



Original Investigation

Mitochondrial sequences yield new insight into the Quaternary history of the edible dormouse on the landbridge Adriatic islands

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ABSTRACT

We studied the phylogeographic structuring of the edible dormice populations occupying the landbridge Adriatic islands which were isolated from the mainland after a transgression of glacial meltwater at about 10 kya. The edible dormouse is well nested into a system-wide biogeography of the archipelago, presumably the consequence of its in situ persistence since the insularisation of the entire system. If so, the genetic profile of island populations was not affected by the presumed population bottleneck at ~2 kya and possibly retained an ancestral genetic diversity which eroded on the mainland. To test the hypothesis, we explored a fragment of a cytochrome *b* gene in 50 dormice from six islands and a further 10 individuals from two eastern Adriatic peninsulas (Istria and Pelješac), one locality in Serbia and three localities in Macedonia. Two new haplotypes from Macedonia clustered into the Macedonian phylogeographic lineage, while the remaining 9 haplotypes formed an unsupported sublineage (the Adriatic haplogroup) within a widespread European lineage. Six Adriatic haplotypes were endemic to a particular island and only one single haplotype was shared between the islands and the mainland. Four islands only had endemic haplotypes and only the widespread haplotype was recorded on a further two islands. A mere 1–2 mutational steps separated the endemic island haplotypes from the widespread haplotype which concurs with the postulated recent population expansion of the European lineage. On the other hand, the suggested timing of the event (i.e. 2 kya) cannot be comfortably accommodated into the environmental dynamics of the Adriatic region since the Last Glacial Maximum.

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Introduction

Many temperate species endured periods of glacial expansions over the last 2.6 million years (my) in geographically restricted refugia. At the end of the Last Glacial Maximum (LGM), some refugial populations with divergent genomes remained restricted to their former glacial refugia, whereas others expanded (Hewitt, 2000; Bilton et al., 1998). By using gene genealogies, numerous phylogeographic studies have shown that peninsulas of Mediterranean Europe have acted as such glacial refugia although some species also survived in more northern areas (Stewart and Lister, 2001). A model of persistence in constrained refugial areas has been used extensively to interpret the Quaternary history of various organisms (e.g. Taberlet et al., 1998; Hewitt, 2000). Each species responded to glacial–interglacial dynamics in its own unique way,

however, and patterns of some taxa and lineages are particularly idiosyncratic.

In this study we focused on the refugial history of the edible dormouse *Glis glis* (Linnaeus, 1766) in the Balkan refugium. Though the overall phylogeographic structuring of the edible dormouse fits the model on the persistence in the southern refugia (Hürner et al., 2010; Castiglia et al., 2012; Naderi et al., 2013), the great majority of extant populations cluster to a single widespread lineage (European lineage *sensu* Hürner et al., 2010). This lineage evidently originates from a recent expansion dated around 2 kya from a single, unknown refugium. Genetic structuring of dormice populations in the Balkans, an area which has acted as one of major glacial refugia, is imperfectly known. The European lineage is widespread in the Balkan peninsula and all dormice sequenced thus far were found to have a single haplotype (Hap02 *sensu* Hürner et al., 2010). This haplotype is also the most common and widespread across Europe and Asia Minor (Hürner et al., 2010; Helvaci et al., 2012). A further two unique and deeply divergent haplotypes were found in the Balkans, one from western Macedonia (Hürner et al., 2010) and the other from the small Greek island of Alonissos (Castiglia et al.,

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2012). Most probably, the Balkan peninsula acted as an important refugium for the edible dormice, however, in the absence of adequate sampling the geographic scope of relict populations and their genetic structure remains enigmatic.

We studied the mitochondrial architecture of dormice populations occupying the landbridge Adriatic islands. During the last glacial cycle, when a sufficient volume of water was removed from the ocean basins and stored in the continental ice sheets (Bell and Walker, 2005), the entire bottom of the northern Adriatic Sea was exposed and the present day islands were part of the mainland throughout the Würmian glacial cycle. Climatic amelioration after the LGM reduced global ice volume and at about 10 kya, a transgression by glacial meltwater isolated the Adriatic islands as we know them today (Van Aandel, 1989; Forenbacher, 2002).

Though the fossil history of the small terrestrial mammals occupying the Adriatic islands is poorly documented (e.g. Malez, 1986) there are other means available to assess the evolutionary history of insular faunal assemblages. For example, the fauna of small terrestrial non-volant mammals of the Adriatic archipelagos show a nested pattern which is more organised than that which would be expected by chance (Kryštufek and Kletečki, 2007) and therefore points to extinction dominated and well-insularised populations (Patterson and Atmar, 1986). The edible dormouse is well nested into the system-wide biogeography of the archipelago. This presumes the post-isolation leakage of dormice between the islands and the mainland to be a less likely event than the in situ persistence of island populations since the insularisation of the entire system.

