

The shaping of mitochondrial DNA phylogeographic patterns of the brown hare (*Lepus europaeus*) under the combined influence of Late Pleistocene climatic fluctuations and anthropogenic translocations

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Abstract

The phylogeographic structure of the brown hare (*Lepus europaeus*) was studied by analysing mtDNA control region sequences of 98 individuals from continental and insular Greece, Bulgaria, Cyprus and northern Israel, together with 44 published sequences from Italy and central Europe. We found two distinct clades separated by an average nucleotide divergence of 6.6%, which may correspond to a Balkan and to an Asia Minor refugium. The estimated time of separation of the two clades was dated back to 105,000–490,000 years ago. These two clades coexist in the area of northeastern Greece and Bulgaria, most likely as a result of a post-glacial northward expansion. Within the southern Balkan refugium, network analyses showed geographical structuring, which supports the hypothesis of several isolated Late Pleistocene populations. The central European and Italian populations appear to have originated from a non-detected northern Balkan population that was genetically closely related to some northern Greek populations, as a result of postglacial expansion, translocations or a combination of both. Moreover, several cases of ancient and recent translocations by humans were detected, especially for some island populations, while the eastern Aegean islands off the Asia Minor coast were most likely colonized naturally through Late Pleistocene land bridge connection. The genetic analysis presented here provides a framework for designing proper conservation and management guidelines for this species.

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1. Introduction

The brown hare (*Lepus europaeus*) is a popular game animal and one of the most frequently translocated mammals in Europe. It is distributed over most of Europe up to 60°N, in Asia Minor and probably south to Israel. Its range has been expanded to the east both by natural dispersion and by translocations to central and far-east Siberia (Flux and Angermann, 1990). It has also been imported in many other areas worldwide, outside

its natural distribution range, such as South and North America, Australia and New Zealand.

Various genetic studies on brown hare populations have revealed different levels of genetic variation across Europe (Hartl et al., 1993; Mamuris et al., 2001; Perez-Suarez et al., 1994; Pierpaoli et al., 1999; Suchentrunk et al., 2000b; Suchentrunk et al., 2001; Suchentrunk et al., 2003; Thulin et al., 1997), but so far there are no studies on the phylogeographic structure and the evolutionary history of the species. Like many other elements of the European fauna and flora, the brown hare was probably influenced by the glaciation cycles of the Pleistocene. The southern peninsulas of Iberia, Italy and the Balkans, as well as Asia Minor, which have acted as

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Pleistocene refugia for diverse European species (e.g., Hewitt, 1999; Taberlet et al., 1998), could have provided a refuge for brown hares as well. After the last glacial maximum, refugial populations expanded to the north, colonized uninhabited central and northern Europe and, in several cases, formed contact zones. Different postglacial colonization patterns have been described (Davison et al., 2001; Hewitt, 1999). In most cases, the Balkans were the main source of European populations, because of the absence of major geographical barriers to the north, compared to the Alps and the Pyrenees for the Italian and the Iberian refugia, respectively (Hewitt, 1999).

For the brown hare no refugial populations have been identified yet. Analyses of mitochondrial DNA (mtDNA) Control Region hypervariable domain I (CR-I) sequences from brown hares of the Italian peninsula showed that they were practically indistinguishable from central European ones and were interpreted as stemming from recently imported hares, while few more divergent haplotypes were suspected to reflect an early colonization wave (Pierpaoli et al., 1999). In the Iberian peninsula, a mtDNA RFLP study revealed the presence of two distinct phylogenetic lineages in brown hare (Perez-Suarez et al., 1994), which later were interpreted as the result of ancient introgression of mountain hare (*Lepus timidus*) mtDNA into brown hare (Alves et al., 2003). Moreover, the southern parts of the Iberian and Italian peninsulas are historically occupied by other hare species (*L. granatensis* and *Lepus castroviejoi* in Iberia, and *Lepus corsicanus* in Italy), while in the Balkans and Asia Minor the brown hare is the only hare species present. The absence of other, possibly competitive hare species in the eastern Mediterranean could have allowed for a long-term presence and evolution of the brown hare there, and this region might indeed have provided a major late glacial refugium. Subfossil remains from the Late Pleistocene of mainland Greece support this assumption (Chevallier, 1973; Jullien, 1981; Payne, 1969; Reisch, 1976).

To study the phylogeographic patterns of the brown hare, one has to consider the extensive human mediated translocations, which may have obscured the historical biogeographical events. Captive-reared hares of various and often unknown origins have been and are still intensively translocated for restocking of the local populations that were extirpated or over-exploited by unsustainable hunting. According to Flux (1983), the indigenous hares in France have been completely replaced by the introduction of hares from eastern Europe, while in Italy many local populations may have been totally replaced by introduced allochthonous ones (Pierpaoli et al., 1999). In Greece, translocations of reared individuals imported mainly from Italy, former Yugoslavia and Bulgaria, were contacted mostly in the last decade but not extensively, thus mtDNA introgression

of allochthonous gene pools into the native populations seems not that high, a fact that could also be attributed to reduced viability of the reared hares in the wild (Mamuris et al., 2001).

Human mediated introductions probably account for the presence of the brown hare on some eastern Mediterranean islands (such as Crete and Cyprus), which have been isolated from the continental coast more than 2.5 million years ago, when the first appearance of the genus *Lepus* is documented by the available fossil record (Lopez-Martinez, 1980). For several others, such as the Aegean islands off the Anatolian coast (e.g., Chios, Samos, Lesbos) and the Ionian islands (e.g., Lefkada), which were connected to the mainland during the last glacial maximum (Andel and Shackleton, 1982), brown hare might have arrived there through natural immigration routes. Depending on the mode of colonization (human mediated or natural) and the source population on the mainland, different islands might have quite distinct mtDNA gene pools or admixtures of different lineages.

The widespread practice of translocations of brown hares throughout Europe tends to replace local gene pools and reduce genetic variability (cf. Flux, 1983; Perez-Suarez et al., 1994; Pierpaoli et al., 1999), thus potentially threatening the long-term viability of the species. It is of great importance for the sustainable management of the species to infer its evolutionary history, identify indigenous gene pools and possible divergent clades, to properly design management practices.

In this study, we analyzed mtDNA CR-I sequences of brown hares from mainland Greece and several major Greek islands, as well as from Cyprus, Bulgaria, and northern Israel and combined the data with published sequences from Italy and central Europe to: (a) reveal the phylogeographic structure of the species and check for divergent lineages and differentiated gene pools, (b) check whether the southern Balkans have acted as source for the colonization of central Europe, (c) infer the colonization history of several islands and (d) consider the impact of translocations on phylogeographic patterns and genetic variability.

2. Materials and methods

2.1. Sample collection

Tissue samples from Greece and Cyprus were collected between 1997 and 2001 with the assistance of the local hunting associations. Samples from Bulgaria and northern Israel were obtained in the course of previous studies on genetic variability of brown hares (Suchentrunk, 2000; Suchentrunk et al., 2000a,b). Sampling locations are given in Fig. 1.

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