western Mediterranean (Corsica and Sardinia) 3000–4000 years later (Poplin 1979; Vigne 1992). This history has contributed to marked genetic differentiation among the three island mouflon populations (Hadjisterkotis et al. 2017), leading scientists to assign them to two subspecies (*Ovis gmelini ophion* and *O. g. musimon* for Cyprus and Corsica/Sardinia, respectively; Festa-Bianchet 2000; Guerrini et al. 2015; Sanna et al. 2015). Note that in aforementioned papers, authors used *O. orientalis* spp., which should be replaced by *O. gmelini* spp., as recommended by Groves and Grubb (2011) and Hadjisterkotis and Lovari (2016). It is also worth mentioning that Cugnasse (1994) suggested referring to Corsican and Sardinian mouflons as *O. g. musimon var. corsicana* and *O. g. musimon var. musimon*, respectively, thus accounting for the demographic disconnection between these island populations occurring since the Neolithic.

Whereas both the genetic structure and the kinship of Cypriot and Sardinian mouflon have been investigated in several studies (e.g. Barbanera et al. 2012; Guerrini et al. 2015; Sanna et al. 2015; Satta et al. 2016; Mereu et al. 2019), the evolutionary history of the Corsican mouflon is still largely unknown. Although previous studies have included a few mouflon samples from Corsica in their analyses (e.g. 2 in Rezaei et al. 2010 and 19 in Guerrini et al. 2015), to date, the population as a whole has not been the subject of any
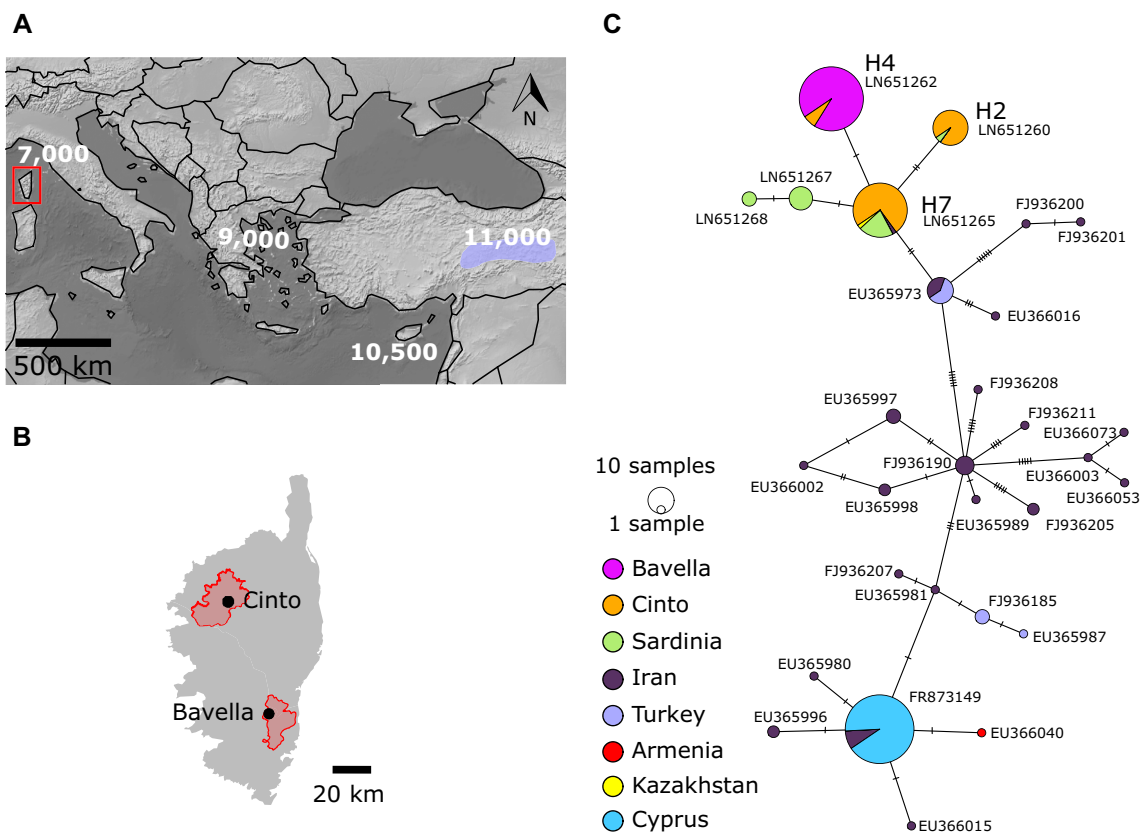
Fig. 1 A Map of the Mediterranean Basin (adapted from Zeder 2008) showing Corsica (red square) and the origin of sheep domestication in Turkey, 11,000 years BP in purple. Approximate dates (in years BP) for the arrival of ancestral farmers across the Mediterranean are reported as well. **B** Locations and spatial range of the two Corsican mouflon populations (see Supplementary Figures S1 and S4 for details on samples locations). **C** *Ovis gmelini* haplotype network for Corsican/Sardinian (*O. g. musimon*), Middle Eastern (Turkey, Armenia and Iran: *O. g. gmelinii*), Central Asian (Kazakhstan) and Cyp-

riot (*O. g. ophion*) populations. Haplotypes were obtained from Rezaei et al. (2010), Demirci et al. (2013), Guerrini et al. (2015), Mereu et al. (2019) and the present study. The numbers of mutational changes between different haplotypes are represented by hatch marks. Names of the three haplotypes found in Corsica are indicated according to those provided in the original paper (H2, H4 and H7 from Guerrini et al. 2015) while other haplotypes are named according to one GenBank sequence representing them

focused study. Nonetheless, the Corsican mouflon is a protected species at both national (French Ministerial order of first March 2019, NOR: TREL1824291A) and international (European Habitat Directive Annexes II and IV, Washington and Berne conventions) levels, and thus deserves attention from conservation professionals. While this taxon has already benefited from some protection plans (European LIFE programme, Rieu 2007; establishment of hunting and wildlife reserves, Sanchis 2018), important information for drafting more comprehensive conservation strategies remains lacking. For instance, although the two Corsican populations are separated by > 45 km (the Cinto and Bavella massifs in the north and south, respectively; Fig. 1B), they have not been investigated on their own. These two populations have limited and non-increasing sizes (the estimated minimum population sizes are approximately 900 and 200 individuals for Cinto and Bavella, respectively; Sanchis 2018; Garel et al. in press) and are moreover threatened by

genetic diversity loss, resource shortage (which may become worse with ongoing global warming), hybridization with domestic sheep (*O. aries*) and poaching, as occurs for their Mediterranean conspecifics (Barbato et al. 2017; Ciuti et al. 2009; Hadjisterkotis et al. 2001; Rieu 2007; Garel et al. in press). In addition, individual phenotypic differences and, based on a preliminary study, genetic differentiation, have been reported between Cinto and Bavella populations (Maudet and Dubray 2002). Overall, research into the evolutionary history of the Corsican populations (i.e. whether they originated following one or more introduction events) as well as their spatial genetic structure, putative gene flow and diversity is crucial to gauging if the two populations should be managed as a single or separate conservation units. Furthermore, studying the Corsican mouflon is important for the conservation of the species as a whole, because this island population (plus potentially some from Sardinia) may represent the most genetically and phenotypically preserved

descendant of the Asiatic mouflon in the Western Mediterranean (Barbato et al. 2017).

In the present study, we investigated the past and recent evolutionary history of the Corsican mouflon. Using a comprehensive phylogeographic framework and mitochondrial *Cytochrome-b* sequences of 109 individuals from both Cinto and Bavella populations, we aimed to determine whether they stemmed from the same part of the Fertile Crescent and then evolved from one or more introduction events (*O. gmelini* spp.; Rezaei et al. 2010; Guerrini et al. 2015). Furthermore, based on 16 microsatellite loci genotyped in 176 individuals, we examined their population genetic structures to assess if gene flow recently occurred between the two Corsican populations. Finally, we combined both mitochondrial and microsatellite DNA data sets and used Approximate Bayesian computation (ABC, Beaumont 2010) to gain knowledge about the demographic history of the Corsican mouflon and prevent the possible failure of phylogeographic and population genetics approaches in discriminating among alternative historical and demographic scenarios (e.g. two introductions from the same source population versus the splitting of one large population into two smaller ones).

Materials and methods

Study area, sample collection and DNA extraction

Two mouflon populations occur in Corsica separated by more than 45 km: one around Monte Cinto (north-west, 42.383° N, 8.898° E; 125–2706 m a.s.l.) and the other in the massif of Bavella (south-east, 41.785° N, 9.266° E; 30–2134 m a.s.l.; Fig. 1A, B). Both populations inhabit mountainous areas characterized by high elevation, rugged terrain and strong slopes (Sanchis 2018), with Mediterranean and Alpine climatic influences. Typical vegetation mostly includes pine forests (*Pinus nigra laricio* and *P. maritimus*), broom and moorlands (*Genista* sp., *Erica arborea*, *Juniperus* sp). Biological samples were collected between 2015 and 2019 across the whole mouflon range in each study area. We obtained faeces from individuals under direct observation in both populations, thus ensuring fresh, high quality samples. Hairs were retrieved from mouflons captured only in the Cinto population using traps baited with salt. DNA extraction was carried out at the Antagene Laboratory (La Tour de Salvagny, France, http://www.antagene.com/) using 96 extraction columns (Nucleospin 96 Tissue, Macherey–Nagel) in the presence of negative and positive extraction controls. The samples were lysed overnight at 56 °C (according to the manufacturer's instructions) and DNA was then purified and isolated using purification columns and vacuum filtration. DNA was subsequently eluted in 140 µl (20–100 ng/µl) and stored in 96-tube plates at −20 °C.

