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Landscape as a determinant of dispersal patterns and population connectivity in a newt species

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ABSTRACT

Landscapes and their structure are important in shaping the distribution of species and the composition of communities. Since a landscape contains elements that are less permeable to dispersal, species use corridors of habitat suitable to movements that maintain the genetic flow among populations. Corridors have been widely used in conservation biology, but less often to study the connectivity between species' allopatric ranges. In this study, we analyzed the distribution and connectivity patterns of the Danube Crested Newt (*Triturus dobrogicus*), a species found in the Danube river basin and whose range is separated by the Carpathian Mountains in two regions, eastern and western. Despite the geographical barrier and clear morphological differentiation between the populations of the two regions, recent genetic analyses suggest maintenance of genetic flow. The aims of our study were (1) to estimate the dispersal ability of the Danube Crested Newt and the connectivity (via corridors) between populations and (2) to identify possible pathways used by the species to cross the Carpathian Mountains barrier. We found that the landscape facilitates a higher population connectivity in the western range than in the eastern range of the species. Moreover, we identified two major migration pathways, along the Iron Gate Canyon and the Timiş – Cerna Gap, that may connect all known occurrences from the two regions separated by the Carpathian Mountains. As an alternative dispersal hypothesis, we also discussed the possibility that the Danube Crested Newt is passively dispersed by water, down the Danube river flow direction. Our study provides support for the assertion that even when a species' distribution is separated in two ranges by a geographical barrier, connectivity between populations via corridors can persist.

1. Introduction

Landscapes are units of usually heterogeneous land (Jobbágy et al., 1996; Wiens, 2002), comprising different geomorphological, anthropogenic, and natural features. Landscapes play an important role in mediating the dispersal and shaping the distribution of species and communities (Atauri and de Lucio, 2001; Coulon et al., 2004; Neville et al., 2006). The gene flow between relatively isolated populations can be maintained through dispersal via corridors (Coulon et al., 2004; Vos et al., 2002). Dispersal corridors represent linear landscape features that ensure connectivity between two or more patches of suitable habitat for the candidate species, isolated by unsuitable habitat (Bennett, 1999; Brooker et al., 1999; Haddad, 1999; LaRue and Nielsen, 2008; Vos et al., 2002; Williams et al., 2005). This concept of connectivity through corridors has been widely used in the field of conservation biology where it serves as a tool for maintaining gene flow between populations of threatened species located in isolated protected areas (Brooker et al., 1999; LaRue and Nielsen, 2008; Williams et al., 2005). However, geostatistical analyses are rarely used to estimate the biogeography and possible connectivity and pathways of migration between allopatric ranges of species, despite their obvious utility (e.g. Murtskhvaladze et al., 2010; Zancolli et al., 2014).

Seven described species of crested newts (*Triturus cristatus*, *T. carnifex*, *T. macedonicus*, *T. dobrogicus*, *T. ivanbureschi*, and *T. karelinii*) form a complex of large bodied newts (*T. cristatus* complex), distributed across the West-Palearctic region (Arntzen, 2003; Arntzen et al., 2007). Rapid evolution and ecological speciation played a fundamental role in the divergence of crested newt species (Furtula et al., 2009; Ivanovic et al., 2008; Vukov et al., 2011). Later, competition and Quaternary climate oscillations shaped the known distribution of crested newts (Wielstra and Arntzen, 2012; Wielstra et al., 2012, 2013). However, ranges of multiple species are not uniform, with areas completely isolated from the main range (e.g., *T. ivanbureschi* in Serbia, *T. cristatus* in Bulgaria and Scandinavia, and *T. karelinii* in Crimean Peninsula and northern Iran) (Arntzen, 2003; Arntzen and Wallis, 1999; Tzankov and Stoyanov, 2008; Wielstra and Arntzen, 2011, 2012). Recently, Wielstra and Arntzen (2012) and Wielstra et al. (2013) used ecological niche modeling and genetic data to show that the last glacial period had an important role in the population isolation of *T. ivanbureschi* and *T. cristatus*. In both cases, it was suggested that the

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isolated populations were "trapped" in their suitable niche in glacial refugia during the Holocene as other sister species expanded their ranges (Wielstra and Arntzen, 2012; Wielstra et al., 2013).

The Danube Crested Newt (*T. dobrogicus*) has an intriguing distribution, with two presumably allopatric ranges separated by the Carpathian Mountains: a western range in the Pannonian plain, and an eastern range in the Lower Danube river plains and around freshwater lake systems along the western Black Sea coast (Arntzen and Wallis, 1999; Gherghel and Iftime, 2009; Litvinchuk, 2005; Litvinchuk and Borkin, 2000). Due to this distribution pattern, the systematic affinities of the Danube Crested Newt have long been debated. Boulenger (1908) described the populations from the western range of the species as a distinct taxon, naming it *macrosoma*. In the most recent systematic revision, Litvinchuk and Borkin (2000) showed differences in morphology and osteology between the proposed *T. dobrogicus* eastern and western subspecies, as well as very low genetic viability of the subspecies hybrids, even lower than hybrids between recognized species. However, recent studies based on allozymes and mitochondrial DNA did not conclusively recognize the two subspecies (Voros and Arntzen, 2010; Wielstra et al., 2013). For the purpose of this study, that of analyzing environmental differences between the two geographic regions, we are using the taxonomy proposed by Litvinchuk and Borkin (2000). Of the Crested Newts, *T. dobrogicus* is the most dependent on aquatic systems, with adults spending up to six months or more in water and exhibiting preference for swamps, marshes, and flooded meadows and riparian forests, as well as plains that are prone to flooding (Arntzen, 2003). Irrigation ditches and flooded agricultural fields can also be used by this species (Gherghel, I. pers. obs.). Previous studies found that, generally, the Crested Newt adults are moving up to 15 m from a pond, but juveniles can move several hundreds of meters (Jehle and Arntzen, 2000; Müllner, 2001).

