An ancient genetic line of European rabbit (*Oryctolagus cuniculus*) from the penitentiary islands of Capraia and Gorgona (Tuscan archipelago, Italy)

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Abstract:
The European rabbit *Oryctolagus cuniculus* comprises *O. c. algirus*, endemic to southwestern Iberia, and *O. c. cuniculus*, which inhabits northeastern Iberia and southwestern France, and it is considered as the source of all introduced populations worldwide. Rabbit populations have long been established for hunting purposes and/or subjected to supplementation with individuals from intensely marketed stocks, with Italy being not an exception. We genotyped 42 fecal samples and 23 specimens (1877-2022) resident in museum collections at the mitochondrial DNA Cytochrome-b gene to infer to which subspecies belong the rabbits from the islands of Gorgona, Capraia, Montecristo, Giglio, and Giannutri (Tuscan archipelago). The Wildlife Refuge Padule di Bolgheri was selected as nearby mainland counterpart, and its population (n = 10) investigated along with 45 GenBank sequences of individuals (also domestic) from different continents. All modern and ancient Tuscan specimens were assigned to *O. c. cuniculus*, an unexpected result for Capraia and Montecristo that were assumed to host *O. c. algirus* on the base of the available literature. The network and the Bayesian clustering defined three groups. Modern rabbits from northern Capraia and most of those from Gorgona, which hosted (1873-1986) or still host (since 1869) an agricultural penal colony, respectively, belonged to a line disclosed in all ancient specimens from Capraia and that was new for the subspecies. The remaining rabbits from Capraia and Gorgona and all those from Montecristo and Giglio were related to European conspecifics while those from Giannutri were close to all the domestic individuals, with Bolgheri representing a mix of these two groups. Overall, the restrictions due to the presence of the penitentiaries likely prevented Capraia and Gorgona from an extended genetic homogenization associated to restocking practices. More broadly, we provided further evidence that the human-mediated rabbit colonization across the Mediterranean was based on *O. c. cuniculus* only.

Keywords: mitochondrial DNA, non-invasive sampling, islands, museum collections, archival samples, agricultural penal colony.

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Introduction

The European rabbit *Oryctolagus cuniculus* (Linnaeus, 1758) comprises two subspecies, namely *O. c. cuniculus* (Linnaeus, 1758), which is distributed across northeastern Iberia and southwestern France and it is considered as the source of either wild or domesticated populations introduced worldwide, and *O. c. algirus* (Loche, 1848), which occurs in southwestern Spain and Portugal (with the Canaries, Azores and Madeira: Fonseca, 2006). The two subspecies are characterized by highly differing (4.5% of nucleotide divergence) mitochondrial DNA (mtDNA) lineages that are referred to as ‘A’ and ‘B’ for *O. c. algirus* and *O. c. cuniculus*, respectively, a separation confirmed also by several studies based on nuclear DNA markers (see Fontanesi et al., 2021 for a comprehensive literature framework).

The European rabbit is included among the 100 world’s worst invasive alien species as it can damage the vegetation cover and speed up the erosion of the soil (Global Invasive Species Database, 2024). On the other hand, in the Iberian Peninsula and southwestern France - the species’ native range possibly with northwestern Africa (e.g., Gibb, 1990) - the rabbit is not only listed ‘Endangered’ by the International Union for Conservation of Nature and Natural Resources (Villafuerte and Delibes-Mateos, 2019) but it also plays a key role for the survival of threatened taxa such as the Spanish imperial eagle (*Aquila adalberti*) and the Iberian lynx (*Lynx pardinus*) (Delibes-Mateos et al., 2007). The same is true also in some parts of the rabbit’s introduced range such as, for instance, Sicily, where the species is the prey of choice of the Bonelli’s eagle (*A. fasciata*) (Di Vittorio et al., 2019). Therefore, *O. cuniculus* represents a so-called ‘conservation paradox’ (Lees and Bell, 2008).

The earliest record for the introduction of rabbits into western Europe dates around to the XV-XIV century BC, when they were carried out from mainland Spain to Minorca (Masseti, 2005). Then, the Phoenicians and later the Romans likely allowed the spread of the species across the Mediterranean (Bodson, 1978); for instance, the Greek historians Polybius - but see Fontanesi et al. (2021) - and Strabo reported its occurrence in Corsica and the Balearics in 204 and 63 BC, respectively (Flux and Fullagar, 1992). In Italy, the first record for *O. cuniculus* deals with the islet of Nisida (Naples) in 230 BC while the earliest evidence for the main islands are the rabbits’ remains of Brucato (Sicily, 1200-1300 AC: Bresc, 1980); hence, in this country, the species is considered as parautochthonous as it became established before 1500 AC (List of alien species excluded from the provisions of the article 2, paragraph 2-bis, of law n. 157/1992).

In northwestern Italy, between the mainland and Corsica, seven main islands are included in the Tuscan Archipelago National Park (Fig. 1). The largest one, Elba, likely hosted wild rabbits since ancient times although their presence was documented by the mid-1600s (Thiebaud de Bernaud, 1808) and especially during the XIX and XX centuries (Damiani, 1923; Repetti, 1839). Likewise, *O. cuniculus* was abundant during the 1800s on the nearby island of Pianosa (e.g., Repetti, 1835), where it became extinct by the mid-1900s as it occurred on Elba (Masseti, 2003).

In the northern part of the archipelago, both Gorgona and Capraia still host a wild rabbit population. On the first island, the species was recorded by the late 1700s (Barbanera, 2021) and reached a high density in the XIX and XX centuries (Bertarelli, 1923; D'Albertis, 1877; Zuccagni-Orlandini, 1842). On the second island, the Romans imported *O. c. huxleyi* (Haeckel, 1874) rabbits from Corsica (Saint Girons, 1973); however, this subspecies is no longer valid and reported as synonymous to *O. c. algirus* (Lo Valvo et al., 2014; Callou, 2000). Rabbits were recorded on Capraia by the early 1600s (Moresco, 2013; Maioli, 1942), in 1770 (Moresco, 2008), and they were still numerous in the following centuries (e.g., De Siervo, 1940; Miller, 1912; Pasquin, 1842). Noteworthy, Gorgona and Capraia are united by hosting (since 1869) or having hosted (1873-1986), respectively, an important penitentiary. On Gorgona, it is still operational across the whole island - the last example of this type in Italy - with around 80 inmates engaged in various working activities. On the other hand, in the northeastern corner of Capraia, an agricultural penal colony was active over about 5 km^2 of territory for several decades before it was converted into a maximum-security penitentiary by the late 1970s and then dismissed after a few years. Today an abandoned place, the inmates of Capraia were involved in fishing, farming, horticulture, the production of olives and wine (De Siervo, 1940).

The southernmost islands of Giannutri and Giglio still host the European rabbit whereas this species became extinct on Montecristo very recently. On Giannutri, rabbits have been always abundant and recorded since 1760 (Masseti, 2003; Bertarelli, 1923; Tanfani, 1890; Garelli, 1870), while the population of Giglio was of relatively recent origin (mid-1930s: Masseti, 2003; Flux and Fullagar, 1992) and underwent numerical control practices (LIFE18 NAT/IT/000828 'LetsGoGiglio' Life Project). On Montecristo, wild rabbits were present since ancient times and they were referred to as belonging to the *O. c. huxleyi* subspecies along with those from Capraia (Angelici et al., 2009; Scalera, 2001; Flux and Fullagar, 1992; Pavan, 1989; Toschi, 1965). Recorded by the XIV century (Caruel, 1864), rabbits were common until the mid-1900s (Toschi, 1953) and even later (170 specimens reported by Spagnesi et al., 1986). Regrettably, a massive aerial delivery of toxic baits to eradicate black rats (*Rattus rattus*) - as part of the LIFE08 NAT/IT/000353 'Montecristo2010' Life Project - led to the extinction of the local rabbit population (Sposimo et al., 2019).

