



# Last but not beast: the fall of the Alpine wolves told by historical DNA

Christophe Dufresnes<sup>1,2</sup> · Christian Miquel<sup>3</sup> · Pierre Taberlet<sup>3</sup> · Luca Fumagalli<sup>1</sup>

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## Abstract

The sociopolitical acceptance necessary for the conservation of controversial species requires scientific knowledge that disentangles empirical facts from myth and misinformation. An epitome of such, the gray wolf (*Canis lupus*) had been eradicated from most of Western Europe by the early twentieth century. However, a few mysteriously re-appeared in the Alps throughout the twentieth century, leading to systematic hunts encouraged by popular folklore and massive waves of panic. These historical events are reminiscent of the hostile context now surrounding the recolonization of the wolf across former ranges. Through historical DNA sequencing of five rare museum specimens shot post-WWII, we tell the true story of these mystery beasts. The oldest ones (1947–1954) were just the very last survivors of an endemic, extremely resilient wolf population, thought to be extinct decades earlier, while recent ones (1978–1990) most likely originated from captivity. This parable reminds that today more than ever, scientific evidence is necessary to conduct an objective societal debate over the management and conservation of controversial species.

**Keywords** *Canis lupus* · Controversial species · Human-wildlife conflicts · Museum samples · Regional extinction

Wolves and humans share a long and complicated history. Alternately viewed as a loyal guardian (e.g., symbolizing the power of the Roman Empire) or as a punishing devil in the Christian culture, over the last centuries the wolf has been feared and despised as a threat to the public and livestock. As deforestation and hunting during the Middle Ages sealed the fate of many wild ungulates, wolf predation pressure on sheep and goats reached a climax. Western societies consequently initiated eradication programs that combined lucrative bounties with popular beliefs to motivate the elimination of the so-called “beasts”. In addition, the improvements of firearms (eighteenth century) and the use of strychnine to poison carrion (nineteenth century) contributed to the rapid decline of this competitive top predator across large parts of its original distribution (Mech and Boitani 2003; Chapron et al. 2014).

Once a stronghold of wolves, the Alps witnessed their progressive eradication; the last self-sustaining populations are thought to have completely disappeared by the turn of the twentieth century (Breitenmoser 1998) (Fig. 1). Recent historical DNA analyses unraveled an unsuspected amount of past genetic diversity before then (Dufresnes et al. 2018): at least 14 mitochondrial haplotypes were present in the extinct Alpine population, representing most European haplogroups identified for this species (Pilot et al. 2010) (Figs. 1 and 2). Only one made it back: the “Italian” haplotype, resulting from the recolonization of the Alps since the early 1990s from the heavily bottlenecked Apennine population in Italy (Valière et al. 2003; Hindrikson et al. 2017) (Fig. 2). Thanks to legal protection and improving environmental conditions, the Alpine population nowadays numbers about 500 individuals (Chapron et al. 2014; Wolf Alpine Group 2018). However, its comeback is once again the theater of recurrent social and political conflicts.

But did wolves really disappear from the Alps a century ago? The appearance of several mysterious “beasts” made the headlines throughout the twentieth century, causing mass hysteria and fueling conspiracy theories. Did some wolves manage to survive the eradication era? Were they vagrants, portending the natural recolonization to come? Or could they have escaped from captivity? Through historical DNA analyses of rare museum specimens (skins and bones, see [Methods](#) below), we revisited

