Assessing beaver origins in North-Western Italy: a mitochondrial DNA comparison with Swiss and French populations

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Abstract:

Mitochondrial DNA sequences can be used to infer haplotype diversity in range-expanding species. The Eurasian beaver *Castor fiber* is experiencing a remarkable recovery in Europe following centuries of exploitation and local extinctions. The species has recently recolonized also Central Italy, likely due to unauthorized releases, whereas the first individuals occurring in North-Eastern Italy may be the results of natural range expansion from neighboring countries. Since the last months of 2023, presence signs were also observed in North-Western Italy, near the border with Switzerland. To assess the genetic diversity and origin of Italian beaver populations, we conducted mitochondrial DNA analysis on samples from this newly colonized area, revealing the occurrence of two mtDNA haplotypes belonging to the western mitochondrial lineage of the Eurasian beaver. Molecular sexing also confirmed the occurrence of both males and females. Therefore, monitoring this population should be urgently established following European laws. Future genetic investigations using nuclear DNA markers will be crucial for understanding the origin of these new populations and informing effective conservation strategies.

Keywords: Castor fiber, mtDNA, molecular identification, range expansion, North-Western Italy.

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Assessing beaver origins in North-Western Italy: a mitochondrial DNA comparison with Swiss and French populations

Genetic monitoring plays a key role in understanding population dynamics of species undergoing range expansions, especially those with complex life histories and distribution patterns (Excoffier et al., 2009). For instance, genetic data can reveal the source populations from which individuals originated, the dispersal routes they followed, and the factors influencing their colonization success or failure (Ibrahim et al., 1996; Ramos et al., 2016; Swan et al., 2022). Ultimately, genetic monitoring provides insights into the dynamics of species range expansion, aiding in the development of effective conservation and management strategies (Schwartz et al., 2007; Fabbri et al., 2014).

- The Eurasian beaver *Castor fiber*, a once ubiquitous species across Eurasia, has experienced a dramatic decline due to centuries of human exploitation, including overhunting and habitat destruction (Halley and Rosell 2003; Wrobel 2020; Halley et al., 2021). Despite this historical population bottleneck, beavers have successfully recolonized much of their former range through reintroduction programs and legal protection (Kodzhabashev et al., 2021; Pucci et al., 2021; Bouroş et al., 2022).
- Reintroduction programs have been crucial for the survival of Eurasian beavers in Europe, though at the same time fostering genetic confusion, as animals from diverse geographical origins have been used in reintroduction efforts, resulting in deeply admixed populations (Ducroz et al., 2005; Durka et al., 2005; Biedrzycka et al., 2014; Frosch et al., 2014).
- Molecular techniques have been used to unravel the genetic origins of recolonizing beavers by tracing the ancestry of newly observed beaver populations (Kropf et al., 2013; Minnig et al., 2016). Previous phylogeographic studies (Durka et al., 2005) identified two mitochondrial lineages in the Eurasian beaver, which corresponded to eastern and western populations, separated from one another in Central-Eastern Europe.
- In Italy, the species was first re-observed in 2018, after about 500 years of absence, in the northeast of
 the country, as a result of natural spreading from the reintroduced populations in Austria (Attili et al.,
 2023; Mori et al., 2024). Furthermore, beaver occurrence has been recorded since 2021 in Central and
 Southern Italy as well, most likely as the result of unauthorized releases (Pucci et al., 2021; Capobianco
 et al., 2023). Currently, the Italian population counts for at least 40-50 individuals, sharing the same
 mitochondrial DNA haplotypes occurring in populations of Switzerland, Austria and the Balkan Peninsula
 (Attili et al., 2023).
- In late 2023 and 2024, at least four more individuals have been recorded in North-Western Italy 31 (provinces of Verbano-Cusio-Ossola, Varese, Novara and Milano), on Lake Maggiore, Toce and Ticino 32 riverbanks, about 50 km south to the southernmost known Swiss records (Mori et al., 2024). Given this 33 geographic distance from the northern areas of beaver occurrence and the lack of signs of presence 34 between these areas, natural spreading might be controversial. Furthermore, in the vicinity of the newly 35 colonized sites, a zoo that formerly housed North American beavers Castor canadensis is still active, 36 37 raising questions about the specific identity of the individuals currently present in the wild. Therefore, we aimed at assessing the origins of these beavers by sequencing mitochondrial DNA from noninvasive 38 samples (hairs) and tissues from beavers collected in North-Western Italy and neighboring countries 39





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50 51 (Switzerland and France). We predicted that 1) individuals from North-Western Italy belong to *C. fiber* and 2) are genetically close to those occurring in Switzerland and France.