The European rabbit, a renowned game species, has always been experiencing an intensive management through introductions and/or supplementation, and peninsular Italy - with both its minor and major islands - was not an exception as many populations have originated for hunting purposes only recently. Therefore, performing genetic analyses is the most reliable way to precisely identify the rabbits currently inhabiting the Italian islands. However, only one investigation of this type has been carried out so far (in Sicily: Lo Valvo et al., 2017). In this study, we used a mtDNA marker relying on both modern samples and museum specimens to infer the subspecies to which belong the rabbits from Gorgona, Capraia, Giglio, Giannutri as well as those disappeared on Montecristo a few years ago.

Materials and methods

Samples collected in the wild

While the islands of Gorgona (2.2 km^2), Pianosa (10 km^2), Montecristo (10.4 km^2), and Giannutri (2.6 km^2) are entirely protected within the National Park, hunting is allowed in the 23%, 50%, and 60% of the territory of Capraia (19.3 km^2), Elba (223.5 km^2), and Giglio (21.2 km^2), respectively (Fig. 1). We collected fresh dark brown, fibrous fecal pellets released by wild rabbits on the ground either at random or in large gathering at latrines (Supplementary Table S1). Each sample was individually housed in a plastic vial (no chemicals added) and transported according to a strict cold chain until the final storage (-40°C) at the Department of Biology of the University of Pisa. Only one pellet was investigated for any given latrine. Samples were collected 2021-2023 on the islands of Gorgona (10), Capraia (12), Giglio

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(10), and along a 2.2 km sandy coastline of the Wildlife Refuge Padule di Bolgheri (Bolgheri hereinafter: 10; total, 42), which is a Special Area of Conservation (Habitats Directive 92/43/EEC)/Special Protection Area (Birds Directive 2009/147/CE) along the Tuscan coast (Fig. 1, Table S1). This protected site (5.8 km^2; cf., Guerrini et al., 2022) was selected as mainland counterpart as it hosted a rabbit population at least by 1941 (P.M. Politi, pers. com. to F. Barbanera, 11th September 2024).

Archival samples

At the present time, no rabbits occur on the islands of Elba, Pianosa, and Montecristo. Whereas specimens originally from the first two islands were not available in museums (e.g., London, Genoa, Pisa, Leghorn, Florence, and Naples), we used a few milligrams of dry skin scraped off from bones of three individuals collected 1976-1983 on Montecristo and resident in the collections of the Natural History Civic Museum 'G. Doria' of Genoa, these being the only achievable to the very best of our knowledge. Moreover, 15 specimens from Capraia dated 1877-1931 were sampled at the museum of Genoa and at the Natural History Museum 'La Specola' of Florence. This latter also provided both modern (n = 3, 2003 and 2021) and ancient (n = 1, 1878) skin fragments of rabbits originally from Giannutri. Finally, another sample (2022) from this latter island was provided by P. Agnelli and included in the Pisa collection (Table S1). In this study, all museum samples from Capraia and the one from Giannutri were referred to as ancient (1877-1931), while the remaining ones as modern (1976-2022).

DNA extraction

In each modern DNA extraction, we included only the outer part of a single fecal pellet (*c*. 200 mg) using a sterile disposable razor blade; then, we employed the QIAamp Fast DNA Stool Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions (final elution, 100 µl: Guerrini and Barbanera, 2009) and including two blanks (no fecal pellets) in each working session. As far as the archival samples are concerned, DNA was extracted in a dedicated and physically separated laboratory. We strictly adhered to ancient DNA protocols throughout all steps, including physically isolated pre-PCR and post-PCR working areas. UV light and 10% bleach were used to sterilize the surfaces of benches and

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laboratory devices. The reliability of each DNA extraction was monitored through two blank controls. Two milligrams of skin - often removed from bones (Table S1) employing a sterile disposable razor blade - were used as starting material. DNA was isolated using the QIAamp DNA Micro Kit (Qiagen) following the manufacturer's instructions (final elution, 100 µl) with some modifications as in Barbanera et al. (2016).

Amplification, sequencing, alignment, and data analysis

We attempted at amplifying a 416 bp-long fragment of the Cytochrome-*b* gene (Cyt-*b*) in 42 wild-collected (Gorgona, Giglio, and Bolgheri: 10 each; Capraia, 12) and 23 archival (Capraia, 15; Montecristo, 3; Giannutri, 5) samples. This region was comprised between positions n. 14,727 and n. 15,142 of the mtDNA genome published by Gissi et al. (1998) (GenBank accession code: NC001913). Modern PCRs were performed as in Guerrini et al. (2015) with the following modifications: 1 µl of 75 µM Bovine Serum Albumin (Merck, Darmstadt, Germany) added to each reaction tube and annealing lasting for 2 min. When no band could be visualized after gel electrophoresis, the product was purified using the Genelute PCR Clean-up Kit (Merck) and 1 µl from the final elution (40 µl) was re-amplified by means of a semi-nested PCR (Guerrini and Barbanera, 2009). In the latter, for each sample two overlapping fragments (length: 1st, 278 bp; 2nd, 262 bp) were targeted in two reaction tubes applying the same thermal profile as that used in the first PCR. As far as all archival PCRs are concerned, we directly amplified the two above-reported fragments in distinct tubes using 5 µl of genomic DNA and preparing reactions as in Barbanera et al. (2016). All modern and archival PCRs were carried out using two blanks for each session. All the primers used for the amplification and the sequencing were specifically designed for this study (Table S2).

Final PCR products were purified using the Genelute PCR Clean-up Kit as above and sequenced in both directions on an ABI 3730 DNA automated sequencer at BioFab (Rome, Italy). We cut our sequences at the 5′ end (final length: 306 nucleotides, from position n. 14,727 to position n. 14,836 of Gissi et al., 1998) to incorporate in the alignment the highest number of *O. cuniculus* GenBank entries as possible (n = 45: Italy, 8; France, 13; Spain, 15; Sweden 1; China, 4; Indonesia, 1; New Zealand, 3) including eight domestic variants (Table S3). Overall, the selected fragment still warranted a significant discriminatory power, with 22 mutational changes recorded between *O. c. cuniculus* and *O. c. algirus* comparing AJ243197 (lineage B: Hardy et al., 1995) and AJ243096 (lineage A: Branco et al., 2000) GenBank entries. The alignment was carried out using CLUSTALX (v. 2.1: Thompson et al., 1997) and inspected with BIOEDIT (v. 7.0.5.3: Hall, 1999). Since all of the Tuscan samples were assigned to *O. c. cuniculus* (see Results), the *O. c. algirus* sequences (n = 10: Spain, 9; France, 1) were discarded and downstream analyses performed with the resulting subset (35 *O. c. cuniculus* GenBank entries: Setiaji et al., 2023; Wang et al., 2021; Mohammadi et al., 2020; Yao et al., 2019; Lo Valvo et al., 2017; Pierpaoli et al., 1999; Hardy et al., 1995; Irwin and Árnason, 1994; Monnerot et al., 1994) (Table S3). Haplotypes (H) were inferred using DNASP (v. 6: Rozas et al., 2017). Summary statistics of diversity (number of haplotypes, N; number of polymorphic sites, S; haplotype diversity, *h*; average number of pairwise differences, *k*; nucleotide diversity, π) were calculated with ARLEQUIN (v. 3.5: Excoffier and Lischer, 2010) only for the Tuscan populations (sample size ≥ 10). We built a network using the Median Joining method of Bandelt et al. (1999) as implemented in NETWORK (v. 10.2.0.0, Fluxus Technology). Moreover, a Bayesian analysis of the structure of the investigated populations was carried out with BAPS (v. 6.0: Cheng et al., 2013) by clustering genetically similar individuals into panmictic groups. We used the module for linked molecular data, and we applied the codon linkage model, which is appropriate for sequencing data.