Mitochondrial DNA

Amplification and sequencing

The entire mitochondrial Cytochrome-*b* gene (mtDNA Cyt-*b*, 1140 bp) was amplified using the two pairs of primers (CYTB_F/CYTB_IN_R and CYTB_IN_F/CYTB_R) published in Pedrosa et al. (2005). Polymerase chain reactions (PCRs) were performed in a final volume of 25 µL, with 11.5 µL of Multiplex PCR Master Mix (Qiagen), 0.5 µL of each 10 µM primer, 0.1 µL of Dream*Taq* DNA Polymerase (Thermo Fisher Scientific), and 25–30 ng of DNA. Following Rezaei et al. (2010), the thermal profile consisted of 10 min of initial denaturation (95 °C), followed by 40 cycles of denaturation (30 s, 95 °C), annealing (30 s at 55 °C and 60 °C for CYTB_F/ CYTB_IN_R and CYTB_IN_F/ CYTB_R pairs of primers, respectively) and extension (1 min, 72 °C). The final extension lasted for 7 min at 72 °C. The PCR products were sequenced on both DNA strands at the Biofidal Laboratory (Vaulx-en-Velin, France). For each individual, chromatograms were checked, edited when necessary (e.g. trimmed) and assembled using CLC Sequence Viewer software (Qiagen Bioinformatics). Following this procedure, Cyt-*b* sequences were obtained for 56 and 53 individuals from the Bavella and Cinto populations, respectively. This data set was enriched with 218 sequences retrieved from GenBank to account for the diversity of all wild *Ovis* species (Supplementary Table S1). All sequences (327 in total) were aligned using Seaview v.4.7 (Galtier et al. 1996; Gouy et al. 2010) and the MUSCLE algorithm (Edgar 2004), and then cut to a final length of 1,042 bp (size of GenBank sequences).

Phylogenetic reconstructions and haplotype network

Haplotypes were determined using DnaSP v.6 (Rozas et al. 2017). In order to precisely infer the relationships among haplotypes, a maximum likelihood phylogenetic tree was reconstructed using PhyML v.3.0 online software (Guindon et al. 2010) with 120 sequences representing the entire haplotype diversity and geographic range of both *O. vignei* (urial) and *O. gmelini* (please note that for each geographic location we removed duplicated haplotypes; Supplementary Table S1). Following Guerrini et al. (2015), we used AJ867266 and EU366039 *O. ammon* (argali) sequences as outgroup. The HKY85 (Hasegawa et al. 1985)+G+I substitution model was chosen using Smart Model Selection (Lefort et al. 2017) as implemented in PhyML and based on the Akaike information criterion (AIC=6138.86; I=0.55,

$\alpha = 0.92$ and transitions/transversion ratio = 10.51). The starting tree was determined using the Neighbor-Joining algorithm (Gascuel 1997) and tree rearrangement was performed using nearest-neighbor interchange (NNI). Branch support was determined using a bootstrap approach ($n = 1000$). The final tree was visualized and edited using FigTree v.1.4.4 (available at https://github.com/rambaut/figtree/releases). A median-joining haplotype network (Bandelt et al. 1999) was also constructed using PopArt v.1.7 (Leigh and Bryant 2015) to visually represent the relationships among all *O. gmelini* haplotypes.

Divergence time estimation

We used BEAST v.2.6 (Drummond et al. 2012; Bouckaert et al. 2019) to determine the time since divergence among the different haplotypes found in Corsica and 18 haplotypes selected among the most divergent ones within each *Ovis* clade: *O. canadensis* (bighorn sheep), *O. dalli* (Dall sheep), *O. nivicola* (snow sheep), *O. ammon*, *O. vignei* and *O. gmelini* (Supplementary Figure S1, Supplementary Table S1). In order to strengthen the power of the analyses, we included in the data set a Cyt-*b* haplotype from one individual sampled in the National Hunting and Wildlife Reserve of Chambord domain (47.617° N, 1.517° E, French mainland). This haplotype, which was held by 11 of the 41 investigated individuals (E. Portanier, unpublished data), has previously been identified only in a Tibetan sheep population (Liu et al. 2016; GenBank accession number KP229045). Following Bibi (2013), we set priors for seven calibration points (see Supplementary Tables S1 and S2). Bayesian model averaging was performed using the *bModelTest* package (Bouckaert and Drummond 2017) as implemented in BEAST v.2.6. We used a Yule process speciation tree prior with estimated base frequencies and assumed a log-normal relaxed molecular clock (Drummond and Rambaut 2007). Two independent runs were carried out with 10,000,000 Markov Chain Monte-Carlo (MCMC) iterations, sampling trees and log files every 1000 iterations. Results files were examined in Tracer v.1.7.1 (Rambaut et al. 2018) by means of a post-processing burn-in of 10% (first 1000 trees discarded) for each run to assess the chain and parameter convergence of independent runs and to verify that the overall effective sample size (ESS) was > 200. Tree files from independent runs were combined using LogCombiner v.2.6.1 (Drummond et al. 2012) and a consensus maximum clade credibility (MCC) tree was created using TreeAnnotator v.2.6.0 (Drummond et al. 2012) after removing 10% of initial trees and using median heights for nodes.

Microsatellite DNA

Genotyping

Individuals were genotyped at 16 microsatellite loci at the Antagene Laboratory following the protocol described in Portanier et al. (2017) (see also Supplementary Table S3). Hairs were genotyped once and faeces twice to obtain at least 13 markers with no missing data. The electropherograms were analyzed using GENEMAPPER software (Applied Biosytems/Life Technologies) independently by two analysts to determine the allele sizes. Reading errors were resolved and ambiguous results were deemed missing data. For samples with two replicates, when an allele drop was observed, consensus was manually generated by keeping the heterozygosity between the two replicates. A quality index (Miquel et al. 2006) was calculated for each faecal sample by comparing the genotypes of the two replicates. The panel was investigated using MICROCHECKER v.2.2.3 (Van Oosterhout et al. 2004) to test for null alleles, putative remaining allele dropout and scoring errors due to stuttering. The discriminatory power was determined using GenAlEx v.6.501 (Peakall and Smouse 2006, 2012) by estimating the probability that two individuals drawn at random from the populations would show identical multilocus genotypes by chance (P_{ID} and P_{IDsibs}; for the latter, we assumed sibling relationships). We tested the data set for the occurrence of twin genotypes; when detected, one of the two individuals was randomly excluded to prevent bias in the downstream analyses (11 samples removed). A factorial correspondence analysis was carried out to detect and subsequently exclude outliers from data sets (one in Cinto, two in Bavella; putative domestic sheep or goats) using Genetix v.4.05.2 (Belkhir et al. 2004). Overall, 117 and 59 individuals genotyped at ≥ 13 loci were obtained for the Cinto and Bavella populations, respectively.

Population genetic diversity and structure

FSTAT v.2.9.3.2 (Goudet 1995, 2001) was used to test for linkage disequilibrium (LD) among all pairs of loci within populations (exact G-test) and departures from the Hardy–Weinberg equilibrium (HWE) for each locus (10,000 randomisations), and to determine F_{IS} values per locus assessing their significance levels relative to zero. When necessary, *p*-values were adjusted for multiple comparisons using Bonferroni correction (Bonferroni 1936). Classical genetic diversity estimates such as the number of alleles per locus (*Na*), allelic richness (*A$_r$*, calculated using the rarefaction method; El Mousadik and Petit 1996) and expected heterozygosity (*He* sensu Nei's gene diversity; Nei 1973) were calculated for each population. Observed heterozygosity (*Ho*) was calculated using the *hierfstat* package (Goudet

and Jombart 2015) for R v.3.6.2 software (R Development Core team 2019).

Population genetic structure was first investigated by calculating F_{ST} (theta estimator, Weir and Cockerham 1984) and assessing its significance using exact G-tests (10,000 permutations) in FSTAT. Subsequently, we used the Bayesian clustering approach as implemented in STRUCTURE (Pritchard et al. 2000) to cluster individuals without a priori information about their geographic origin. We used the admixture and correlated allele frequency models for a varying number of clusters (*K*, from 1 to 10), with 20 independent repetitions for each *K* value and a MCMC length of 1,000,000 iterations (burn-in: 300,000). The optimal number of clusters was determined using both the likelihood of each *K* (Ln Pr(X|K)) and the method described by Evanno et al. (2005) as implemented in STRUCTURE HARVESTER v.0.6.94 (Earl and vonHoldt 2012). Independent runs for the optimal *K* were combined using CLUMPAK (Kopelman et al. 2015), additionally implementing the DISTRUCT procedure to display graphical results (Rosenberg 2004).

Approximate Bayesian computation

We used ABC analyses implemented in DIYABC v.2.1.0 (Cornuet et al. 2014) to gain insights into the demographic history of the Corsican mouflon populations. ABC relies on the simulation of numerous data sets, which are, like the observed data set, summarized by statistics calculated within or among populations. The posterior probabilities of different demographic scenarios and the posterior distribution of demographic parameters are assessed by comparing observed and simulated statistics (Cornuet et al. 2014). We used microsatellites in combination with mitochondrial DNA data to trace back the history of Corsican mouflon on both recent and ancient time scales. Such an approach has been shown to improve the estimation of ancient divergence times (Cornuet et al. 2010). Nevertheless, in the preliminary runs we also evaluated the results based on microsatellites only. These were qualitatively the same as those obtained using the combined data set. Therefore, we ran the final analyses using the latter, which included 176 individuals genotyped at 16 microsatellite DNA loci, among which 98 were also sequenced at the 1,042 bp-long *Cyt-b* gene, along
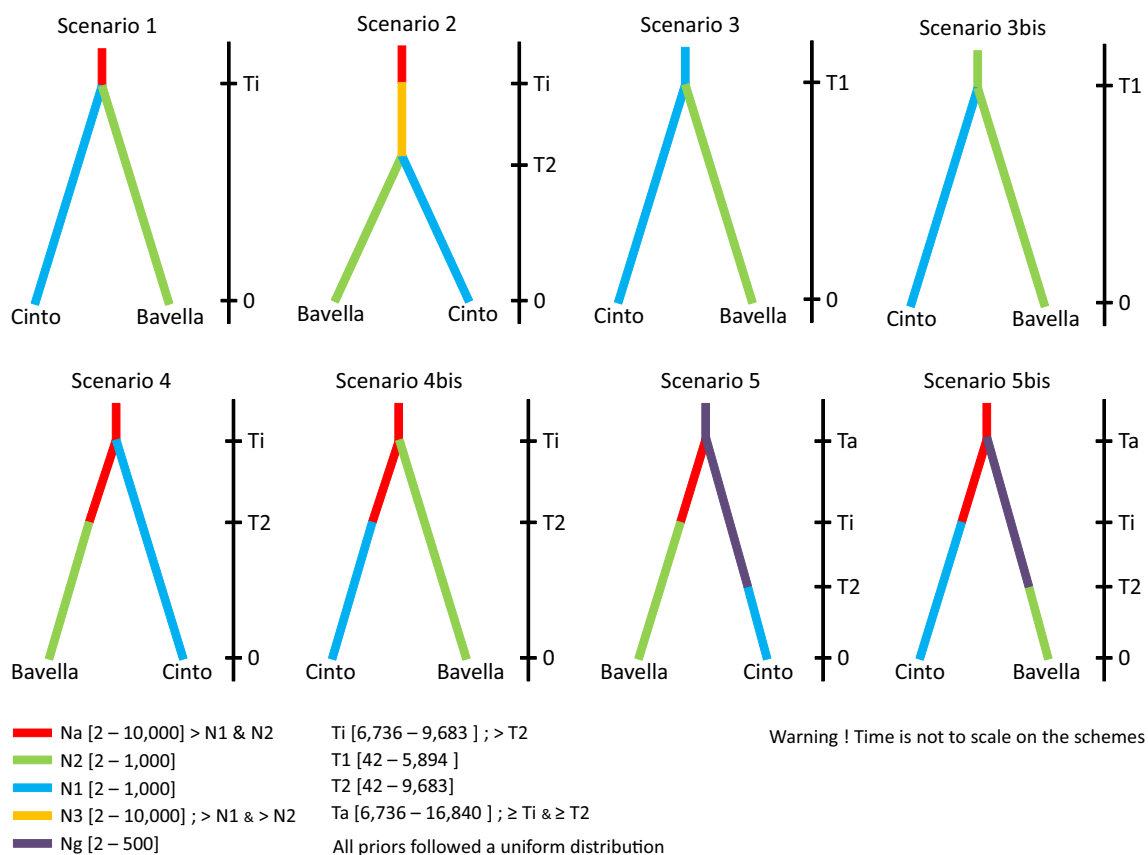