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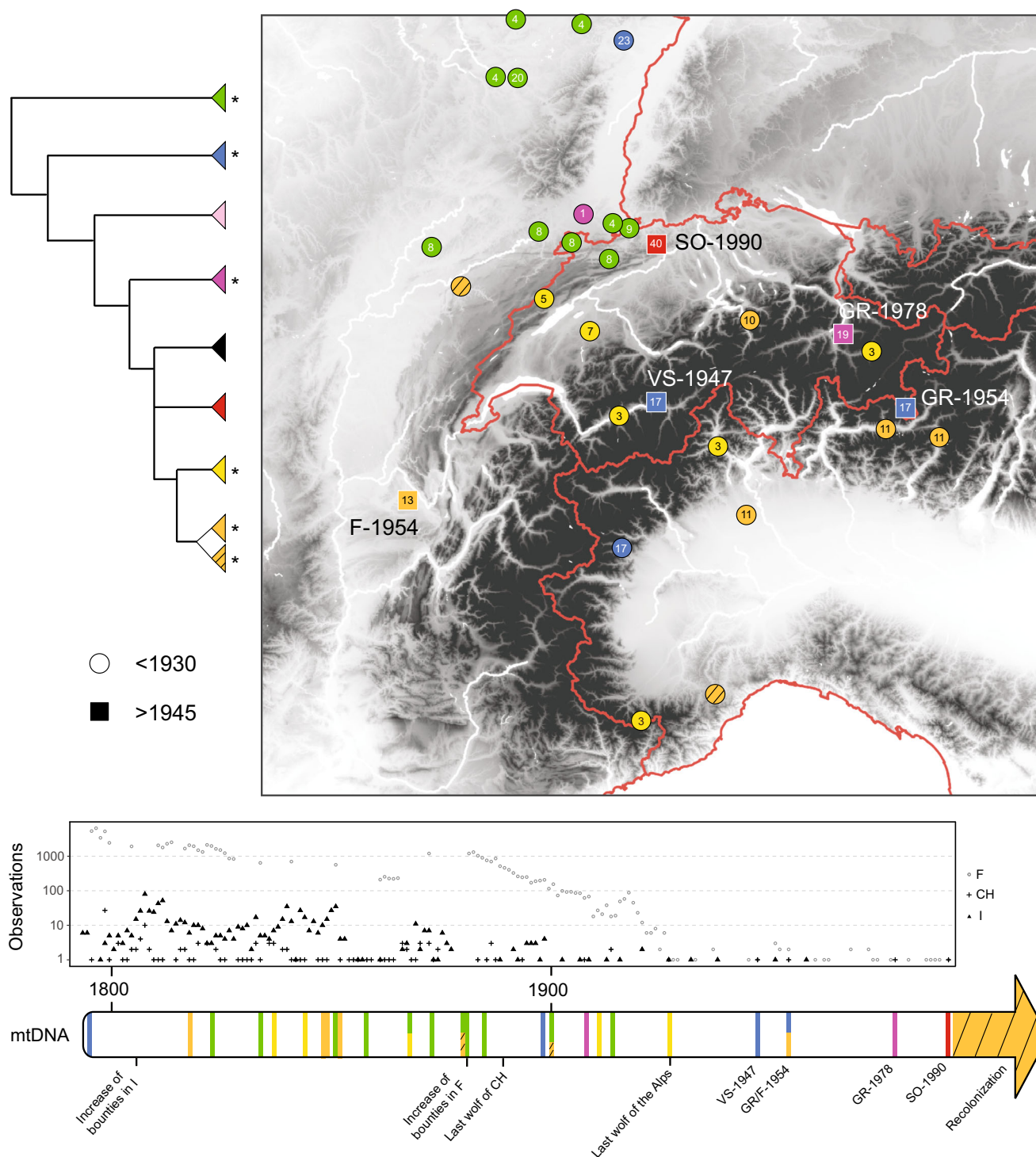
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✉ Luca Fumagalli  
luca.fumagalli@unil.ch

<sup>1</sup> Laboratory for Conservation Biology, Department of Ecology and Evolution, Biophore Building, University of Lausanne, CH-1015 Lausanne, Switzerland

<sup>2</sup> Department of Animal & Plant Sciences, University of Sheffield, Alfred Denny Building, Western Bank, Sheffield S10 2TN, UK

<sup>3</sup> Laboratoire d'Écologie Alpine (LECA), UMR 5553, BP53, 38041 Grenoble Cedex 9, France