Arntzen et al. (1997) suggested that the western and eastern ranges might be connected along the Danube river through the Iron Gate Canyon, but the lack of *T. dobrogicus* records from that region does not support this assumption. Interestingly, the Iron Gate region was identified as a hotspot of sampling effort in amphibian research in Romania (Cogălniceanu et al., 2013), yet no studies reported *T. dobrogicus* in that region (e.g. Cogălniceanu et al., 2013; Covaciu-Marcov et al., 2009; Iftime, 2005; Sahlean et al., 2008). Our goals were (1) to estimate the dispersal ability of the Danube Crested Newt and the connectivity (via corridors) between populations across its range; and (2) to identify possible pathways used by this species to cross the Carpathian Mountains and maintain gene flow between the eastern and western range populations. We used a landscape resistance raster specifically built for the Danube Crested Newt, comprising geomorphological characteristics to which the species may be highly sensitive due to ecological adaptations that shaped its distribution (Arntzen et al., 1997).

2. Materials and methods

2.1. Study area

The study area covered 1.5 million km^2 in central and eastern Europe, representing the known distribution of the Danube Crested Newt (Fig. 1) (Arntzen et al., 1997; Gherghel and Iftime, 2009; Litvinchuk, 2005; Litvinchuk and Borkin, 2000). The landscape in the region comprises mountains (Carpathian, Balkan, and Tatra Mountains) and plains (Pannonian, Romanian, and the western part of Eastern European Plain), the plateaus occupying only a small portion, in the eastern part of the region (e.g., Moldavian Plateau and Dnieper Upland; Fig. 1). The main hydrographic network is represented by the Danube river and its major tributaries (Sava, Drava, Tisa, Olt, Siret, and Prut), and in smaller proportion by other drainage basins like Dnieper, Dniester, or Vistula (Fig. 1). The Danube river floodplains with marshes and flooded forests represent the primary suitable habitat for the Danube Crested Newt (Arntzen, 2003; Arntzen et al., 1997). However, in the Carpathian Mountains, the Danube River passes through the narrow Iron Gate Canyon that does not hold suitable habitat for the Danube Crested Newt due to the high slopes of the canyon (up to 90 degrees) and lack of flooding riparian area. As such, the species' range is divided into two regions, east and west of the Carpathian Mountains (Fig. 1).

2.2. Occurrence records

A total of 586 Danube Crested Newt records were gathered from the scientific literature (Appendix 1) and field observations from Romania (I.G.) and Hungary (Voros, pers. comm.), spanning from 1905 to 2013. The general survey methods used to identify newts were direct observation, pit-fall traps, or netting. The sampling covered the entire known range of the Danube Crested Newt. Of the initial set of occurrences, we retained only the records with location accuracy of at least 1 km in order to match them with the resolution of environmental data used in the analysis, thus each occurrence corresponded to one pixel (cell) in the landscape data. The final dataset used in the analysis consisted of 221 unique occurrences, of which 61 were identified as *T. d. dobrogicus* and 155 were identified as *T. d. macrosoma*.

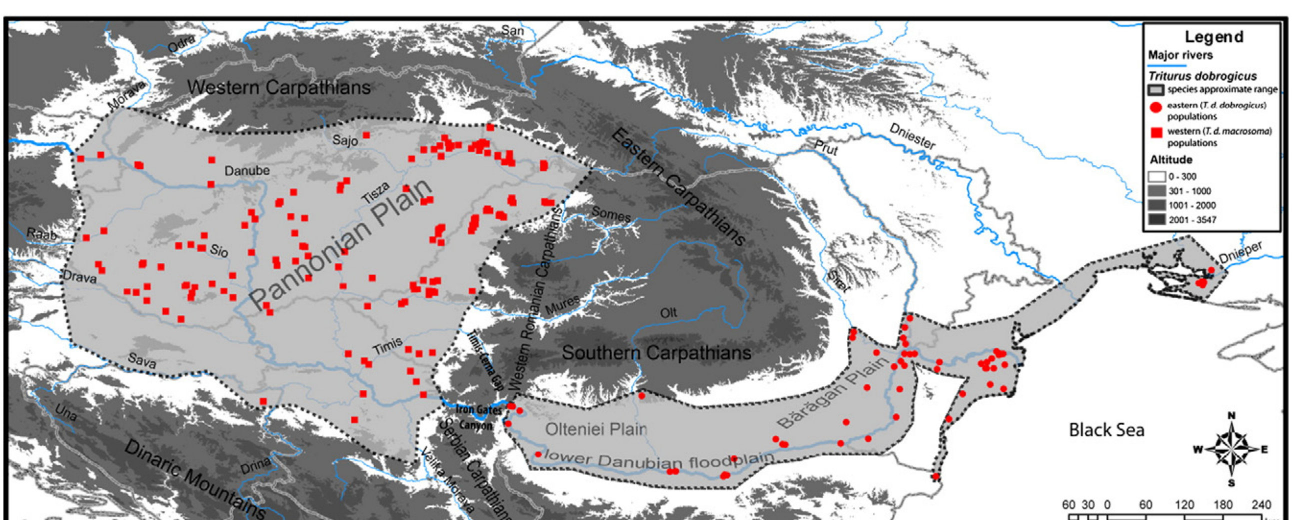

Fig. 1. The eastern and western ranges of the Danube Crested Newt (*T. dobrogicus*), with known records of the two populations, relief, and geographic features in the studied region.