Three hair samples were collected in 2024 from North-Western Italy, at two different sites along Toce river (Verbano-Cusio-Ossola province, PIE1, PIE2) and Lake Maggiore (Varese province, LOM1), supplemented by a blood sample from a live beaver rescued along Ticino river (Milano province, LOM2). Nine muscle tissue samples were also gathered from Switzerland (n=7, from deceased individuals due to natural causes or car accidents, in Canton of Fribourg, Canton of Valais, Canton of Obwalden and Canton of Neuchâtel) and South-Western France, Rhone river basin in Savoie Department (n=2) (Tab.1, Fig.1). DNA was isolated from approximately 15 mg of muscle, 5–10 hairs and 200 µl of whole blood in EDTA using the Maxwell16 Instrument (Promega, Madison, USA) and following the producer's handbook.

A fragment of 330 base pair (bp) in a highly variable section of the mtDNA Control Region (CR) was 52 amplified and sequenced using the beaver-specific primers CR_Castor F and R (Attili et al. 2023). PCR 53 reactions contained 2.5 µl of 10X Gold buffer (Thermo Fisher Scientific, Waltham, MA, USA), 200 µM of 54 each dNTP, 2.5 mM MgCl₂, 10 pm of each primer, 1U of AmpliTagGold polymerase (Thermo Fisher 55 Scientific), 3 µl template DNA (10–50 ng) and PCR grade H₂O in a final volume of 25 µl. PCR tubes 56 57 were loaded onto an ABI Veriti® 96-Well Thermal Cycler (Thermo Fisher Scientific) under the following conditions: an initial activation step at 94°C for 3 min; 38 cycles of 94°C for 30 s, 56°C for 30 s, 72°C for 58 30 s, followed by a final extension of 5 min at 72°C. Negative and positive controls were included to 59 check success of amplifications and monitor contaminations. 60

61 PCR products were cleaned up with the QIAquick PCR purification kit (QIAGEN) and sequenced 62 bidirectionally using the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems). Unincorporated 63 dyes and contaminants were removed with the Agencourt® CleanSEQ solution (Beckman Coulter, 64 Beverly, MA, USA), then loaded on ABI 3130 Genetic Analyzer (Applied Biosystems).

CR sequences were edited and aligned with 31 sequences downloaded from GenBank, covering the
current Eurasian range of *C. fiber* (Ducroz et al., 2005; Durka et al., 2005; Horn et al., 2011; Kropf et al.,
2013; Frosch et al., 2014; Senn et al., 2014) using MEGA11 (Tamura et al., 2021). The final alignment
was trimmed to the common 330 bp fragment. The software DnaSP 6.0 (Rozas et al., 2017) was used
to determine the number of haplotypes and a median-joining network (Bandelt et al., 1999) was
constructed using the software PopArt (Leigh and Bryant 2015) to visualize their relationships.

Given the lack of sexual size dimorphism in Eurasian beavers, sex of individuals from North-Western
 Italy was molecularly determined following the protocol of Goldberg et al. (2011).

Sequencing of mitochondrial partial CR from all Eurasian beaver samples collected in this study
 produced three different haplotypes: ga1, JF7 and fi1, following the nomenclature in Munclinger et al.
 (2022) (Tab. 1; Fig. 1). One hair sample from North-Western Italy (PIE1) yielded only a partial fragment
 of 150 bp that matched *Castor fiber* sequences (100% of identity in BLAST NCBI
 http://www.ncbi.nlm.nih.gov/blast), but it was not possible to identify the haplotype and we excluded it
 from subsequent analyses. No evidence of *C. canadensis* was found in our beaver samples. In North Western Italy we found ga1 and JF7 haplotypes only. These haplotypes were first described as native





to the relict populations in France (Durka et al., 2005) and Russia (Voronezh) (Senn et al., 2014)
respectively, but currently they are widespread across Europe (Biedrzycka et al., 2014; Frosch et al.,
2014; Minnig et al., 2016; Kropf et al., 2013; Horn et al., 2011; Munclinger et al., 2022). Molecular sexing
suggested that a male and a female at least occur in the study area.

Among beavers from Switzerland, we identified ga1 and fi1 haplotypes, while in France only ga1 was found, in agreement with the literature (Durka et al., 2005; Senn et al., 2014; Minnig et al., 2016; Attili et al., 2023: Fig. 1). In regions near the Alps, the ga1 haplotype was identified, while in the Swiss Plateau (northeast), the fi1 haplotype was observed.