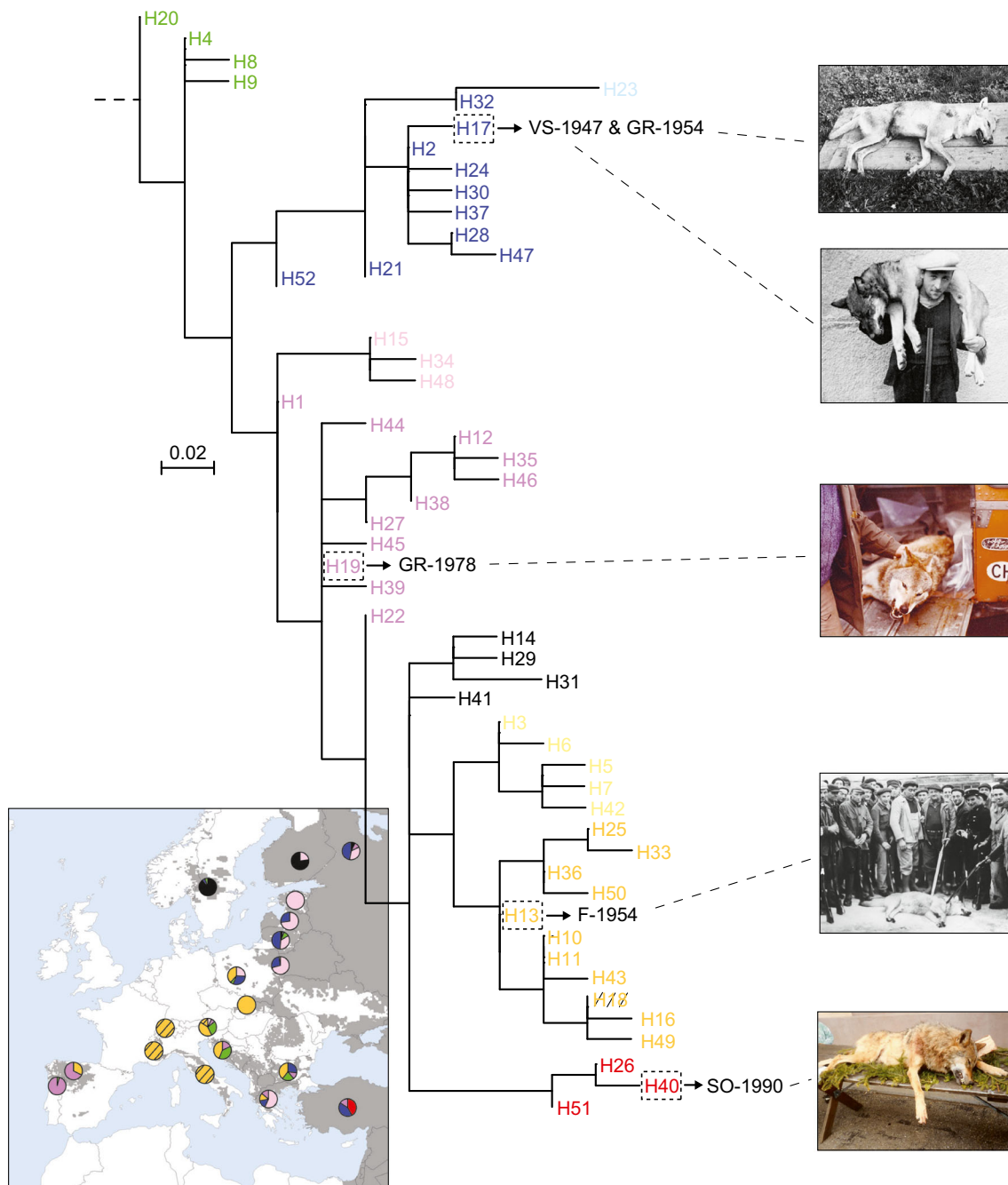


**Fig. 1** Simplified phylogeny of mitochondrial DNA CR haplogroups (\*haplogroups found in the Alps) and their historical occurrence (1795–1990) in space (map) and time (bottom chronological arrow). Circles and squares show the place of death for sequenced wolves killed from 1795 to 1930 (Dufresnes et al. 2018), and after 1945 (this study), respectively. The identity of haplotypes is indicated within the symbols. The “Italian”