Fig. 2 Schematic representations of the 8 scenarios modelled and compared using the ABC approach as implemented in DIYABC v.2.1.0 (Cornuet et al. 2014). See Supplementary Table S4 for bio-logical interpretation. Prior settings are given within brackets and a detailed description of their definition can be found in Supplementary Data 1

with 11 additional individuals for which only the *Cyt-b* was available.

We compared eight scenarios that might have led to the present-day spatial genetic structure of the Corsican mouflon (see Fig. 2 and Supplementary Table S4 for a detailed description). Briefly, we took into account cases where the Cinto and Bavella populations were formed simultaneously or successively from either the same (scenarios 1, 4, 4bis) or different (scenarios 5, 5bis) source populations. The tested scenarios also took into account the circumstance that only one population was introduced during the Neolithic whereas the other stemmed from this ancestral population either by splitting due to demographic and/or genetic bottlenecks (scenarios 2) or by virtue of some recent human-mediated translocations (scenarios 3, 3bis).

All scenarios were considered equally probable and the prior values were chosen after preliminary analyses according to both their biological meaning and our knowledge of the history of the Corsican mouflon (Fig. 2; see also Supplementary data 1 for a detailed explanation). All priors were set to follow a uniform distribution. Mutation models were retained as the default setting implemented in DIYABC v.2.1.0 (i.e. generalized stepwise mutation model for microsatellites with default parameters, and default parameters with a HKY85 + G + I substitution model (I = 0.55, α = 0.92, see above) for *Cyt-b*, see Supplementary data 1 for details). As regards the summary statistics, for the microsatellite DNA we included: the mean number of alleles and the mean genetic diversity across loci per- and among populations, the mean M index per population, the F_{ST} and the $(d\mu)^2$ distance between populations. For mitochondrial DNA, the summary statistics comprised the mean number of haplotypes and the number of segregating sites per and among populations, the mean pairwise differences per population, and the F_{ST} between population pairs. We generated 8,000,000 simulated data sets; the pre-evaluation of scenario-prior combinations was undertaken using a principal component analysis (PCA) as well as numerical values from the summary statistics. The posterior probabilities of scenarios and distributions of demographic parameters were computed using the closest 1% of simulated data sets to the observed data. Finally, as recommended by Cornuet et al. (2015), the reliability of the most supported model was tested using the 'model checking' analysis in DIYABC. This step assesses model goodness-of-fit by comparing observed and simulated data under the posterior predictive distribution. The comparison was carried out using both PCA and numerical values from all available summary statistics in DIYABC (i.e. the 19 used for the scenario choice plus all others available, 37 in total; see Supplementary Table S6).

Results

Mitochondrial DNA

A total of 135 haplotypes were inferred from the 327 aligned sequences (56 and 53 sequences from the Bavella and Cinto populations, respectively, plus 218 sequences retrieved from GenBank). The 109 sequences obtained in the present study corresponded to the haplotypes already published by Guerrini et al. (2015) (H2, H4 and H7 with GenBank accession numbers LN651260, LN651262 and LN651265, respectively). Three haplotypes were present in the Cinto population: H2 was found in 17 individuals (32% of the investigated population sample), H4 in 4 (8%) and H7 in 32 (60%). All 56 Bavella mouflon held haplotype H4 (Fig. 1C, Supplementary Figure S2).

Phylogenetic reconstruction and haplotype network

Phylogenetic reconstruction was performed relying on 120 sequences representing haplotype diversity and geographic range (i.e. removing for each geographic location duplicate haplotypes; see Supplementary Table S1). The findings pointed to a clear separation between *O. gmelini* and *O. vignei* (Fig. 3). Within *O. gmelini,* individuals from the Middle East (Turkey, Armenia and Iran) mostly grouped together with strong statistical support and significantly diverged from the Western Mediterranean mouflon. Nevertheless, several Iranian and Turkish haplotypes were very close to those held by Corsican and Sardinian mouflons. One individual from Kazakhstan and one from Iran clustered within the Corsican (Cinto)/Sardinian clade (Fig. 3). Among the 120 haplotypes used in the phylogenetic reconstruction, 29 were unambiguously associated with *O. gmelini* from either the Middle East or the Mediterranean (Fig. 3). Interestingly, no *O. gmelini × O. vignei* hybrid individuals were included in the Corsica/Sardinia clade, while eight grouped within the Middle East clade. This latter also included the single Cypriot haplotype, which was the only Mediterranean mouflon close to the Asiatic mouflon from Armenia.

When focusing on the 29 haplotypes unambiguously assigned to *O. gmelini*, the network confirmed the evolutionary picture provided by the phylogenetic reconstruction (Fig. 1C). Indeed, one haplotype (EU365973) found in Turkey and Iran was very close to those from Corsica and Sardinia, while haplotype H7 was shared by mouflons from Sardinia, Iran, Kazakhstan and Cinto. The Cypriot haplotype was also close to several from the Middle East—the single Armenian haplotype included—and was shared with Iranian individuals only. Haplotype H2 was found only in Cinto and in the Sardinian population, while H4 was private to Corsica.
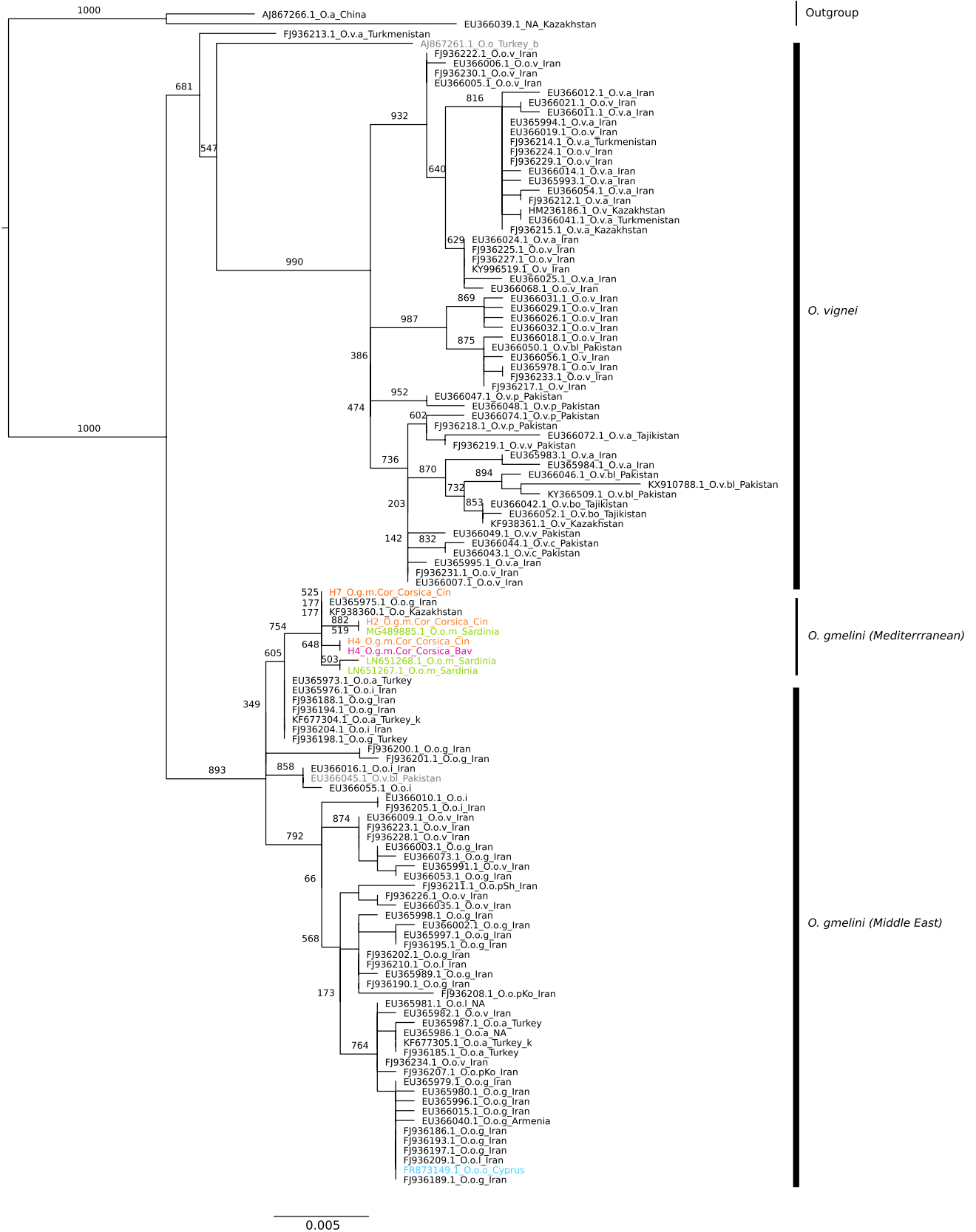
◀**Fig. 3** Maximum likelihood tree of Eurasian *Ovis* species. Main branch supports are indicated (bootstraps, *n* = 1000). Grey labels represent taxa for which an incoherence exists between the species name indicated along the published DNA sequence and its position in the tree. Nomenclature is composed of the GenBank accession number followed by an acronym standing for the species (according to how it was named in the original paper, see Supplementary Table S1 and below) and the locality (if known) where the individual was sampled. Mediterranean mouflon sequences are coloured according to their geographic origin and following the colours of the haplotype network (Fig. 1C). For species names, O.a stands for *Ovis ammon*, O.v.a: *Ovis vignei arkal*, O.o: *Ovis orientalis*, O.o.v: *Ovis orientalis × Ovis vignei*, O.v.bl: *Ovis vignei blandfordi*, O.v.p: *Ovis vignei punjabensis*, O.v.v: *Ovis vignei vignei*, O.v.bo: *Ovis vignei bochariensis*, O.v: *Ovis vignei*, O.v.c: *Ovis vignei cycloceros*, O.g.m.Cor: *Ovis gmelini musimon var. Corsicana*, O.o.g: *Ovis orientalis gmelini*, O.o: *Ovis orientalis*, O.o.m: *Ovis orientalis musimon*, O.o.a: *Ovis orientalis anatolica*, O.o.i: *Ovis orientalis isphahanica*, O.o.pKo: *Ovis orientalis population Ko*, O.o.l: *Ovis orientalis laristanica*. It should be noted here that *Ovis orientalis* is a deprecated name and *Ovis gmelini* should be used instead (Groves and Grubb 2011; Hadjisterkotis and Lovari 2016)