Because the historical processes of divergence, persistence in refugia, and migration all leave their footprints in the genealogies of DNA sequences (Taberlet et al., 1998; Hewitt, 2000),

molecular markers can uncover the evolutionary history of the edible dormouse in the Balkan refugium. Several partly overlapping hypotheses are feasible. If dormice were recently transported to the islands, then one can expect their genetic makeup to closely match the conditions found on the mainland. Hence, a single widespread haplotype Hap02 should also be present on the islands. Assuming that the insular populations of the edible dormouse indeed resulted from the isolation at ~10 kya, then their genetic profile was not affected by a presumed population bottleneck at ~2 kya (Hürner et al., 2010) and retained the ancestral genetic diversity which was lost on the mainland.

Material and methods

Samples, DNA extraction, PCR amplification and sequencing

DNA samples were obtained from 60 individuals of edible dormouse from 12 locations in the Balkans. Localities in Croatia included six Adriatic islands (Cres, Krk, Hvar, Brač, Korčula and Mljet) and two east Adriatic peninsulas (Kršete, Istria and Pelješac). Further samples originated from one location in Serbia, Kladovo and three locations in Macedonia, Bituša, Mavrovo and Mt. Karađica (Fig. 1, Table 1).

From ethanol-preserved samples we dissected a 2 × 2 mm piece of tissue and air-dried it under sterile conditions. DNA extraction was performed using QIAamp DNA Mini Kit (Qiagen, Valencia, CA, USA). For the amplification of the cytochrome *b* gene (*cytb*), we used the following primers: L15408Marv (Haynes et al. 2003), H15497 (Shen and Nakamura, 1999), L14727-SP and H15915-SP (Jaarola and Searle, 2002). A polymerase chain reaction (PCR) was performed in a total volume of 15 µl containing: 2.5 mM MgCl₂, 0.3 µM

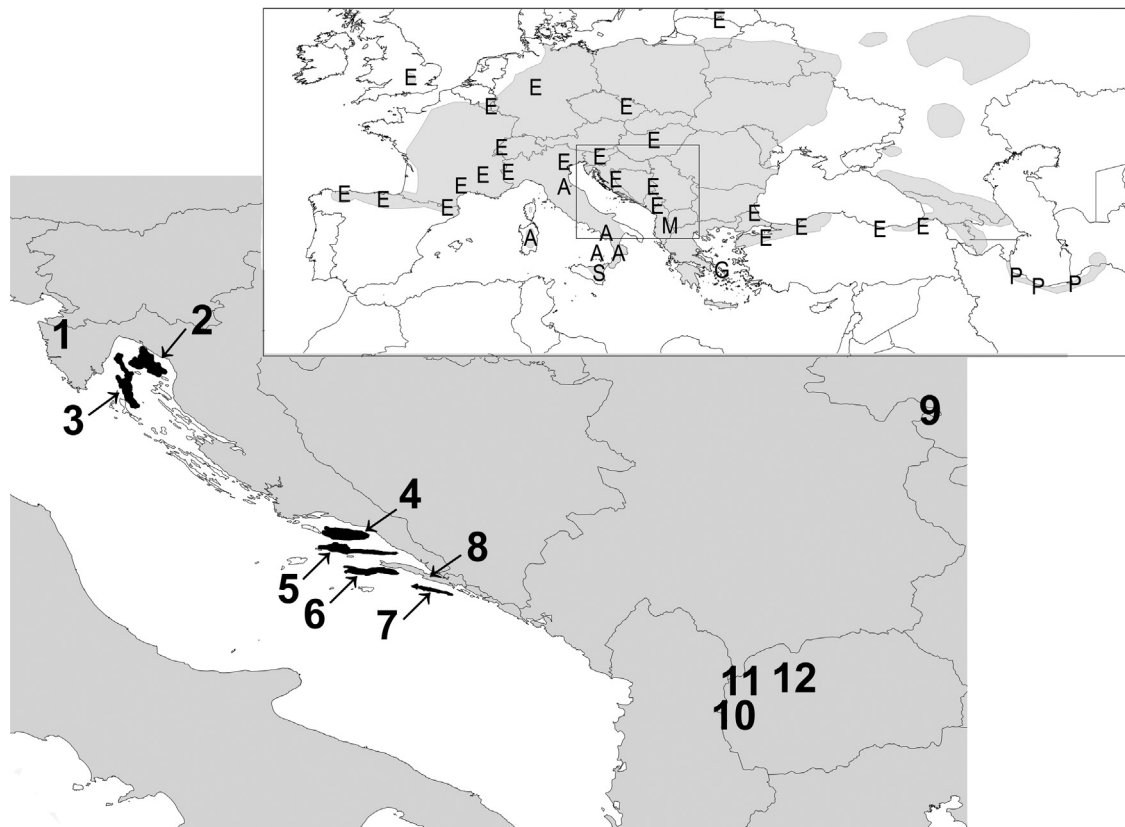


Fig. 1. Geographical distribution of samples of the edible dormouse (*Glis glis*) used in this study. Capital letters in the top inset tentatively show the ranges of major phylogenetic lineages (from Hürner et al., 2010; Lo Brutto et al., 2011; Castiglia et al., 2012; Helvacı et al., 2012; and Naderi et al., 2013): A—Italian, E—European, G—Greek, M—Macedonian P—Iranian. The approximate range of the species (shaded) is adopted from Amori et al. (2008). For sample localities see Table 1. Island populations are shaded black.

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