- 89 When the sequences from this study were added to published sequences, two clades were visible in 90 the median-joining network (Figure 2), consistent with previous phylogeographic studies (Durka et al., 91 2005).
- 92 All beavers analyzed in the present survey were grouped into the alleged Western lineage, although it is currently recognized that there is not clear correspondence between mtDNA clades and geographic 93 populations (Senn et al., 2014; Munclinger et al., 2022). A mixture of haplotypes currently occurs in most 94 beaver populations in Europe, following reintroduction events both legal and unofficial (Senn et al., 95 2014). In North-Western Italy we detected two haplotypes, which are very widespread in neighboring 96 countries (Durka et al. 2005; Minnig et al., 2016; Attili et al., 2023). Therefore, our findings are consistent 97 98 with the hypothesis that at least two individuals may have spontaneously dispersed from the Swiss population following ecological corridors linking Switzerland to Northern Piedmont and Lombardy 99 100 (Treves et al., 2020; Falaschi et al., 2023). However, the possibility of unauthorized releases of individuals descending from a genetically mixed stock, as the case of Central Italy, cannot be discarded 101 (Attili et al., 2023; Bertolino et al., 2023). 102
- 103 The recent arrival of Eurasian beavers in North-Western Italy, following their expansion from 104 Switzerland, may represent an opportunity for ecological restoration and biodiversity enhancement. 105 However, it is also possible that the beavers found in this region originate from Central Europe, sharing 106 the same haplotype with populations from that area (see Attili et al., 2023). This raises the hypothesis 107 that some individuals may have been introduced from Central Europe rather than arriving solely through 108 natural expansion. None of these hypotheses could be actually ruled out.
- The Eurasian beaver is listed in Annex II of the Habitats Directive (92/43/EEC); thus, Piedmont and 109 110 Lombardy should actively contribute to the recovery of a keystone species that is naturally returning after centuries of local extinction (Treves et al., 2020). Furthermore, Eurasian beavers, as ecosystem 111 engineers, play a crucial role in shaping aquatic environments; their dam-building activities create 112 wetland habitats that support a multitude of plant and animal species (Viviano et al., 2022) and provide 113 114 essential ecosystem services such as flood mitigation, water filtration, and carbon sequestration. By protecting and promoting beaver populations, Piedmont and Lombardy can not only restore natural 115 processes but also contribute to climate change mitigation and adaptation strategies (Treves et al., 116 2022). Additionally, the presence of beavers can attract eco-tourism, generating economic benefits for 117 local communities (Treves and Comino, 2024). While potential conflicts with human activities may arise, 118





careful management and public education can mitigate these issues and foster coexistence between 120 humans and beavers (Falaschi et al., 2023). 121

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236**Table 1** List of *Castor fiber* samples analyzed in this study. H= hair, B = blood T = tissue. CR haplotype237nomenclature follows Munclinger et al. (2022). - = not identified.

238	Sample ID	Locality (Country)	Biological	CR	Sex
239			material	haplotype	
240	PIE1	Fondotoce, Verbania Province (Italy)	Н	-	-
241	PIE2	Fondotoce, Verbania Province (Italy)	Н	ga1	Μ
242	LOM1	Lake Maggiore, Varese Province (Italy)	Н	JF7	F
243	LOM2	Ticino Park, Milano Province (Italy)	В	JF7	Μ
244	S1	Canton of Fribourg (Switzerland)	Т	ga1	-
245	S2	Canton of Neuchâtel (Switzerland)	Т	ga1	-
246	S3	Canton of Valais (Switzerland)	Т	ga1	-
247	SWISS 1	Canton of Fribourg (Switzerland)	Т	ga1	-
248	SWISS 2	Canton of Fribourg (Switzerland)	Т	fi1	-
249	SW6	Canton of Obwalden (Switzerland)	Т	fi1	-
250	SW7	Canton of Fribourg (Switzerland)	т	ga1	-
251	FR1	Le Bourget-du-Lac, Savoie department	Т	ga1	-
252		(France)			
253	FR2	Arenthon, Haute-Savoie department (France)	Т	ga1	-





255 256	Figure 1. Map of sampling sites. Localities are described in detail in Tab.1. Made with QGIS using Natural Earth Data.
257 258	Figure 2. Median-joining network of mitochondrial CR haplotypes in Eurasian beavers. Eastern lineage and Western lineage are shown according to Durka et al. (2005). The haplotypes found in this study are

259 marked in blue (JF7), red (ga1) and yellow (fi1).







Map of sampling sites. Localities are described in detail in Tab.1. Made with QGIS using Natural Earth Data.









Median-joining network of mitochondrial CR haplotypes in Eurasian beavers. Eastern lineage and Western lineage are shown according to Durka et al. (2005). The haplotypes found in this study are marked in blue (JF7), red (ga1) and yellow (fi1).





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Map of sampling sites. Localities are described in detail in Tab.1. Made with QGIS using Natural Earth Data.

Figure 2 - Download source file (143.54 kB)

Median-joining network of mitochondrial CR haplotypes in Eurasian beavers. Eastern lineage and Western lineage are shown according to Durka et al. (2005). The haplotypes found in this study are marked in blue (JF7), red (ga1) and yellow (fi1).