Divergence time estimation

The divergence between Corsican/Sardinian and Cypriot lineages was dated 560,000 years BP [292,400–963,500]$_{95\% \text{ HPD}}$ (Supplementary Figure S1). A second event separated Iranian/Turkish and Corsica/Sardinia haplotypes 320,000 years BP [143,000–567,300]$_{95\% \text{ HPD}}$. Corsica and Sardinia diverged more recently. Haplotype H2, which can be found in both Corsica (Cinto) and Sardinia, departed from H4 and H7 110,000 years BP [36,100–227,400]$_{95\% \text{ HPD}}$. Haplotype H4, which was found only in Corsica, separated from H7 (Corsica/Sardinia) 70,000 years BP [2,300–166,400]$_{95\% \text{ HPD}}$ (Supplementary Figure S1). Interestingly, the other two haplotypes found in Sardinia only diverged from those occurring in Corsica 190,000 years BP [71,800–344,100]$_{95\% \text{ HPD}}$.

Microsatellite DNA

Genotyping errors

The microsatellite panel was powerful in discriminating the mouflons. The probabilities of identity considering unrelated or sibling individuals were $P_{ID} = 3.0 \times 10^{-9}$ and $P_{IDsibs} = 1.2 \times 10^{-4}$ for the Cinto and $P_{ID} = 3.0 \times 10^{-8}$ and $P_{IDsibs} = 3.9 \times 10^{-4}$ for the Bavella populations. The average quality index for faeces was 0.95, indicating a very good quality for this kind of sample. In Cinto, no evidence of allele dropout and scoring errors was found using MICROCHECKER v.2.2.3, while null alleles were recorded at 6 loci. However, their frequencies were relatively low ($f = 0.11, 0.10, 0.08, 0.13, 0.07, 0.12$ for BM8125, HUJ616, MCM140, OarCP34, OarHH47 and SRCRSP1, respectively; Van Oosterhout et al.'s estimator from Van Oosterhout et al. 2004) and the occurrence

of a strong intra-population genetic structure was deemed the most likely explanation for this finding (Chapuis and Estoup 2007). Indeed, when the structure of the Cinto population was investigated, two strongly supported clusters were found (see Supplementary Figures S3 and S4 and Portanier 2018) and no null alleles were disclosed when the analysis was carried out within each group (Portanier 2018). In Bavella, no genotyping errors were detected using MICROCHECKER and, as above, the occurrence of null alleles at loci OarHH47 and OarJMP29 ($f = 0.10$ for both loci) was attributed to a significant level of intra-population genetic structure (Supplementary Figure S3 and S4 and Portanier 2018). Again, within clusters, only OarHH47 was still suspected to include null alleles ($f = 0.20$, one cluster only), this outcome likely due to the relatively low number of genotyped individuals in this cluster ($n = 20$).

Population genetic diversity and structure

In the Cinto population, seven pairs of loci were in LD (HUJ616-OarCP34, HUJ616-SRCRSP1, MAF70-OarHH47, OarCP34-OarHH47, OarCP34-SRCRSP1, OarHH47-SRCRSP1 and OarVH72- SRCRSP1). At least one locus for each pair was suspected to include null alleles (see above). In the Bavella population, two pairs of loci (HUJ616-OarCP34 and HUJ616-OarVH72) were in LD. In both populations, the level of genetic diversity was relatively low. The Bavella population did not depart from HWE, unlike the Cinto population, which held significant positive F_{IS} values, suggesting an excess of homozygotes at three loci (Table 1, Supplementary Table S3). Nevertheless, departure from HWE disappeared when the loci suspected to include null alleles were removed (Supplementary Table S3). In order to ensure that the downstream analyses would not be biased by the occurrence of loci believed to include null alleles or being in LD, we used either the whole data set (16 loci) or a subset without the problematic loci. These included BM8125, HUJ616, MCM140, OarCP34, OarHH47 and SRCRSP1 for the Cinto population and OarJMP29 for the Bavella one. The reduced data set therefore comprised 9 loci. The results were qualitatively and quantitatively very similar to each other and only those obtained by relying on the whole data set are provided in the manuscript.

Genetic differentiation between the two Corsican populations was high ($F_{ST} = 0.23$ [0.13; 0.32]$_{95\%}$, $p < 0.0001$). In addition, 15 and 17 alleles were private to the Bavella and the Cinto populations, respectively. Bayesian clustering with STRUCTURE highlighted the occurrence of a strong genetic divergence between the two populations. The Evanno method clearly indicated an optimal number of two

Table 1 Genetic diversity estimates (mean over loci ± SD) and F_{IS} values for both Corsican mouflon populations

Population	n	Na	Ar	Ho	He	F_{IS}
Bavella	59	3.06 ± 1.29	3.03 ± 1.24	0.41 ± 0.22	0.44 ± 0.23	0.085
Cinto	117	3.19 ± 1.05	3.09 ± 1.03	0.45 ± 0.18	0.50 ± 0.19	0.114*

n sample size, Na number of alleles, Ar allelic richness, Ho observed heterozygosity, He expected heterozygosity

*F_{IS} values are significantly different from zero (Bonferroni-adjusted nominal level = 0.002)
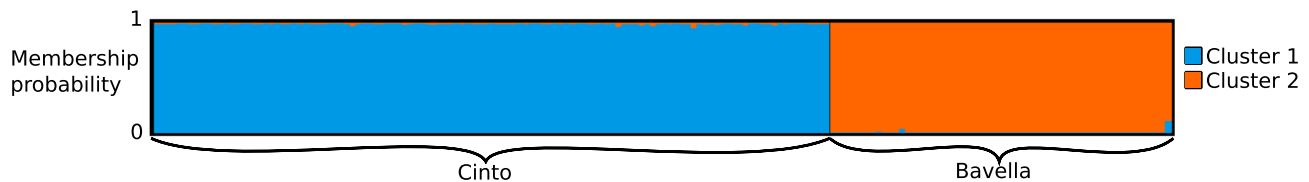
Fig. 4 Bayesian analysis of microsatellite DNA multilocus genotypes as computed with STRUCTURE. Each individual is represented as a vertical bar partitioned in K segments, whose length is proportional to the estimated membership to the K clusters

clusters (Supplementary Figure S5). Maximum K likelihood also gave strong support for $K = 2$ (although K = 3 received maximal support as a result of the Cinto intra-population genetic structure; see Supplementary Figures S4 and S5) and the assignment success was 100% because both the first and the second clusters included all individuals from the Cinto and the Bavella populations, respectively (Fig. 4). The posterior probability of membership ranged from 0.955 to 0.998 and from 0.888 to 0.998 for the Cinto and the Bavella clusters, respectively (Fig. 4).

Approximate Bayesian computation

Based on the PCA and the numerical values of the summary statistics, we observed a good congruence between the scenarios-priors combination and the observed data set, revealing that the former was able to produce simulated data sets that were close enough to the latter. Indeed, in the PCA, observed data were nested in prior distributions (Supplementary Figure S6) and only a few summary statistics calculated on simulated data provided values that were significantly different from those observed (7 to 8 out of 19 according to the considered scenario, Supplementary Table S5). A comparatively higher posterior probability (all < 0.01; see Supplementary Figure S7) was disclosed for scenario 2 (logistic approach: 0.9896 [0.9881; 0.9910]$_{95\% HPD}$ based on the 80,000 simulated data sets closest to the observed data). The second-most supported scenario was 4bis (posterior probability: 0.0087 [0; 0.14]$_{95\% HPD}$). Other posterior probabilities were 0.001 [0; 0.13]$_{95\% HPD}$, 0.0004 [0; 0.13]$_{95\% HPD}$, 0.0001 [0; 0.13]$_{95\% HPD}$, 0.0011 [0; 0.14]$_{95\% HPD}$, 0.00 [0; 0.13]$_{95\% HPD}$ and 0.00 [0; 0.13]$_{95\% HPD}$, for scenarios 1, 3, 3bis, 4, 5 and 5bis, respectively. Model checking revealed good congruence between observed data and data simulated

Table 2 Mean, median and 2.5–97.5% quantiles of historical parameter estimates under demographic scenario 2 modelled in DIYABC

	Mean	Median	95%CI	Prior values
N_1	478	447	109–947	2–1000
N_2	391	374	95–837	2–1000
N_3	5580	5550	1290–9770	2–10,000
N_a	8150	8530	4390–9940	2–10,000
T_2	606	497	126–1794	42–9683
T_i	7957	7873	6778–9557	6736–9683

Time parameters are expressed in years BP (mouflon generation time: 4.21 years; Hamel et al. 2016). For details about prior definitions, see Supplementary Data 1

under scenario 2 from the posterior predictive distribution and the prior distribution (Supplementary Figure S8). Only a few observed summary statistics were found in the tails of distributions of summary statistics computed from the simulated data (5 out of 37 among which none had a tail-area probability lower than 0.001; Supplementary Table S6), thus indicating good reliability for this most supported model (Estoup et al. 2018). Historical parameter estimates under scenario 2 suggested that the founders of the Corsican ancestral population could have been introduced around 8000 years BP (T_i), before splitting (T_2) 606 years BP into Cinto and Bavella populations (Table 2, Supplementary Figure S9).