Results

All wild-collected samples (42) and most (20 out of 23) of the archival ones were successfully amplified, sequenced, and assigned to the *O. c. cuniculus* subspecies only (mtDNA lineage B). The alignment (42 + 20 + 35 = 97 sequences) comprised 40 polymorphic sites. We inferred 21 haplotypes, with 10 from the modern and archival Tuscan rabbits of this study (Table S1, including the GenBank accession codes). All individuals from Giglio shared the same haplotype (H8) with a few individuals from Gorgona and France, whereas the population of Capraia held the highest values of diversity; nonetheless, the highest number of haplotypes was retrieved from the archival specimens of Capraia (Table 1).

The Median Joining Network returned three distinct haplogroups. The first (I, Fig. 2) included rabbits from Spain, France, Italy (Sicily), Sweden as well as all those from the island of Giglio, the southern part of Capraia (cf., Fig. 4) and Montecristo, plus a minor part of the representatives from Gorgona and Bolgheri. The second (II, Fig. 2) included the remaining rabbits from Bolgheri and Italy, all the domestic breeds (Table S3), and the single Indonesian representative. The only ancient (dated 1878) and all modern individuals sampled in Giannutri stemmed from H1 - with a few rabbits mostly from France - thus linking the second to the third haplogroup (III, Fig. 2: H17-H20). This latter included all ancient rabbits from Capraia and all the modern ones originally from the northern part of this island (Fig. 4), plus the 80% of the samples from Gorgona.

The Bayesian clustering method defined genetically distinct X, Y, and Z clusters (p = 0.99, optimal partition, log likelihood = - 276.79: Fig. 3, Table S4) perfectly overlapping with haplogroups I, II, and III, respectively; in particular, BAPS assigned all the investigated samples from Giannutri to cluster Y (cf., II, Fig. 2).

Discussion

Taxonomical identity and pattern of diversity

All modern (Gorgona, Capraia, Montecristo, Giglio, Giannutri, and Bolgheri) and ancient (Capraia, Giannutri) Tuscan rabbits investigated in this study turned out to belong to *O. c. cuniculus*. Therefore, although several literature records (see Introduction) reported that especially Capraia and Montecristo should have hosted populations of *O. c. algirus*, we did not find any molecular evidence for the occurrence of this taxon. On the one hand, it is worth noting that the same result was obtained by Lo Valvo et al. (2017) in Sicily (minor islands included), and that even the whole rabbit population resident in Corsica - a stronghold in the human-mediated spreading of the species across the Mediterranean - is the result of recent *O. c. cuniculus* importations (Marchandeau et al., 2003). More broadly, our result agrees with Fontanesi et al. (2021), who reported that the colonization across the Mediterranean - opposed to that involving the Atlantic archipelagos of the Canaries, Azores, and Madeira (Fonseca, 2006) - was likely based on *O. c. cuniculus* only, as it was suggested by the discovery of the mtDNA B lineage alone in ancient and modern rabbits from the islands of Zembra (Tunisia, *c*. 130-390 AC: Hardy et al., 1994) and Mallorca (Seixas et al., 2014), respectively. On the other hand, the extinction of the local population (Sposimo et al., 2019) made the sample size available for Montecristo so small to considerably hinder any potential discovery of *O. c. algirus* representatives.

We inferred the occurrence of three *O. c. cuniculus* haplogroups (Fig. 2). All the rabbits from Giglio and Montecristo, part of those from Gorgona, Capraia (only the modern ones from the northern side of the island), and Bolgheri were included in the haplogroup I with European conspecifics (Italy included: Sicily). The remaining rabbits from Bolgheri and Italy clustered into haplogroup II with all the representatives of domestic breeds from France, Asia and Oceania plus an Indonesian individual, a complex picture clearly pointing to the import of marketable stocks. Finally, haplogroup III included all ancient rabbits from Capraia and the modern ones from the northern part of this island (Fig. 4) plus the majority of those from Gorgona, thus indicating the persistence of an ancient *O. c. cuniculus* line that existed at least between 1877 and 1931. This result was fully returned also by the Bayesian analysis (Fig. 3, Table S4) that assigned all ancient specimens from Capraia and most of the modern ones from Capraia and Gorgona (III, Fig. 2) to a genetic cluster (Z, Fig. 3) different with respect to those including all the individuals investigated so far either in Italy (13, Sicily, Lo Valvo et al., 2017; 1, unknown origin, Pierpaoli et al., 1999) or in Giannutri and across Europe/other continents (X and Y, Fig. 3). Based on the literature (see Introduction), we expected that the rabbits from the extinct population of Montecristo were incorporated into both haplogroup III (Fig. 2) and cluster Z (Fig. 3). On the contrary, all the specimens from this island turned out to belong to haplogroup I and were assigned to cluster X. In this respect, it is worth recalling here that Montecristo has long been a private hunting reserve - e.g., for the royal family of Savoy since 1899 and most recently between 1955 and 1970 - and thus subjected to the introduction of many allochthonous taxa over the centuries (e.g., Pavan, 1989). Likewise, on Giannutri, where the local rabbits were heavily hunted as well (Ghigi, 1911), the local population could have been intensely supplemented by the late 1800; not surprisingly, this was the only island of the archipelago with individuals genetically related to domestic rabbit breeds. To sum up, while we paved the way to the knowledge of the genetic identity of the rabbits from the Tuscan archipelago, the investigation of further specimens from Montecristo (where available) would be required to get a more complete picture. More broadly, we are aware that the relatively small number of GenBank sequences from Iberia, where most of the genetic diversification of the European rabbit has occurred, and the unavailability of others, for instance, from the United Kingdom, may represent a potential inherent limitation of the study design.

The estimators of genetic variability returned the highest values for Capraia and null for Giglio, with the population of Bolgheri being much closer to the former than to the second island (Table S1). Whereas the pattern of diversity disclosed in the penitentiary islands of Capraia (1873-1986) and Gorgona (1869-) deserves a careful discussion through the time (see next paragraph), the haplotype composition of Bolgheri reflected a history of releases for hunting purposes carried out in a private estate before the Wildlife Refuge was established by the will of the Marquis Mario Incisa della Rocchetta in 1959. On the other hand, the lack of diversity disclosed on Giglio pointed to the release of a low number of founders in the mid-1930s (Masseti, 2003; Flux and Fullagar, 1992) and/or to the effects of the practices for the numerical control of the local population carried out since 2018 (cf., Introduction).