haplotype (H18), nowadays fixed in the Apennines and the Alps, is in dashed orange. The middle panel plots (log-scale) direct observations/shootings of wolves over the 1795–1990 period in France and Switzerland (whole country) and the Italian Alps, inferred from historical sources (See Methods). F: France; I: Italy; CH: Switzerland

some of these cases by investigating the genetic legacy of five famous wolves killed after WWII in the Western Alps, decades after their official eradication (Table 1).

We sequenced a commonly used ~300 bp fragment of the mitochondrial DNA control region (CR) and identified haplotypes based on our database of extinct and extant



**Fig. 2** Phylogeny of mitochondrial DNA CR haplotypes (adapted from Dufresnes et al. 2018) for the identification of the five post-WWII historical wolf specimens sequenced, and illustrated. The bottom-left map shows the current distribution of wolves in Europe (gray area) and the proportion of each haplogroup (pie charts) according to published

regional studies (Dufresnes et al. 2018 and references therein). The “Italian” haplotype is in dashed orange. Photos are credited as follows, from top to bottom. GR-1954: Museo Poschiavino; VS-1947: UVT, Médiathèque du Valais, Martigny; GR-1978: Archiv Bündner Naturmuseum; F-1954: Archives Dauphiné Libéré; SO-1990: E. Plattner

lineages of the Western Palearctic (Dufresnes et al. 2018, Fig. 2).

The first wolf, the “monster of Valais” (VS-1947), caused tremendous turmoil in Switzerland in 1946–1947, as hundreds of livestock were slaughtered and rumors transformed into collective psychosis, even suspecting a panther or a giant snake

(Bachmann 2009). Its mtDNA lineage was last detected in the region a century before (haplotype H17; Dufresnes et al. 2018). A second specimen shot a few years later (1954 in Graubünden, Switzerland; GR-1954) bears the same genetic signature (H17). Based on skull analysis, the London British Museum first concluded that it was a dog, and it took almost

**Table 1** Details on the wolf specimens sequenced; CR: control region mitochondrial haplotypes (according to Dufresnes et al. 2018)

| ID      | Sex    | Sample       | Place of killing            | Date of killing | Museum   | Museum code             | CR  | Origin                              |
|---------|--------|--------------|-----------------------------|-----------------|--|-------------------------|-----|-------------------------------------|
| VS-1947 | Male   | bone         | Eischoll, Valais, CH        | 27.11.1947      | Musée de la Nature du Valais, Sion (CH)                        | 128                     | H17 | Relict Alpine population            |
| F-1954  | Male   | bone         | Vignieu, Isère, F           | 12.01.1954      | Muséum d'Histoire Naturelle, Lyon (F)                          | 50.000276               | H13 | Relict Alpine population            |
| GR-1954 | Female | bone         | Poschiavo, Graubünden, CH   | 09.09.1954      | Bündner Naturmuseum, Chur (CH)                                 | BNM13170                | H17 | Relict Alpine population            |
| GR-1978 | Male   | bone         | Lenzerheide, Graubünden, CH | 13.12.1978      | Bündner Naturmuseum, Chur (CH)                                 | BNM8203                 | H19 | Presumably captive (Eastern Europe) |
| SO-1990 | Male   | bone<br>skin | Hägendorf, Solothurn, CH    | 15.05.1990      | Naturhistorisches Museum, Bern (CH)<br>Naturmuseum, Olten (CH) | NMBE1028210<br>NMO33035 | H40 | Captive (Asia Minor)                |

two decades to consider its genuine wolf nature, despite general disbelief (von Lehmann 1971). By killing several dogs, another wolf (F-1954) spread terror in the north of Isère (France) during the winter of 1953/1954. The hunt involved 3000 people, including the entire police force of the department. Its mitochondrial haplotype (H13) was previously known only from nineteenth century specimens present in Italy and Central Europe. Wolves were scarcely observed again in the Alps over the following decades. The two individuals killed in Switzerland in 1978 (GR-1978, resulting in school closings) and 1990 (SO-1990, terrifying the population over three weeks) possessed Eastern European (H19) and Middle Eastern haplotypes (H40), respectively, suggesting captive origins (Fig. 1). Barely two years later (1992), the species made its official comeback to the Alps (Breitenmoser 1998).