Discussion

This study is the first large-scale genetic study performed on Corsican mouflon populations. Mitochondrial DNA sequencing revealed the occurrence of three haplotypes in

Corsica, which were either shared with or were very close to those held by Kazakh, Iranian and Turkish individuals (Figs. 1C and 3), thus reaffirming that the Corsican mouflon is a descendant of the Asiatic mouflon introduced into the Mediterranean Basin. Therefore, the Corsican population should be unvaryingly referred to as *O. g. musimon*, i.e. as a subspecies of the Asiatic mouflon. Both divergence time estimates and population genetic structure suggested that gene flow between the two Corsican populations has been restricted for many generations. ABC supported the introduction of a unique ancestral population, with two demes stemming later on and evolving separately during the past centuries.

Past Corsican mouflon population history

Numerous studies have investigated the history of domestic sheep (e.g. Chessa et al. 2009; Demirci et al. 2013; Ciani et al. 2020). Consequently, the genus *Ovis* is probably one of the most extensively studied taxon from a phylogenetic point of view. However, whereas Sardinian and Cypriot mouflon have been widely investigated (e.g. Guerrini et al. 2015; Sanna et al. 2015; Mereu et al. 2019), the same attention has not been paid to the Corsican mouflon. Studying both Cinto and Bavella as distinct mouflon populations for the first time, we found that they differed from each other in their haplotypic composition. On the other hand, haplotypes found in Corsica also occurred in Sardinia, Iran and Kazakhstan (Fig. 1C). The Kazakh individual (KF938360, Lv et al. 2015) with H7 was regarded as a possible hybrid by Mereu et al. (2019), as it clustered with German mouflons in their reconstructions based on the mitochondrial D-loop. Haplotype H7 has also been detected in wild Iranian individuals (Rezaei et al. 2010, EU365975; Meadows et al. 2011, HM236185) as well as in domestic sheep (see for instance Niu et al. 2016). Overall, this may suggest that the Kazakh mouflon descended from a domestic ewe. Apart from this doubtful individual, the Corsica/Sardinia clade was phylogenetically close to other Iranian and Turkish haplotypes (Fig. 3), a result in perfect agreement with the expected Middle Eastern origin of the Corsican mouflon (Chessa et al. 2009; Rezaei et al. 2010). More importantly, by relying on a sample size much larger than those investigated in previous studies (Rezaei et al. 2010; Guerrini et al. 2015; Mereu et al. 2019), we provided clear genetic evidence for the descent of Corsican and Sardinian mouflon from their Asiatic counterpart, with their Cypriot conspecifics being the closest relative to the latter (Chessa et al. 2009). Therefore, the Corsican mouflon along with some Sardinian populations may represent the most genetically and phenotypically preserved descendant of the Asiatic mouflon in the Western Mediterranean (Barbato et al. 2017).

In the Cinto population, only a few individuals held haplotype H4. Although H2, H4 and H7 diverged from one another much more recently than the Cypriot one did with respect to the Iranian haplotypes, such differentiation nevertheless seems to have predated the introduction of the mouflon into Corsica (70,000–110,000 BP). The occurrence of a haplotype (H4) shared by the populations of Cinto and Bavella makes it difficult to establish whether these populations originated from the same or different sources. The second hypothesis may find support in the phenotypic differences observed between Cinto and Bavella individuals (Maudet and Dubray 2002; Sanchis 2018) as well as in the results of human genetic studies performed in Corsica. Indeed, a similar north–south differentiation has been detected in the settlement across the island of different human groups originating from diverse geographic areas, including Iran (Tofanelli et al. 2001; Vona et al. 2003; Di Cristofaro et al. 2018). Such a scenario, namely genetically different populations following distinct introduction events, nevertheless received very low support in the ABC compared to the one suggesting a single group of founders and a subsequent split (Supplementary Figure S7).

Although mouflons might have persisted across most of the Corsican mountains after their introduction (e.g. Giustiniani 1531 in Dubray and Roux 1985; Pfeffer 1967; Simonpoli 1995; but see Dubray 1984), population size variations and genetic bottlenecks or local adaptations might have led diverging haplotypes to persist in different/distant geographic areas after the split, thereby contributing to the present-day population structure. This pattern might have also resulted from the tendency of mouflons to display strong female philopatry (Dubois et al. 1992, 1994; Dupuis et al., 2002) and poor dispersal abilities (Dubois et al. 1996; Portanier et al. 2017), alongside landscape features that are highly resistant to gene flow between the two populations (e.g. ridges and thalwegs; Marchand et al. 2017; Portanier et al. 2018). This may further explain the similar north–south spatial structure detected at an intra-population scale within both Cinto and Bavella populations (Supplementary Figures S1, S3 and S4). Finally, the few mouflons sharing haplotypes between Cinto and Bavella populations may be descendant of better represented ancient lineages, and/or the result of human-mediated translocations.

According to ABC, Corsican mouflon would have been introduced around 8000 years B.P (T_i in Table 2). Although paleontological studies have dated the occurrence of the mouflon to 6000 years BP (Vigne 1988, 1992), our estimates suggested that Neolithic people might have reached Corsica much earlier (see also Poplin 1979). This estimation may nevertheless also represent the time at which the divergence between the flock travelling with Neolithic people and the ancestral source population became large enough to be detectable. This might have occurred slightly earlier than the

actual introduction of the mouflon into Corsica. The split leading to two distinct populations seemed to have occurred around 600 [126–1793]$_{95\%IC}$ years BP. During this period, a number of human conflicts occurred in Corsica (under the government of the Republic of Genoa), and an increase in non-endemic faunal diversity has been described as a result of intense maritime activities leading to the extinction of endemic species and the decline of taxa such as the mouflon (Vigne 1992). Demographic decline and habitat loss might have contributed to strong bottlenecks and the fragmentation of the mouflon population. Nevertheless, in this study, the confidence intervals around parameter estimates were large (Table 2). Although this is commonly observed in ABC analyses (e.g. Cabrera and Palsbøll 2017; Stone et al. 2017; Allen et al. 2020), it may represent an important drawback and it should be kept in mind when interpreting the results.

Recent Corsican mouflon population history

With the exception of Guerrini et al. (2015), which included some individuals genotyped at microsatellite loci, this study was the first to be carried out on the Corsican mouflon at large spatial scale and with large sample size while focusing on Cinto and Bavella as distinct populations. We found strong genetic differentiation between the two populations, as revealed by both F_{ST} and Bayesian genetic clustering approaches (Fig. 4). In addition, numerous private alleles were detected, reinforcing the hypothesis of a lack of gene flow between the two populations, either in the present or the recent past (i.e. a few ten or hundred generations ago; Landguth et al. 2010; Haasl and Payseur 2011; Safner et al. 2011). This result was in accordance with our expectations, as the natural dispersion of mouflons between Cinto and Bavella was deemed very unlikely due to limited dispersal abilities and the occurrence of barriers to gene flow (see above).

In both investigated populations, heterozygosity and allelic richness were low (Table 1), probably as a consequence of genetic bottlenecks related to declines in the population size (Pfeffer 1967). More generally, low levels of genetic diversity are typical of mouflon populations (Ozüt 2001; Barbato et al. 2017). Although this may be of concern in terms of fitness, population persistence and adaptive potential for the species (Gaggiotti 2003; Frankham et al. 2004; Kaeuffer et al. 2008; Portanier et al. 2019), it is worth recalling that numerous introduced populations have proved to be able to reach a high level of genetic diversity with no concern for their persistence, even as descendants of a very small group of founders (Uloth 1972; Giffin 1979; Weller 2001; Kaeuffer et al. 2007; Portanier et al. 2017). Therefore, resource shortage (Ciuti et al. 2009) rather than low genetic diversity could be the main threatening factor in the long term (Boussès and Réale 1998; Garel et al. 2005),

especially in the light of currently rampant climate change (Paeth and Hense 2005).

Conservation perspectives for the Corsican mouflon

Mouflon hunting has been forbidden across the entire island of Corsica since 1953, hence the species has benefited from early albeit not comprehensive preservation. Nevertheless, the Corsican mouflon has very recently been recognized as an officially protected species (Ministerial order of 1 March 2019, NOR: TREL1824291A) and will hence benefit from a more adequate conservation strategy in the future. However, the latter must consider important issues such as establishing whether Cinto and Bavella populations should be managed in the same way and whether their genetic connectivity should be restored or not. Two main categories of conservation units have been described so far: evolutionarily significant units (ESUs; Ryder 1986; Moritz 1994) and management units (MUs; Moritz 1994, Taylor and Dizon 2005). Whereas reciprocal monophyly and divergence of allele frequency at mitochondrial and nuclear DNA loci, respectively, is required to be recognized as ESUs, MUs are defined as 'demographically independent populations whose population dynamics (e.g. population growth rate) depend largely on local birth and death rates rather than on immigration' (Palsbøl et al. 2007). Given that reciprocal monophyly was not disclosed between the mtDNA lineages of the two Corsican populations, Bavella and Cinto mouflons cannot be referred to as ESUs. However, both their strong genetic differentiation and demographic independence (since approximately 600 years BP according to ABC) allow us to recommend viewing them as two distinct and, as such, independently managed, MUs.

Based on the results obtained in the present study, two types of management strategies may be considered. The common origin inferred for Cinto and Bavella populations may call for conservation strategies aiming to restore genetic connectivity between them. Indeed, gene flow among MUs is expected to be not only harmless but potentially beneficial to increasing genetic diversity and thus adaptive potential maintenance (Frankham et al. 2004; Mills 2013). However, natural inter-population genetic exchanges between Cinto and Bavella seem to have been impaired for approximately 144 mouflon generations (around 600 years). In addition, the dynamics observed in introduced mouflon populations (e.g. high reproductive success and rapid restoration of genetic variability; Garel et al. 2005; Kaeuffer et al. 2007, 2008) suggest that evolution can be very rapid in this taxon. Altogether, this may lead to the hasty appearance of local adaptations, for instance, as a result of differences existing between the two habitats (e.g. Cinto: 40.6% open habitats; Bavella: 19.7%). Present-day strong genetic divergence and potential risks related to the translocation of highly divergent

individuals (such as outbreeding depression and loss of local adaptations; Edmands 2007) should inspire caution regarding conservation strategies encompassing the exchange of individuals between the two populations. More studies (e.g. genome-wide sequencing and identification of adaptive genetic variation, genome-environment association studies; Holenhole et al. 2020; Dudaniec et al. 2018; González-Serna et al. 2020) are needed to assess the risks that such translocations would entail.