The penal colonies of Capraia and Gorgona: a retrospective look at the local rabbits

The history of the connections between the local people and the rabbit populations living on Capraia and Gorgona deserves attention. The residents of Capraia struggled powerfully to protect their crops from the rabbits since the very early 1600s, as the extension of cultivable land was quite limited on such a mountainous and rocky island (Moresco, 2013). The same was true also for Gorgona where, however, rabbits were intentionally introduced only much later to supply the canteens of the Grand Duke Pietro Leopoldo in Florence (*Archivio di Stato di Livorno, Governo civile e militare di Livorno, inv. n. 31, Lettera del 27 novembre 1785*). When the penitentiary of Capraia was opened in 1873, after the creation of wide-ranging dry-stone walls and the development of a notable extension of overlapping terraces, the prisoners have made the cultivation of the land not only possible but also productive in almost one third of the island, the entire northeastern portion (De Siervo, 1940). Therefore, in the early 1900s the abundance of rabbits could be hardly tolerated. However, according to a local hunting society the agricultural yield of the penal colony was not negatively impacted by the rabbits, which were referred to as in demographic decline. Hence, the hunters suggested that captive-bred individuals were released into the southern tip of Capraia (Zenobito, Le Saline: Fig. 4) - a land more arid and less suitable for agriculture than that in the northern side - to start restocking the island rabbit population (Brizi, 2005). The Italian government not only rejected this request but also established that the animals could be captured all the yearlong to protect the crops (upon authorization of the mayor only to the landowners and the prisoners: Ministero dell’Agricoltura, 1916). This decision was valid also for Gorgona, where the rabbits - a real scourge for the agriculture since the former century - could be persecuted also using leghold traps. Listed among the harmful species of the province of Leghorn by the 1st of July 1949, the European rabbit was reinstated with a decree of the Ministry of Agriculture and Forestry (*Gazzetta Ufficiale della Repubblica Italiana*, *n. 228*) on 10th September 1962 only in Capraia (not in Gorgona and in the rest of the province). In the following three decades rabbits were released on Capraia in 1967 and on Gorgona around 1974 (Flux and Fullagar, 1992). To the very best of our knowledge no further restocking events were carried out on Capraia (with certainty after 2008: D. Giustini, Ambito Territoriale di Caccia 9-10, Leghorn, pers. com. to F. Barbanera, 2nd July 2024) whereas no additional information was available for Gorgona.

The restrictions on access and exploitation of the territory due to the presence of a penal colony have certainly helped to protect the environment of Capraia and Gorgona over decades. However, the historical documents collected in this study unequivocally indicate that the European rabbit was strongly persecuted on both islands mostly - but not exclusively - by the prisoners. On the one hand, this struggle did not lead to the extinction of the local populations. On the other hand, limitations due to the presence of the penitentiaries prevented Capraia and Gorgona from an extended genetic homogenization (Olden and Rooney, 2006) associated to restocking practices with rabbits from intensely marketed stocks (II, Fig. 2; X and Y, Fig. 3). While a few rabbits were incorporated in the haplogroup I, most of the present-day individuals from these two islands, indeed, belong to the same line of the conspecifics that lived (at least) on Capraia by the late 1800 onwards (III, Fig. 2; Z, Fig. 3) and that was not disclosed in Sicily by Lo Valvo et al. (2017).

The spatial genetic structure of the rabbit population of Capraia represented another interesting finding (Fig. 4). This island, which is about 8 km long and 4 km wide, is crossed North-to-South by a series of long and steep valleys hosting streams at their bottom. Among these, the so-called Vado del Porto is 3 km long and the only perennial of the island. All the modern rabbits included in the haplogroup III/cluster Z (Figs. 2 and 3) were sampled (numbers in yellow, Fig. 4) North of the canyon connecting the only lake of the island - Lo Stagnone, on the western coast - to the harbour on the eastern side. On the other hand, the rabbits sampled in the southern part of Capraia (numbers in red, Fig. 4) were assigned to haplogroup I/cluster X (Figs. 2 and 3), namely those including most of the animals from Bolgheri and all those from Giglio and Montecristo, among others. Rabbits are vagile animals, although a familiar group is used to live within 1 ha (on average, maximum 5-10 ha). They usually displace between their shelter and the feeding areas, the dispersal over a few km being limited to a few young individuals (Trocchi and Riga, 2005). One may argue that the valleys and their streams (e.g., Vado del Porto) may hinder the movement of the rabbits across Capraia, the furthest reaches of the upper part of the village likely representing the most affordable North-South corridor (towards the plain, Il Piano: see Fig. 4). Since historical times, indeed, rabbits could be spotted in the village as they can still today. We hypothesized that the lack of releases for hunting purposes in the North, as opposed to the remaining part of Capraia, and the physical geography of the island have altogether concurred to shape the spatial genetic structure of the local population. Regrettably, the locations of the ancient specimens from Capraia were not available in the archives of the museums of Genoa and Florence, hence, we could not assess if the genetic divergence between northern and southern rabbits had occurred also in the past.

In conclusion, we wish that an approach such as ours, which relied on modern and archival specimens, will inspire new studies including a larger sample size and the use of genomic tools. Especially for Capraia, we recommend the National Park and, where operational in the territory of this island, the local hunting body (Ambito Territoriale di Caccia 9-10, Leghorn) to strictly avoid the release of rabbits imported from abroad to aid the persistence of the *O. cuniculus* genetic line inherited from the past.

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References

Angelici F.M., Laurenti A., Nappi A., 2009. Checklist of the mammals of small Italian islands. Hystrix It. J. Mamm. 20: 3-27.

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

Barbanera F., 2021. On the origins and history of the red-legged partridge (*Alectoris rufa*) from Elba Island (Tuscan Archipelago, Italy). Atti Soc. Toscana Sci. Nat. Mem. Serie B 128: 45-55.

Barbanera F., Moretti B., Guerrini M., Al-Sheikhly O.F., Forcina G., 2016. Investigation of ancient DNA to enhance natural history museum collections: misidentification of smooth-coated otter (*Lutrogale perspicillata*) specimens across multiple museums. Belg. J. Zool. 146: 101-112.

Bertarelli L.V., 1923. Guida d'Italia del Touring Club Italiano. Italia centrale. Volume 3. Tipografia Sociale del Cav. Carlo Sironi, Milano. 1-618 (in Italian).

Bodson L., 1978. Ancient zoogeographical data: expansion of Leporidae in the Mediterranean of classical times. Nat. Belg. 59: 66-81.

Branco M., Ferrand N., Monnerot M., 2000. Phylogeography of the European rabbit (*Oryctolagus *cuniculus*) in the Iberian Peninsula inferred from RFLP analysis of the cytochrome *b* gene. Heredity 85: 307-317.

Bresc H., 1980. La chasse in Sicile (XIIe-XVe siècles). La chasse au moyen âge. Actes du colloque du Centre d'Etudes Médiévales de Nice. Paris, Belles Lettres. 201-217 (in French).

Brizi F., 2005. L'isola ritrovata. Comune di Capraia Isola, Provincia di Genova (1861-1925). Fratelli Frilli Editori, Genova. 1-237 (in Italian).

Callou C., 2000. La diffusion du lapin (*Oryctolagus cuniculus*) en Europe Occidentale: aspects historiques, biogéographiques, évolutifs et anthropologiques. Thèse doctorale 3e cycle, Université Paris I. 1-486 (in French).