These findings somehow rewrite the history of the gray wolf in Europe, which was presumed extinct in the Alps by the 1890s (Switzerland and France) and the 1920s (Italy) (Fig. 1). Indeed, the mid-twentieth century specimens we analyzed carried ancestral haplotypes and thus likely descended from the original Alpine population. The closest alternative source, the Apennine population (at that time restricted to the southern part), had already fixed the private H18 haplotype ever since the 1900s (Dufresnes et al. 2018). The relict population of Alpine wolves must thus have remained at a very low density to avoid detection, and benefited from the respite offered by WWII, during which capture and hunting programs were interrupted. Similarly, French wolves episodically recovered during the wars of 1870 and 1914–1918 (de Beaufort 1987), demonstrating their amazing resilience over very short time periods. The last Alpine wolves ultimately became extinct in the 1950s, decades after their presumed eradication. Subsequent observations (1970–1990) appear to be wolves of oriental ancestry, bearing haplotypes that were not previously found in the studied area (Fig. 1). Therefore, these individuals are presumably of captive origin.

Our elders, affected by the loss of livestock, but mostly influenced by popular credulity, reacted with fear and disproportionate measures towards the few last survivors of this natural population. Decades later, rumors spread more than ever as wolves return to their former ranges, casting again doubts about their origin, genetic integrity and actual socio-economic impact, hence hindering an objective public debate over the species management. Knowledge and acceptance of controversial species is a crucial element to their long-term conservation (Bruskotter et al. 2011; Treves and Bruskotter 2014; Behr et al. 2017; Treves et al. 2017; Killion et al. 2019), so history does not repeat itself. Scientific evidence is instrumental to demystify popular beliefs and counter misinformation campaigns on (social) media (e.g., Lewandowsky et al. 2016; Loss and Marra 2018). In a time of unprecedented propagation of fake news undermining scientific credibility, this remains a major societal challenge, years after the last mystery beasts roamed the Alpine mountains.

## Methods

Skin and bone samples were obtained from five gray wolf *Canis lupus* specimens provided by French and Swiss museums. All samples originated from wolves killed between 1947 and 1990, decades after the official extinction of the species in the Alpine range and adjacent regions (Table 1).

Haplotype identification was assessed through mitochondrial DNA (mtDNA) control region (CR) sequencing following Dufresnes et al. (2018). Briefly, all samples were processed in a physically separated laboratory exclusively devoted to the analysis of museum and low DNA-content samples, and negative controls were included in each extraction and amplification experiment to monitor contaminations. Three short (111–225 bp), partially overlapping sequences were PCR-amplified, resulting in a 317 bp fragment of the mtDNA control region and adjacent Pro-tRNA gene. In order to confirm the haplotypes obtained by capillary Sanger-sequencing of each of the three amplified fragments/sample (in duplicate), the full experimental procedure was independently replicated in two different laboratories (University of Lausanne, Switzerland and University of Grenoble, France).

The five resulting haplotypes were compared with a database of historical ( $n = 177$ ) and modern ( $n = 1814$ ) homologous CR wolf sequences from the Western Palearctic, totaling 52 haplotypes (Dufresnes et al. 2018).

In order to illustrate wolf population declines in the studied region, we collected historical data on wolf kills, bounties and direct observations (France and Switzerland: full country; Italy: Alpine region only), according to the following publications: Association des lieutenants de louveterie de France (1929), Baillon (2014), de Beaufort (1988), Brunetti (1984), Comincini (1991), Etter (1992), Farina et al. (2005), Molinier (2002), Mostini (1997), Oriani et al. (2014), Villequez (1884).

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