As long as neither population is declining, especially the smaller one in Bavella, we do not recommend using one population to supplement the other one. Accordingly, we propose a more wary approach for their management. When reintroductions are needed, they will be planned using individuals from captive breeding programmes relying on mouflons sampled in the concerned population. This perfectly fits with what is ongoing for the Bavella population to increase spatial range, population size and genetic diversity (Rieu 2007). A future reintroduction plan can also account for the existence of within-population substructures (Supplementary Figures S3 and S4; Portanier 2018). Although larger sample sizes in the Bavella population would likely be needed to confirm F_{ST} values between its own clusters, the high value reported in this study ($F_{ST} = 0.16$ and 0.20 in Bavella and Cinto populations, respectively) was of the same order of magnitude as that found between the two populations, a result that can have implications in terms of conservation strategies. It is noteworthy that the ABC analyses revealed an estimate of the effective Cinto population size (Ne) in good agreement with previous knowledge. Indeed, the latest estimate of the census size (Nc) in the Cinto population was 900 individuals (Garel et al. in press), leading to an Ne/Nc *ratio* of around 0.5, a high but nevertheless congruous value when compared to those obtained for other ungulates and *Ovis* species (e.g. *Ovis canadensis*; Hoban et al. 2020). In addition, the methods used to estimate the census size are known to often result in underestimated Nc (Morellet et al. 2007). Conversely, an effective population size of approximately 400 individuals for the Bavella population appears highly optimistic when compared to the latest Nc estimate (around 200 individuals). Although the census may be downward-biased (Morellet et al. 2007), effective size estimates must be considered carefully because they are associated with wide confidence intervals (Table 2) and can show sensitivity to prior definition (as we observed in our preliminary analyses).

Although we do not recommend human-mediated interpopulation exchanges, the preservation of mouflon-favourable habitats in both massifs (e.g. grass-rich areas, covered areas; Garel et al. 2007; Marchand et al. 2015) as well as between them may enhance the natural restoration of interpopulation gene flow. Finally, the survival of the Corsican mouflon would benefit from additional studies regarding its phylogenetic relationships with domestic sheep. Indeed, while sheep domestication had started 11,000 years BP (Zeder 2008), divergence times of 110,000–171,000 years BP between sheep and mouflon haplotypes have been reported for Sardinian and Cypriot populations (Sanna et al. 2015; Mereu et al. 2019). Therefore, these populations should not be regarded as descendants of domestic sheep but instead as wild taxon that evolved separately, namely as unique gene pools to be conserved (Chessa et al. 2009; Guerrini et al. 2015). The same can be expected for the Corsican mouflon because they seem to share a large part of their history with those from Sardinia. Regrettably, following International Commission on Zoological Nomenclature recommendations (see also Wilson and Reeder 2005; the Washington and Bern Conventions), the Corsican (and more generally Western Mediterranean) mouflon is still considered by several authors a domestic subspecies (*O. aries musimon*). Such a taxonomic designation may underestimate the importance of protecting the unique Corsican mouflon gene pool, beyond being advantageous to people charged with crimes against mouflon (e.g. poachers), a risk also suggested to occur for the Cypriot mouflon (Guerrini et al. 2015). Unvaryingly referring to Corsican mouflon as *O. gmelini musimon* would thus favour its conservation and lessen the extinction risk of Mediterranean mouflon in general (Hughes et al. 1997).

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All captures, handling and sampling were conducted according to the appropriate national laws for animal welfare, following the ethical conditions detailed in the specific accreditations delivered by the Préfecture de Paris (prefectorial decree n°2009–014) in agreement with the French environmental code (Art. R421-15 to 421–31 and R422-92 to 422–94-1).

Consent to participate Not applicable.

Consent for publications Not applicable.

References

Allen A, Guerrero J, Byrne A, Lavery J, Presho E, Courcier E, O'Keeffe J, Fogarty U, Delahay R, Wilson G, Newman C, Buesching C, Silk M, O'Meara D, Skuce R, Biek R, McDonald RA (2020) Genetic evidence further elucidates the history and extent of badger introductions from Great Britain into Ireland. R Soc Open Sci 7:200288

Bandelt H, Forster P, Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. Mol Biol Evol 16:37–48

Barbanera F, Guerrini M, Beccani C, Forcina G, Anayiotos P, Panayides P (2012) Conservation of endemic and threatened wildlife: molecular forensic DNA against poaching of the Cypriot mouflon (*Ovis orientalis ophio*n, Bovidae). Forensic Sci Int Genet 6:671–675

Barbato M, Hailer F, Orozco-terWengel P, Kijas J, Mereu P, Cabras P, Mazza R, Pirastru M, Bruford MV (2017) Genomic signatures of adaptive introgression from European mouflon into domestic sheep. Sci Rep 7:7623

Beaumont MA (2010) Approximate Bayesian computation in evolution and ecology. Annu Rev Eco Evol Syst 41:379–406

Belkhir K, Borsa P, Chikhi L, Raufaste N, Bonhomme F (2004) GENETIX 4.05, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier (France)

Bibi F (2013) A multi-calibrated mitochondrial phylogeny of extant Bovidae (Artiodactyla, Ruminantia) and the importance of the fossil record to systematics. BMC Evol Biol 13:166

Biebach I, Keller L (2009) A strong genetic footprint of the re-introduction history of Alpine ibex (*Capra ibex ibex*). Mol Ecol 18:5046–5058

Bonferroni CE (1936) Teoria statistica delle classi e calcolo delle probabilità. Pubbl R Istituto Super Sci Econ Commer Firenze 8:3–62

Bouckaert RR, Drummond AJ (2017) bModelTest: Bayesian phylogenetic site model averaging and model comparison. BMC Evol Biol 17:1–11

Bouckaert R, Vaughan TG, Barido-Sottani J, Duchêne S, Fourment M, Gavryushkina A, Heled J, Jones G, Kühnert D, De Maio N, Matschiner M, Mendes FK, Müller NF, Ogilvie HA, du Plessis L, Popinga A, Rambaut A, Rasmussen D, Siveroni I, Suchard MA, Wu CH, Xie D, Zhang C, Stadler T, Drummond AJ (2019) BEAST 25: an advanced software platform for Bayesian evolutionary analysis. PLoS Comput Biol 15:e1006650

Boussès P, Réale D (1998) Biology of twinning and origin of an unusually high twinning rate in an insular mouflon population. Z Für Säugetierkunde 63:147–153

Bozzuto C, Biebach I, Luff S, Ives AR, Keller LF (2019) Inbreeding reduces long-term growth of Alpine ibex populations. Nat Ecol Evol 3:1359–1364

Cabrera AA, Palsbøll PJ (2017) Inferring past demographic changes from contemporary genetic data: a simulation-based evaluation of the ABC methods implemented in DIYABC. Mol Ecol Resour 17:e94–e110

Chapuis MP, Estoup A (2007) Microsatellite null alleles and estimation of population differentiation. Mol Biol Evol 24:621–631

Chessa B, Pereira F, Arnaud F, Amorim A, Goyache F, Mainland I, Kao RR, Pemberton JM, Beraldi D, Stear MJ, Alberti A, Pittau M, Iannuzzi L, Banabazi MH, Kazwala RR, Zhang YP, Arranz JJ, Ali BA, Wang Z, Uzun M, Dione MM, Olsaker I, Holm LE, Saarma U, Ahmad S, Marzanov N, Eythorsdottir E, Holland MJ, Ajmone-Marsan P, Bruford MW, Kantanen J, Spencer TE, Palmarini M (2009) Revealing the history of sheep domestication using retrovirus integrations. Science 324:532–536

Ciani E, Mastrangelo S, Da Silva A, Marroni F, Ferenčaković M, Ajmone-Marsan P, Baird H, Barbato M, Colli L, Delvento C, Dovenski T, Gorjanc G, Hall SJG, Hoda A, Li M, Marković B, McEwan J, Moradi MH, Ruiz-Larrañaga O, Ružić-Muslić D, Šalamon D, Simčič M, Stepanek O, Curik I, Cubric-Curik V, Lenstra J (2020) On the origin of European sheep as revealed by the diversity of the Balkan breeds and by optimizing population-genetic analysis tools. Genet Sel Evol 52:25

Ciuti S, Pipia A, Grignolio S, Ghiandai F, Apollonio M (2009) Space use, habitat selection and activity patterns of female Sardinian mouflon (*Ovis orientalis musimon*) during the lambing season. Eur J Wildl Res 55:589–595

Coltman DW, Pilkington JG, Smith JA, Pemberton JM (1999) Parasite-mediated selection against inbred Soay sheep in a free-living, island population. Evolution 53:1259–1267

Cornuet JM, Ravigné V, Estoup A (2010) Inference on population history and model checking using DNA sequence and microsatellite data with the software DIYABC (v10). BMC Bioinform 11:401

Cornuet JM, Pudlo P, Veyssier J, Dehnegarcia A, Gautier M, Leblois R, Marin JM, Estoup A (2014) DIYABC v2.0: A software to make approximate Bayesian computation inferences about population history using single nucleotide polymorphism, DNA sequence and microsatellite data. Bioinformatics 30:1187–1189

Cornuet JM, Pudlo P, Veyssier J, Loire E, Santos F, Dehne-Garcia A, Estoup A (2015) A user-friendly software for inferring population history through Approximate Bayesian Computations using microsatellite, DNA sequence and SNP data. http://www1.montpellier.inra.fr/CBGP/diyabc/diyabc-2.1.0/tmp/diyabc-2.1.0-UserManual.pdf. Accessed 3 Aug 2020

Courchamp F, Hoffman BD, Russel JC, Leclerc C, Bellard C (2014) Climate change, sea-level rise, and conservation: keeping island biodiversity afloat. Trends Ecol Evol 29:127–130

Cugnasse JM (1994) Révision taxinomique des mouflons des îles méditerranéennes. Mammalia 58:507–512

Demirci S, Koban B, Evren D, Nihan D, Piskin E, Engin A, Togan I (2013) Mitochondrial DNA diversity of modern, ancient and wild sheep (*Ovis gmelinii anatolica*) from Turkey: new insights on the evolutionary history of sheep. PLoS ONE 8:e81952

Di Cristofaro J, Mazières S, Tous A, Di Gaetano C, Lin AA, Nebbia P, Piazza A, King RJ, Underhill P, Chiaroni J (2018) Prehistoric migrations through the Mediterranean basin shaped Corsican Y chromosome diversity. PLoS ONE 13:e0200641

Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol Biol 7:214

Drummond AJ, Suchard MA, Xie D, Rambaut A (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol Biol Evol 29:1969–1973

Dubois M, Gerard J, Maublanc ML (1992) Seasonal movements of females Corsican mouflon (*Ovis ammon*) in a Mediterranean mountain range, southern France. Behav Process 26:155–166