Caruel T., 1864. Florula di Montecristo. Tipografia Bernardoni, Milano.1-38 (in Italian).

Cheng L., Connor T.R., Sirén J., Aanensen D.M., Corander J., 2013. Hierarchical and spatially explicit clustering of DNA sequences with BAPS software. Mol. Biol. Evol. 30: 1224-1228.

D'Albertis E.A., 1877. Crociera del Violante: comandato dal capitano armatore Enrico D'Albertis durante l'anno 1876. Tipografia del Regio Istituto dei Sordomuti, Genova, Italia. 1-320 (in Italian).

Damiani G., 1923. La Fauna. In: Foresi S. (Ed.) L'Elba illustrata. Editore Sandro Foresi, Portoferraio, Livorno, Italia. 103-129 (in Italian).

De Siervo V., 1940. Colonia penale agricola di Capraia. Ministero di Grazia e Giustizia, Direzione Generale Istituti di Prevenzione e di Pena. Relazione dell'Ispettore Agricolo. Roma. 1-38 (in Italian).

Di Vittorio M., Lo Valvo M., Di Trapani E., Sanguinetti A., Ciaccio A., Grenci S., Zafarana M., Giacalone G., Patti N., Cacopardi S., Rannisi P., Scuderi A., Luiselli L., La Grua G., Cortone G., Merlino S., Falci A., Spinella G., López-López P., 2019. Long-term changes in the breeding period diet of Bonelli's eagle (*Aquila fasciata*) in Sicily, Italy. Wildlife Res. 46: 409-414.

Excoffier L., Lischer H.E.L., 2010. Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. Mol. Ecol. Resour. 10: 564-567.

Flux J.E.C., Fullagar P.J., 1992. World distribution of the rabbit *Oryctolagus cuniculus* on islands. Mammal Rev. 22: 151-205.

Fonseca A., 2006. Análise da origem e dispersão das populações de elho-bravo (*Oryctolagus cuniculus*) dos arquipélagos dos Açores, Madeira e Canárias através da utilização de marcadores genéticos nucleares e de DNA-mitocondrial. PhD Thesis, University of the Azores (in Portuguese).

Fontanesi L., Utzari V.J., Ribani A., 2021. The Evolution, Domestication, and World Distribution of the European Rabbit (*Oryctolagus cuniculus*). In: Fontanesi L. (Ed.) The Genetics and Genomics of the Rabbit. CABI, Wallingford (UK) and Boston (USA). 1-22.

Garelli V., 1870. Delle colonie di beneficenza e di pena: lettere sull'arcipelago toscano. Editore Moreno, Torino, Italia. 1-120 (in Italian).

Ghigi A., 1911. Ricerche faunistiche e sistematiche sui mammiferi d'Italia che formano oggetto di caccia. Natura 2: 289-320 (in Italian).

Ghigi A., 1964. Il Rifugio Faunistico di Bolgheri. Natura e Montagna, serie II, anno IV, 3: 95-103 (in Italian).

Gibb J.A., 1990. The European Rabbit *Oryctolagus cuniculus*. In: Chapman J.A., Flux J.E.C. (Eds.)

Rabbits, hares and pikas: Status survey and conservation action plan. IUCN, Oxford, UK. 116-120.

Gissi C., Gullberg A., Árnason U., 1998. The Complete Mitochondrial DNA Sequence of the Rabbit, *Oryctolagus cuniculus*. Genomics 50: 161-169.

Global Invasive Species Database, 2024. Available from: http://www.iucngisd.org/gisd/100_worst.php [14th May 2024].

Guerrini M., Barbanera F., 2009. Non-invasive genotyping of the red-legged partridge (*Alectoris rufa*, Phasianidae): semi-nested PCR of mitochondrial DNA from feces. Biochem. Genet. 47: 873-883.

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.

Guerrini M., Politi P.M., Puglisi L., Barbanera F., 2022. Primo dato genetico per il fratino (*Charadrius alexandrinus*) in Italia e confronto su scala continentale. Riv. Ital. Ornit. 92: 21-32 (in Italian).

Hall T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucl. Acids. Symp. Ser. 41: 95-98.

Hardy C., Vigne J.-D., Casañe D., Dennebouy N., Mounolou J.-C., Monnerot M. 1994. Origin of European rabbit (*Oryctolagus cuniculus*) in a Mediterranean island: Zooarchaeology and ancient DNA examination, J. Evol. Biol. 7: 217-226.

Hardy C., Callou C., Vigne J.-D., Casañe D., Dennebouy N., Mounolou J.-C., Monnerot M., 1995. Rabbit mitochondrial DNA diversity from prehistoric to modern times. J. Mol. Evol. 40: 227-237.

Irwin D.M., ÁArnason U.,1994. Cytochrome b gene of marine mammals: phylogeny and evolution. J Mammal. Evol. 2: 37-55.

Lees A.C., Bell D.J., 2008. A conservation paradox for the 21st century: the European wild rabbit *Oryctolagus cuniculus*, an invasive alien and an endangered native species. Mammal Rev. 38: 304-320.

Lo Valvo M., La Scala A., Scalisi M., 2014. Biometric characterisation and taxonomic considerations of European rabbit *Oryctolagus cuniculus* (Linnaeus, 1758) in Sicily (Italy). World Rabbit Sci. 22: 207-214.

Lo Valvo M., Russo R., Mancuso F.P., Palla F., 2017. mtDNA diversity in a rabbit population from Sicily (Italy). Turk. J. Zool. 41: 645-653.

Maioli G., 1942. La descrizione della Corsica di Giovanni Antonio Magini. Archivio Storico di Corsica. XVIII, 1-289 (in Italian).

Marchandeau S., Pascal M., Vigne J.-D., 2003. Le Lapin de garenne: *Oryctolagus cuniculus* (Linné, 1758). In: Pascal M., Lorvelec O., Vigne J.-D., Keith P., Clergeau P. (Eds.) Évolution holocène de la faune de Vertébrés de France: invasions et disparitions. Institut National de la Recherche Agronomique, Centre National de la Recherche Scientifique, Muséum National d’Histoire Naturelle. Rapport au Ministère de l’Écologie et du Développement Durable (Direction de la Nature et des Paysages). Paris, France. 329-332 (in French).

Masseti M., 2003. Fauna toscana. Galliformi non migratori, Lagomorfi e Artiodattili. Arsia, Firenze. 1-311 (in Italian).

Masseti M., 2005. Note paleontologiche, genetiche e archeozoologiche sul coniglio selvatico *Oryctolagus* *cuniculus*. In: Trocchi V., Riga F. (Eds.) I Lagomorfi in Italia. Linee guida per la conservazione e la gestione. Ministero delle Politiche Agricole e Forestali, Istituto Nazionale della Fauna Selvatica, Documenti Tecnici, n. 25. 11-12 (in Italian).

Miller G.S., 1912. Catalogue of the Mammals of Western Europe (Europe exclusive of Russia) in the collection of the British Museum. Trustees of the British Museum, London. 1-1019.

Ministero per l'Agricoltura, 1916. Bollettino dei ministeri per l'agricoltura e per l'industria, il commercio ed il lavoro. Serie A: Parte ufficiale. Anno XV, volume II, fascicolo I. Tipografia L. Cecchini Editore, Roma. 287-307 (in Italian).

Mohammadi Z., Aliabadian M., Ghorbani F., Moghaddam F.Y., Lissovsky A.A, Obst M., Olsson U., 2020. Unidirectional Introgression and Evidence of Hybrid Superiority over Parental Populations in Eastern Iranian Plateau Population of Hares (Mammalia: *Lepus* Linnaeus, 1758). J. Mammal. Evol. 27: 723-743.

Monnerot M., Vigne J.-D., Biju-Duval C., Casañe D., Callou C., Hardy C., Mougel F., Soriguer R., Dennebouy N., Monoulou J.-C., 1994. Rabbit and man: genetic and historical approach. Genet. Sel. Evol. 26: 167-182.

Moresco R., 2008. L'isola di Capraia. Carte e vedute tra cronaca e storia. Secoli XVI-XIX. Debatte Editore, Livorno. 1-208 (in Italian).

Moresco R., 2013. 1608 - I Capraiesi contro ratti e conigli. Available from: https://storiaisoladicapraia.com/2013/04/07/1608-i-capraiesi-contro-ratti-e-conigli/ [8th May 2024].

Olden J.D., Rooney T.P., 2006. On defining and quantifying biotic homogenization. Glob. Ecol.

Biogeogr. 15: 113-120.

Pasquin V., 1842.Viaggi alle isole di Corsica, d'Elba, e di Sardegna del signor Valery. Volume I. Pirotta e C., Milano. 1-301 (in Italian).

Pavan M., 1989. Isola di Montecristo. Riserva naturale. Collana Verde, volume 77. Ministero dell'Agricoltura e delle Foreste. Corpo Forestale dello Stato. Roma. 1-125 (in Italian).

Pierpaoli M., Riga F., Trocchi V., Randi E., 1999. Species distinction and evolutionary relationships of the Italian hare (*Lepus corsicanus*) as described by mitochondrial DNA sequencing. Mol. Ecol. 8: 1805-1817.

Repetti E., 1835. Dizionario geografico fisico storico della Toscana contenente la descrizione di tutti i luoghi del granducato. A. Tofani Editore, Firenze, volume II. 1-955 (in Italian).

Repetti E., 1839. Dizionario geografico fisico storico della Toscana contenente la descrizione di tutti i luoghi del granducato. A. Tofani Editore, Firenze, volume III. 1-710 (in Italian).

Rozas J., Ferrer-Mata A., Sánchez-DelBarrio J.C., Guirao-Rico S., Librado P., Ramos-Onsins S.E., Sánchez-Gracia A., 2017. DnaSP 6: DNA Sequence Polymorphism Analysis of Large Datasets. Mol. Biol. Evol. 34: 3299-3302.

Saint Girons M.-C.,1973. Les Mammifères de France et du Bénélux (faune marine exceptée). Doin, Paris. 1-481 (in French).

Scalera R., 2001. Invasioni biologiche. Le introduzioni di vertebrati in Italia: un problema tra conservazione e globalizzazione. Collana Verde, volume 103. Ministero delle Politiche Agricole e

Forestali. Corpo Forestale dello Stato. Roma. 1-368 (in Italian).

Seixas F.A., Juste J., Campos P.F., Carneiro M., Ferrand N., Alves P.C., Melo-Ferreira J., 2014. Colonization history of Mallorca Island by the European rabbit, *Oryctolagus cuniculus*, and the Iberian hare, *Lepus granatensis* (Lagomorpha: Leporidae). Biol. J. Linn. Soc. 111: 748-760.

Setiaji A., Lestari D.A., Pandupuspitasari N.S., Agusetyaningsih I., Khan FA., 2023. Genetic characteristics of complete mtDNA genome sequence of Indonesian local rabbit (*Oryctolagus cuniculus*). J. Genet. Eng. Biotechnol. 21, 96.

Spagnesi M., Cagnolaro L., Perco F., Scala C., 1986. La capra di Montecristo (*Capra aegagrus hircus* Linnaeus, 1758). Ric. Biol. Selv. 76: 1-147 (in Italian).

Sposimo, P., Capizzi D., Cencetti T., De Pietro F., Giannini F., Gotti C., Puppo F., Quilghini G., Raganella Pelliccioni E., Sammuri G., Trocchi V., Vagniluca S., Zanichelli F., Baccetti N., 2019. Rat and lagomorph eradication on two large islands of central Mediterranean: differences in island morphology and consequences on methods, problems and targets. In: Veitch C.R., Clout M.N., Martin A.R., Russell J.C., West C.J. (Eds.) Island invasives: scaling up to meet the challenge. Occasional Paper SSC no. 62. Gland, Switzerland: IUCN. 231-235.

Tanfani E., 1890. Florula di Giannutri. Nuovo Giorn. Bot. Ital. 2: 153-216 (in Italian).

Thiebaut De Berneaud A., 1808. Voyage à l’Isle d’Elbe, suivi d’une notice sur les autres isles de la Mer Tyrrhénienne. D. Colas, Paris (in French).

Thompson J.D., Gibson T.J., Plewniak F., Jeanmougin F., Higgins D.G., 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic

Acids Res. 25: 4876-4882.

Toschi A., 1953. Note sui vertebrati dell'Isola di Montecristo. Ric. Zool. Appl. Caccia 23: 1-52 (in Italian).

Toschi A., 1965. Fauna d'Italia. Mammalia. Lagomorpha, Rodentia, Carnivora, Ungulata, Cetacea. Edizioni Calderini, Bologna (in Italian).

Trocchi V., Riga F. (Eds.), 2005. I Lagomorfi in Italia. Linee guida per la conservazione e la gestione. Min. Politiche Agricole e Forestali - Ist. Naz. Fauna Selvatica, Documenti Tecnici, 25:1-128 (in Italian)

Villafuerte R., Delibes-Mateos M., 2019. *Oryctolagus cuniculus*. The IUCN Red List of Threatened Species 2019: e.T41291A170619657. Available from: https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T41291A170619657.en [29th March 2024].

Wang X., Zeng H.M., Wang Y., Luo Y., Yao X.P., Yang Z., 2021. The complete mitochondrial DNA sequence of Chuanbai Rex rabbit (*Oryctolagus cuniculus*). Mitochondrial DNA B Resour. 6: 129-130.

Yao C.Y., Li Y.Y., Liu L.X., Ma C., Liu Y.G., Liu Y.H., 2019. The complete mitochondrial DNA sequence of Yimeng wool rabbit. Mitochondrial DNA B Resour. 4: 3858-3859.

Zuccagni-Orlandini A., 1842. Corografia fisica, storica e statistica dell'Italia e delle sue isole corredata da un atlante di mappe geografiche e topografiche e di altre tavole illustrative. Volume 12: Isole. 1-844 (in Italian).