Dubois M, Bon R, Cransac N, Maublanc ML (1994) Dispersal patterns of Corsican mouflon ewes: importance of age and proximate influences. Appl Anim Behav Sci 42:29–40

Dubois M, Khazrziie K, Guilhem C, Maublanc ML, Le Pendu Y (1996) Philopatry in mouflon rams during the rutting season:psycho-ethological determinism and functional consequences. Behav Processs 35:93–100

Dubray D (1984) Achat de mouflon Corses pour le compte du gouvernement: étude des correspondances échangées entre 1820 et 1823. Office National de la Chasse, Service technique Corse

Dubray D, Roux D (1985) Recueil de 15 textes historiques relatifs au mouflon en Corse (1531–1960). Rapports scientifiques de l'Office National de la Chasse

Ducrocq V (2016) Climate change in the Mediterranean region. In: Moatti J-P, Thiébault S (eds) The Mediterranean region under climate change: a scientific update. IRD Editions, Marseille

Dudaniec RY, Yong CJ, Lancaster LT, Svensson EI, Hansson B (2018) Signatures of local adaptation along environmental gradients in a range-expanding damselfly (*Ischnura elegans*). Mol Ecol 27:2576–2593

Dupuis J, Badia J, Maublanc ML, Bon R (2002) Survival and spatial fidelity of mouflon (*Ovis gmelini*): a Bayesian analysis of an age-dependent capture-recapture model. J Agric Biol Environ Stat 7:277–298

Earl DA, vonHoldt BM (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conserv Genet Resour 4:359–361

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res 32:1792–1797

Edmands S (2007) Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. Mol Ecol 16:463–475

El Mousadik A, Petit RJ (1996) High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. Theor Appl Genet 92:832–839

Escoriza D, Hernandez A (2019) Using hierarchical spatial models to assess the occurrence of an island endemism: the case of *Salamandra corsica*. Ecol Process 8:15

Estoup A, Verdu P, Marin JM, Robert C, Dehne-Garcia A, Cornuet JM, Pudlo P (2018) Application of ABC to infer the genetic history of Pygmy hunter-gatherer populations from Western Central Africa. Handbook of approximate Bayesian computation. Chapman & Hall/CRC, London

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software structure: a simulation study. Mol Ecol 14:2611–2620

Festa-Bianchet M (2000) A summary of discussion on the taxonomy of mountain ungulates and its conservation implications. In: Workshop on Caprinae taxonomy, Ankara

Fitzsimmons NN, Buskirk SW, Smith MH (1995) Population history, genetic variability, and horn growth in bighorn sheep. Conserv Biol 9:314–323

Frankham R, Ballou JD, Briscoe DA (2004) A primer of conservation genetics. Cambridge University Press, New York

Gaggiotti OE (2003) Genetic threats to population persistence. Ann Zool Fenn 40:155–168

Galtier N, Gouy M, Gautier C (1996) SEAVIEW and PHYLO_WIN: two graphic tools for sequence alignment and molecular phylogeny. Comput Appl Biosci 12:543–548

Garel M, Cugnasse JM, Gaillard JM, Loison A, Gibert P, Douvre P, Dubray D (2005) Reproductive output of female mouflon (*Ovis gmelini musimon* × *Ovis* sp.): a comparative analysis. J Zool 266:65–71

Garel M, Cugnasse JM, Maillard D, Gaillard JM, Hewison AJM, Dubray D (2007) Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. Ecol Appl 17:1607–1618

Garel M, Marchand P, Bourgoin G, Santiago-Moreno J, Portanier E, Piegert H, Hadjisterkotis E, Cugnasse JM (in press) Mouflon *Ovis gmelini*, Blyth 1841. In: Corlatti L, Zachos F (Eds.) Terrestrial Cetartiodactyla, Handbook of the mammals of Europe. Springer International Publishing, New York

Gascuel O (1997) BIONJ: an improved version of the NJ algorithm based on a simple model of sequence data. Mol Biol Evol 14:685–695

Giffin JG (1979) Ecology of the Mouflon Sheep on Mauna Kea. Pittman-Robertson project No. W-17-R, Study no. R-III 1975–1979. Rapport technique, State of Hawaii - Department of land and natural resources—Division of Forestry and Wildlife

Giorgi F (2006) Climate change hot-spots. Geophys Res Lett 33:L08707

González-Serna MJ, Cordero PJ, Ortego J (2020) Insights into the neutral and adaptive processes shaping the spatial distribution of genomic variation in the economically important Moroccan locust (*Dociostaurus maroccanus*). Ecol Evol 10:3991–4008

Goudet J (1995) FSTAT (Version 1.2): a computer program to calculate F-Statistics. J Hered 86:485–486

Goudet J (2001) FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). http://www2.unil.ch/popgen/softwares/fstat.htm. Updated from Goudet (1995). Accessed 29 September 2021.

Goudet J, Jombart T (2015) Estimation and tests of hierarchical F-statistics. R Core Team, Vienna

Gouy M, Guindon S, Gascuel O (2010) SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Mol Biol Evol 27:221–224

Grill A, Casula P, Lecis R, Menken S (2007) Endemism in Sardinia. In: Weiss S, Ferrand N (eds) Phylogeography of southern European refugia. Springer, Dordrecht

Groves C, Grubb P (2011) Ungulate taxonomy. The Johns Hopkins University Press, Baltimore

Guerrini M, Forcina G, Panayides P, Lorenzini R, Garel M, Anayiotos P, Kassinis N, Barbanera F (2015) Molecular DNA identity of the mouflon of Cyprus (*Ovis orientalis ophion*, Bovidae): near Eastern origin and divergence from Western Mediterranean conspecific populations. Syst Biodivers 13:472–483

Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New Algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Syst Biol 59:307–321

Haasl RJ, Payseur BA (2011) Multi-locus inference of population structure: a comparison between single nucleotide polymorphisms and microsatellites. Heredity 106:158–171

Hadjisterkotis E, Lovari S (2016) Results and resolutions of the 6th World Congress on Mountain Ungulates and the 5th International Symposium on Mouflon. In: Book of Abstracts, 3rd edn. 28 August -1 September, Nicosia, pp 20–23

Hadjisterkotis E, Nahlik A, Uloth W (2001) The Cyprus mouflon, a threatened species in a biodiversity "hotspot" area. In: Proceedings of the Third International Symposium on Mouflon.

Hadjisterkotis E, Mereu P, Masala B (2017) Resolutions of the 6th World Congress on Mountain Ungulates and the 5th International Symposium on Mouflon and their effect on Mouflon taxonomy. In: 33rd IUGB Congress & 14th Perdix Symposium, Montpellier

Hamel S, Gaillard JM, Yoccoz NG, Albon S, Côté SD, Craine JM, Festa-Bianchet M, Garel M, Lee P, Moss C, Nussey DH, Pelletier F, Stien A, Tveraa T (2016) Cohort variation in individual body mass dissipates with age in large herbivores. Ecol Monogr 86:517–543

Hasegawa M, Kishino H, Yano TA (1985) Dating of the human–ape splitting by a molecular clock of mitochondrial DNA. J Mol Evol 22:160–174

Hoban S, Bruford M, Jackson DJ, Lopes-Fernandes M, Heuertz M, Hohenlohe PA, Paz-Vinas I, Sjögren-Gulve P, Segelbacher G, Vernesi C, Aitken S, Bertola LD, Bloomer P, Breed M, Rodríguez-Correa H, Funk WC, Grueber CE, Hunter ME, Jaffe R, Liggins L, Mergeay J, Moharrek F, O'Brien D, Ogden R, Palma-Silva C, Pierson J, Ramakrishnan U, Simo-Droissart M, Tani N, Waits L, Laikre L (2020) Genetic diversity targets and indicators in the CBD post-2020 Global Biodiversity Framework must be improved. Biol Conserv 248:108654

Hohenlohe PA, Funk WC, OmP R (2020) Population genomics for wildlife conservation and management. Mol Ecol 30:62–82

Hughes JB, Daily GC, Ehrlich PR (1997) Population diversity: its extent and extinction. Science 278:689–692

Jeanmonod D, Naciri Y, Schlüssel A, Gamisans J (2015) Floristic analyses of the Corsican flora: biogeographical origin and endemism. Candollea 70:21–41

Kaeuffer R, Coltman DW, Chapuis JL, Pontier D, Réale D (2007) Unexpected heterozygosity in an island mouflon population founded by a single pair of individuals. Proc R Soc B 274:527–533

Kaeuffer R, Réale D, Pontier D, Chapuis JL, Coltman DW (2008) Local effects of inbreeding on embryo number and consequences for genetic diversity in Kerguelen mouflon. Biol Lett 4:504–507

Keller LF, Waller DM (2002) Inbreeding effects in wild populations. Trends Ecol Evol 17:230–241

Keller SR, Fields PD, Berardi AE, Taylor DR (2014) Recent admixture generates heterozygosity–fitness correlations during the range expansion of an invading species. J Evol Biol 27:616–627

Kier G, Kreft H, Ming Lee T, Jetz W, Ibish PL, Nowicki C, Mutke J, Barthlott W (2008) A global assessment of endemism and species richness across island and mainland regions. PNAS 106:9322–9327

Kopelman NM, Mayzel J, Jakobsson M, Rosenberg NA, Mayrose I (2015) CLUMPAK: a program for identifying clustering modes and packaging population structure inferences across K. Mol Ecol Resour 15:1179–1191

Lande R (1988) Genetics and demography in biological conservation. Science 241:1455–1460

Landguth EL, Cushman SA, Schwartz MK, McKelvey KS, Murphy M, Luikart G (2010) Quantifying the lag time to detect barriers in landscape genetics. Mol Ecol 19:4179–4191

Lefort V, Longueville JE, Gascuel O (2017) SMS: smart model selection in PhyML. Mol Biol Evol 34:2422–2424

Leigh JW, Bryant D (2015) POPART: full-feature software for haplotype network construction. Methods Ecol Evol 6:1110–1116

Liu J, Ding X, Zeng Y, Yue Y, Guo X, Guo T, Chu M, Wang F, Han J, Feng R, Sun X, Niu C, Yang B, Guo J, Yuan C (2016) Genetic diversity and phylogenetic evolution of Tibetan sheep based on mtDNA D-Loop sequences. PLoS ONE 11:e0159308

Loso JB, Ricklefs RE (2009) Adaptation and diversification on islands. Nature 457:830–836

Lv FH, Peng WF, Yang J, Zhao YX, Li WR, Liu MJ, Ma YH, Zhao QJ, Yang GL, Wang F, Li JQ, Liu YG, Shen ZQ, Zhao SG, Hehua EE, Gorkhali NA, Vahidi SMF, Muladno M, Naqvi AN, Tabell J, Iso-Touru T, Bruford MW, Kantanen J, Han JL, Li MH (2015)

Mitogenomic meta-analysis identifies two phases of migration in the history of eastern Eurasian sheep. Mol Biol Evol 32:2515–2533

Marchand P, Garel M, Bourgoin G, Dubray D, Maillard D, Loison A (2015) Coupling scale-specific habitat selection and activity reveals sex-specific food/cover trade-offs in a large herbivore. Anim Behav 102:169–187

Marchand P, Garel M, Bourgoin G, Duparc A, Dubray D, Maillard D, Loison A (2017) Combining familiarity and landscape features helps break down the barriers between movements and home ranges in a non-territorial large herbivore. J Anim Ecol 86:371–383

Maudet C, Dubray D (2002) Comparison of the genetic structures of two Corsican mouflon (*Ovis gmelini musimon*) populations (Cinto/Asco and Bavella). In: Poster. IV International Mouflon Symposium

Meadows JRS, Hiendleder S, Kijas JW (2011) Haplogroup relationships between domestic and wild sheep resolved using a mitogenome panel. Heredity 106:700–706

Mereu P, Pirastru M, Barbato M, Satta V, Hadjisterkotis E, Manca L, Naitana S, Leoni GG (2019) Identification of an ancestral haplotype in the mitochondrial phylogeny of the ovine haplogroup B. PeerJ 7:e7895

Milberg P, Tyrberg T (1993) Naïve birds and noble savages—a review of man caused prehistoric extinctions of island birds. Ecography 16:229–250

Mills LS (2013) Conservation of wildlife populations, 2nd edn. Wiley, Hoboken

Miquel C, Bellemain E, Poillot C, Bessière J, Durand A, Taberlet P (2006) Quality indexes to assess the reliability of genotypes in studies using noninvasive sampling and multiple-tube approach. Mol Ecol Notes 6:985–988

Morellet N, Gaillard JM, Hewison AJM, Ballon P, Boscardin Y, Duncan P, Klein F, Maillard D (2007) Indicators of ecological change: new tools for managing populations of large herbivores. J Appl Ecol 44:634–643

Moritz C (1994) Defining 'evolutionary significant units' for conservation. Trends Ecol Evol 9:373–375

Myers N, Mittermeier R, Mittermeier C, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nei M (1973) Analysis of gene diversity in subdivided populations. Proc Natl Acad Sci USA 70:3321–3323

Niu L, Chen X, Xiao P, Zhao Q, Zhou J, Hu J, Sun H, Guo J, Li L, Wang L, Zhang H, Zhong T (2016) Detecting signatures of selection within the Tibetan sheep mitochondrial genome. Mitochondrial DNA Part A 28:801–809

Ozüt D (2001) Conservation genetics of Anatolian mouflon (*Ovis gmelinii anatolica*). MSc dissertation, Middle East Technical University

Paeth H, Hense A (2005) Mean versus extreme climate in the Mediterranean region and its sensitivity to future global warming conditions. Meteorol Z 14:329–347

Palsbøl PJ, Bérubé M, Allendorf FW (2007) Identification of management units using population genetic data. Trends Ecol Evol 22:11–16

Peakall R, Smouse PE (2006) GenAlEx 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288–295

Peakall R, Smouse PE (2012) GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research-an update. Bioinformatics 28:2537–2539

Pedrosa S, Uzun M, Arranz JJ, Gutierrez-Gil B, San Rimitivo F, Bayon Y (2005) Evidence of three maternal lineages in near eastern sheep supporting multiple domestication events. Proc R Soc B 272:2211–2217

Pfeffer P (1967) Le mouflon de Corse (*Ovis ammon musimon* Schreber, 1782): position systématique, écologie et éthologie comparées. Mammalia 31(Suppl):1–262

Poplin F (1979) Origine du mouflon de Corse dans une nouvelle perspective paléontologique, par marronnage. Ann Genet Sel Anim 11:133–143

Portanier E (2018) Parasitisme et structuration génétique et spatiale: exemple chez le mouflon méditerranéen, *Ovis gmelini musimon* × *Ovis* sp. Doctoral thesis, Université de Montpellier

Portanier E, Garel M, Devillard S, Marchand P, Andru J, Maillard D, Bourgoin G (2017) Introduction history overrides social factors in explaining genetic structure of females in Mediterranean mouflon. Ecol Evol 7:9580–9591

Portanier E, Larroque J, Garel M, Marchand P, Maillard D, Bourgoin G, Devillard S (2018) Landscape genetics matches with behavioural ecology and brings new insight on the functional connectivity in Mediterranean mouflon. Landsc Ecol 33:1069–1085

Portanier E, Garel M, Devillard S, Maillard D, Poissant J, Galan M, Benabed S, Poirel MT, Duhayer J, Itty C, Bourgoin G (2019) Both candidate gene and neutral genetic diversity correlate with parasite resistance in female Mediterranean mouflon. BMC Ecol 19:1–14

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

R Development Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. Syst Biol 67:901–904

Rezaei HR, Naderi S, Chintauan-Marquier IC, Taberlet P, Virk AT, Naghash HR, Rioux D, Kaboli M, Pompanon F (2010) Evolution and taxonomy of the wild species of the genus *Ovis* (Mammalia, Artiodactyla, Bovidae). Mol Phylogenet Evol 54:315–326

Rezaei H (2007) Phylogénie moléculaire du genre *Ovis* (Mouton et Mouflons)—Implications pour la conservation du genre et pour l'origine de l'espèce domestique. Doctoral thesis, Université Joseph Fourier Grenoble 1

Ricketts TH, Dinerstein E, Boucher T, Brooks TM, Butchart SHM, Hoffmann M, Lamoreux JF, Morrison J, Parr M, Pilgrim JD, Rodrigues ASL, Sechrest W, Wallace GE, Berlin K, Bielby J, Burgess ND, Church DR, Cox N, Knox D, Loucks C, Luck GW, Master LL, Moore R, Naidoo R, Ridgely R, Schatz GE, Shire G, Strand H, Wettengel W, Wikramanayake E (2005) Pinpointing and preventing imminent extinctions. PNAS 102:18497–18501

Rieu L (2007) LIFE NATURE Conservation et extension des populations de mouflons corses en Corse. Projet LIFE03NAT/F/000099 (2003–2007). Rapport technique, Parc Naturel Régional de Corse

Rosenberg NA (2004) DISTRUCT: a program for the graphical display of population structure. Mol Ecol Notes 4:137–138

Rozas J, Ferrer-Mata A, Sanchez-DelBarrio JC, Guirao-Rico S, Librado P, Ramos-Onsins SE, Sanchez-Gracia A (2017) DnaSP v6:DNA sequence polymorphism analysis of large datasets. Mol Biol Evol 34:3299–3302

Ryder OA (1986) Species conservation and systematics: the dilemma of subspecies. Trends Ecol Evol 1:9–10

Safner T, Miller MP, McRae BH, Fortin MJ, Manel S (2011) Comparison of bayesian clustering and edge detection methods for inferring boundaries in landscape genetics. Int J Mol Sci 12:865–889

Sanchis F (2018) Etude de l'utilisation et de la sélection de l'habitat chez le mouflon de Corse à différentes échelles spatiales et temporelles. Ecole Pratique des Hautes Etudes, Montpellier

Sanna D, Barbato M, Hadjisterkotis E, Cossu P, Decandia L, Trova S, Pirastru M, Leoni GG, Naitana S, Francalacci P, Masala B, Manca L, Mereu P (2015) The first mitogenome of the Cyprus mouflon (*Ovis gmelini ophion*): new insights into the phylogeny of the genus *Ovis*. PLoS ONE 10:e0144257

Satta V, Lereu P, Doro M, Casula S, Casu G, Bassu G, Frongia G, Berlinguer F, Masala B, Manca L, Naitana S, Leoni GG (2016) Habitat fragmentation causes genetic differentiation of Sardinian mouflon. In: 6th World Congress on Mountain Ungulates and the 5th International Symposium on Mouflon. Book of Abstracts, 3rd edn, Nicosia, pp 72–73

Simonpoli P (1995) Le mouflon dans le massif de Bavella. In: Simonpoli P (ed) La chasse en Corse. PNRC, Ajaccio, pp 153–175

Stone GN, White SC, Csoka G, Melika G, Mutun S, Pénzes Z, Sadeghi SE, Schönrogge K, Majid T, Nicholls JA (2017) Tournament ABC analysis of the western Palaearctic population history of an oak gall wasp, *Synergus umbraculus*. Mol Ecol 26:6685–6703

Taylor BL, Dizon AE (2005) First policy then science: why a management unit based solely on genetic criteria cannot work. Mol Ecol 8:S11–S16

Taylor HR, Colbourne RG, Robertson HA, Nelson NJ, Allendorf FW, Ramstad KAM (2017) Cryptic inbreeding depression in a growing population of a long-lived species. Mol Ecol 26:799–813

Tofanelli S, Taglioli L, Varesi L, Paoli G (2001) Genetic history of the population of Corsica (Western Mediterranean) as inferred from autosomal STR analysis. Hum Biol 76:229–251

Uloth W (1972) To the history of the distribution, introduction and cross-breeding of the Tyrrhenis mouflon in Europe and oversea. Acta Theriol 17:412–413

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4:535–538

Vigne JD (1988) Paléontologie, archéologie et mammalogie. XIème Colloque Francophone de Mammalogie, Maison-Alfort

Vigne JD (1992) Zooarchaeology and the biogeographical history of the mammals of Corsica and Sardinia since the last ice age. Mammal Rev 22:87–96

Vona G, Moral P, Memmi M, Ghiani ME, Varesi L (2003) Genetic structure and affinities of the Corsican population (France): classical genetic markers analysis. Am J Hum Biol 15:151–163

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370

Weller KE (2001) The status of mouflon (*Ovis musimon*) in Europe. In: Náhlik A, Uloth W (eds) Proceedings of the Third International Symposium on Mouflon, Sopron, 27–29 October 2000

Whittaker RJ, Fernández-Palacios JM (2007) Island biogeography, 2nd edn. Oxford University Press, Oxford

Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton

Wilson DE, Reeder DM (2005) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore

Wright S (1931) Evolution in Mendelian populations. Genetics 16:97–159

Zeder MA (2008) Domestication and early agriculture in the Mediterranean Basin: origins, diffusion, and impact. Proc Natl Acad Sci USA 105:11597–11604

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