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Table 1. Estimates of mtDNA genetic diversity for each population of this study with a sample size ≥ 10. Legend: n, number of samples; S, number of polymorphic sites; N, number of haplotypes; *h*, haplotype diversity; *k*, average number of pairwise differences; π, nucleotide diversity.

	n	S	N	*h* ± S.E.	*k* ± S.E.	*π* ± S.E. (%)
Bolgheri	10	3	2	0.47 ± 0.13	1.40 ± 0.93	0.46 ± 0.34
Ancient Capraia	12	3	4	0.45 ± 0.17	0.50 ± 0.45	0.16 ± 0.16
Capraia	12	6	3	0.59 ± 0.11	2.82 ± 1.60	0.92 ± 0.59
Giglio	10	0	1	-	-	-
Gorgona	10	6	3	0.38 ± 0.18	1.98 ± 1.22	0.65 ± 0.45

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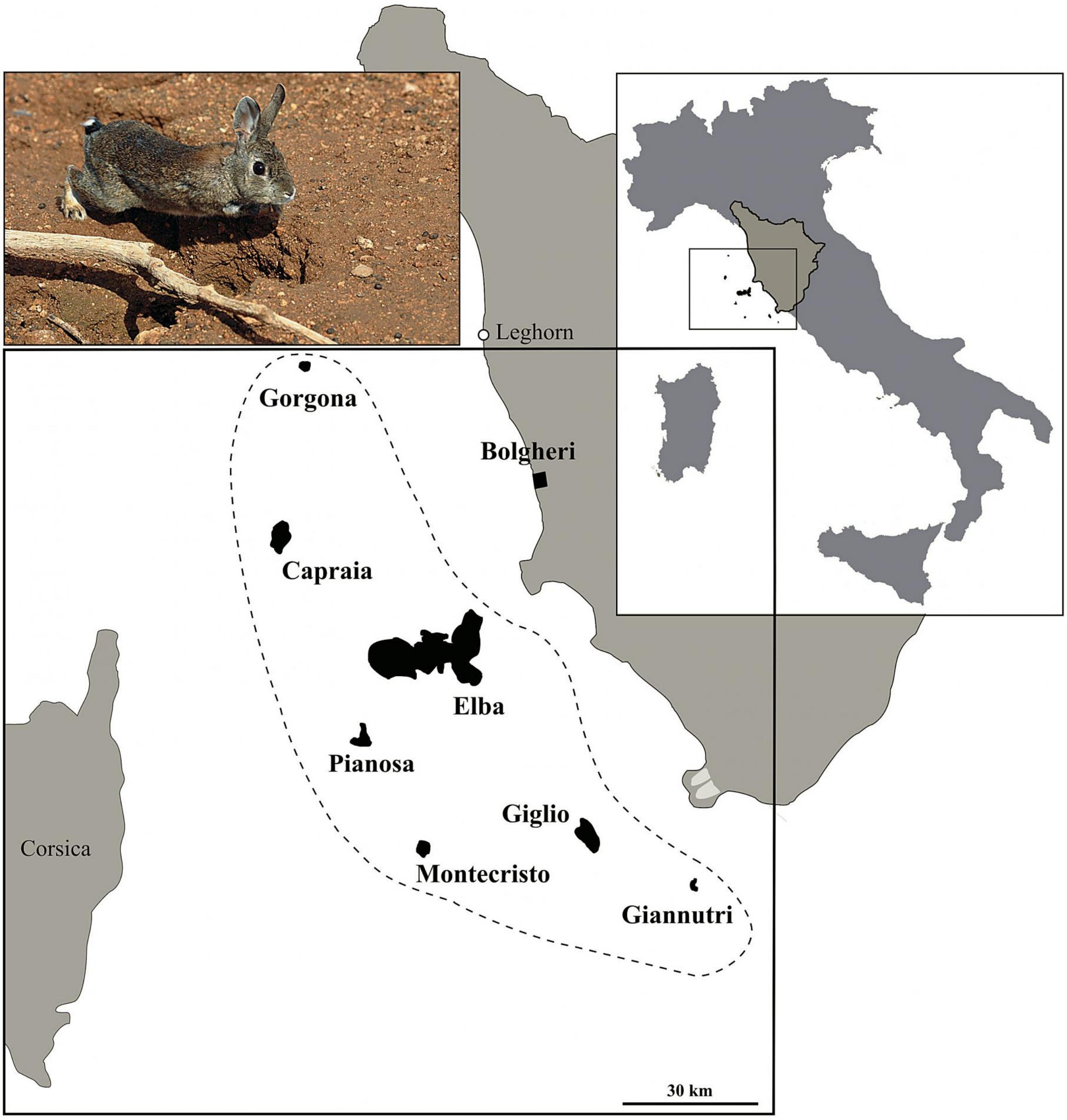

The study area in Tuscany with the seven main islands of the Tuscan Archipelago National Park and the Wildlife Refuge Padule di Bolgheri along the mainland coast. Photo: European wild rabbit, courtesy of J.A. Blanco-Aguiar (University of Castilla-La Mancha, Spain).

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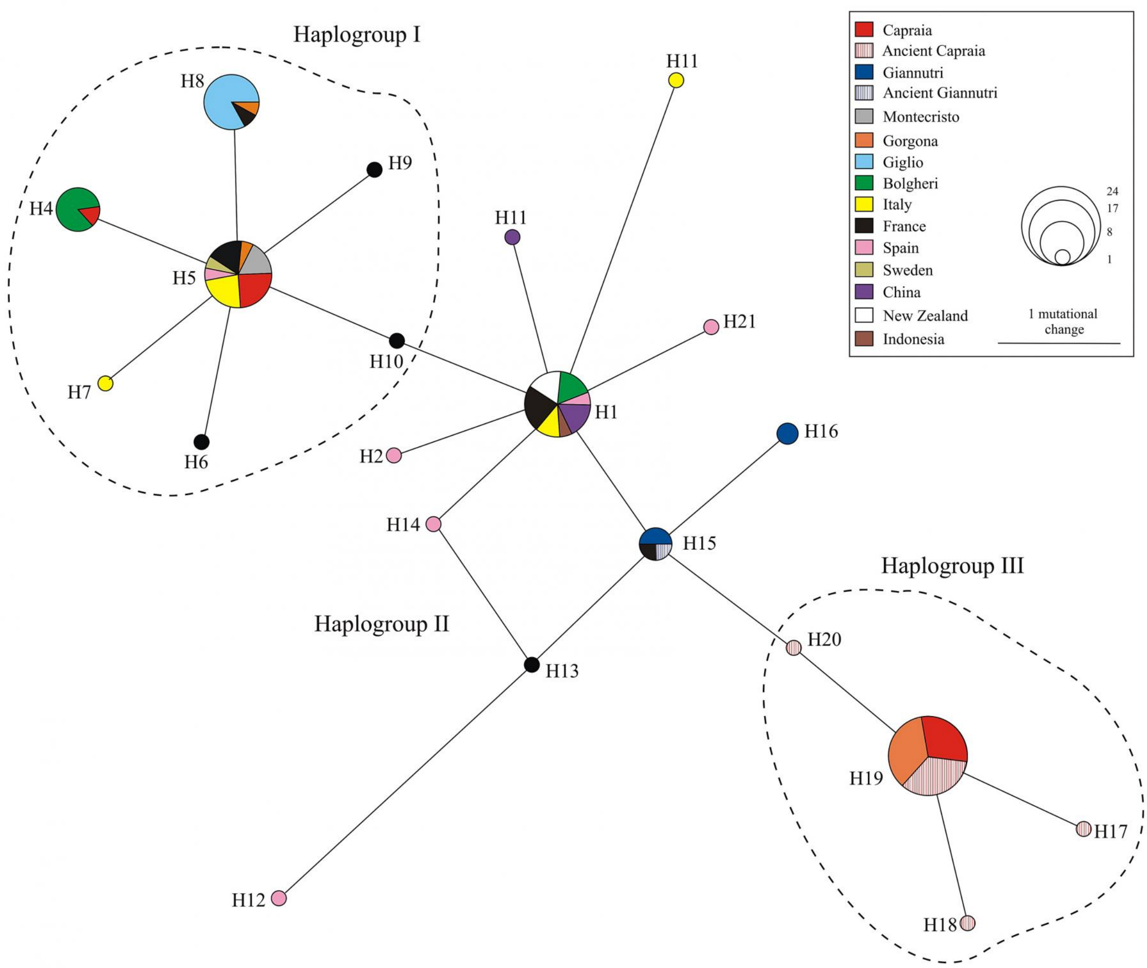

Haplotype network including all the O. c. cuniculus rabbits investigated in this study. A scale to infer the number of haplotypes (H, 1-21) for each pie is provided together with a length bar to compute the number of mutational changes. The colour of each population is indicated as well as the number of the haplotypes within the three haplogroups (I, II, and III) (see Table S1). Note that most of the domestic variants (Fauve de Bourgogne, Yimeng Wool, Chuanbai Rex, Jiuyi Mountain, and New Zealand White) were assigned to H1, with the Fujian Yellow being the only exception (H11) (see Table S3).

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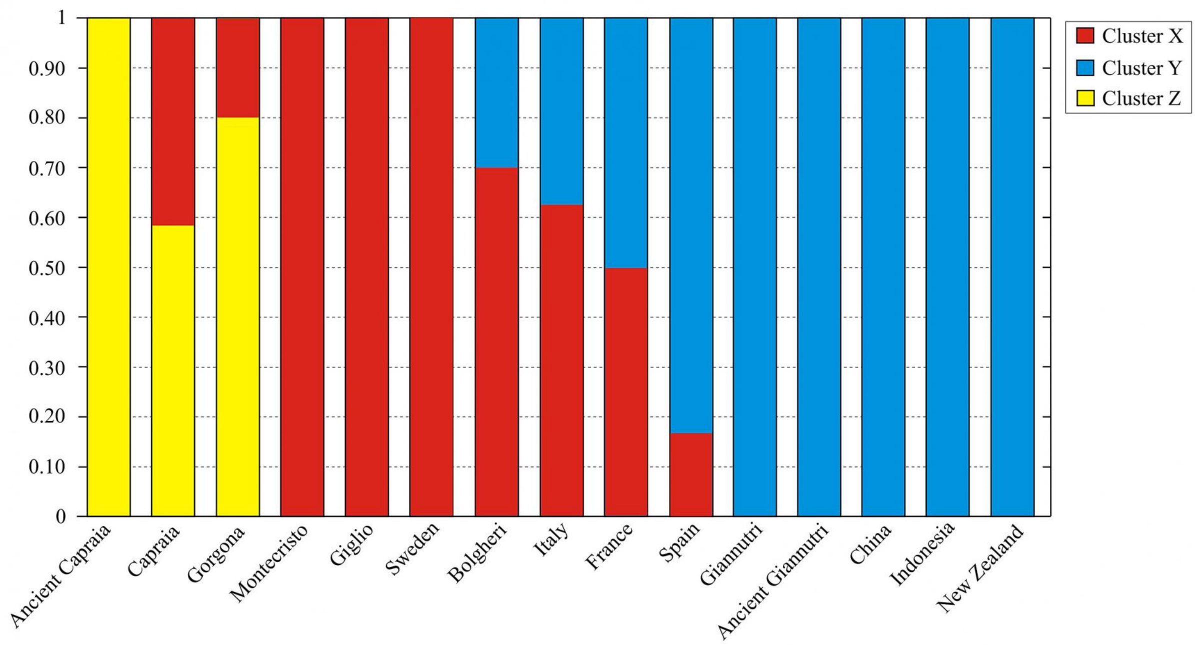

The genetic structure of the rabbit populations investigated in this study (abscissas) as inferred with BAPS is given by means of a histogram where the length of the vertical bars (ordinates) indicates the proportion of individuals with an estimated membership to the clusters X, Y, and Z (cf., Table S3 for the posterior probability values of membership).

Aerial photo of Capraia (M. Steele, www.flickr.com/photos/21022123@N04/27219061013/, CC BY 2.0, 2016). The perimeter (white thick line) of the area corresponding to the agricultural penal colony is indicated in the northern side of the island as well as the position of the only village. On the western side, the positions (white squares) of the three main mountain peaks - with elevation in metres - are reported from North to South as it follows: Mt. Castello, the highest one, Mt. Forcone and Mt. Arpagna. The only lake of Capraia - Lo Stagnone - is indicated by a blue spot on the western side as well as the main streams flowing towards East (white dotted lines); in particular, Vado del Porto is given in black. Finally, the areas of Zenobito, Le Saline, and Il Piano are indicated as well. Samples n. 1-4 and 10 (in red) are assigned to haplotypes H4 and H5 (I, Fig. 2), while samples n. 5, 9, 11, 14, 17, 19 and 20 (in yellow) are assigned to haplotype H19 (III, Fig. 2). Sample n. 5 is the only one collected outside the limits of the National Park.

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Table 1. Estimates of mtDNA genetic diversity for each population of this study with a sample size ≥ 10. Legend: n, number of samples; S, number of polymorphic sites; N, number of haplotypes; h, haplotype diversity; k, average number of pairwise differences; □, nucleotide diversity.

Figures

Figure 1 - Download source file (2.64 MB)

The study area in Tuscany with the seven main islands of the Tuscan Archipelago National Park and the Wildlife Refuge Padule di Bolgheri along the mainland coast. Photo: European wild rabbit, courtesy of J.A. Blanco-Aguiar (University of Castilla-La Mancha, Spain).

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Haplotype network including all the O. c. cuniculus rabbits investigated in this study. A scale to infer the number of haplotypes (H, 1-21) for each pie is provided together with a length bar to compute the number of mutational changes. The colour of each population is indicated as well as the number of the haplotypes within the three haplogroups (I, II, and III) (see Table S1). Note that most of the domestic variants (Fauve de Bourgogne, Yimeng Wool, Chuanbai Rex, Jiuyi Mountain, and New Zealand White) were assigned to H1, with the Fujian Yellow being the only exception (H11) (see Table S3).

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The genetic structure of the rabbit populations investigated in this study (abscissas) as inferred with BAPS is given by means of a histogram where the length of the vertical bars (ordinates) indicates the proportion of individuals with an estimated membership to the clusters X, Y, and Z (cf., Table S3 for the posterior probability values of membership).

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Aerial photo of Capraia (M. Steele, www.flickr.com/photos/21022123@N04/27219061013/, CC BY 2.0, 2016). The perimeter (white thick line) of the area corresponding to the agricultural penal colony is indicated in the northern side of the island as well as the position of the only village. On the western side, the positions (white squares) of the three main mountain peaks - with elevation in metres - are reported from North to South as it follows: Mt. Castello, the highest one, Mt. Forcone and Mt. Arpagna. The only lake of Capraia - Lo Stagnone - is indicated by a blue spot on the western side as well as the main streams flowing towards East (white dotted lines); in particular, Vado del Porto is given in black. Finally, the areas of Zenobito, Le Saline, and Il Piano are indicated as well. Samples n. 1-4 and 10 (in red) are assigned to haplotypes H4 and H5 (I, Fig. 2), while samples n. 5, 9, 11, 14, 17, 19 and 20 (in yellow) are assigned to haplotype H19 (III, Fig. 2). Sample n. 5 is the only one collected outside the limits of the National Park.

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