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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*.

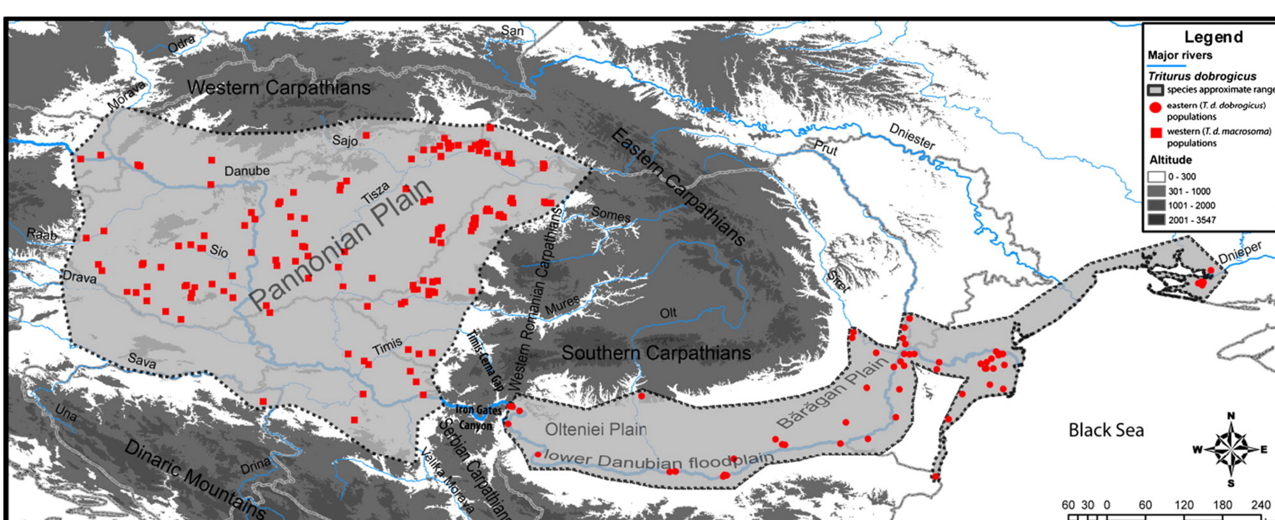

Fig. 1. The eastern and western ranges of the Danube Crested Newt (*T. dobrogicus*), with known records of the two populations, relief, and geographic features in the studied region.

2.3. Landscape data

Our overall approach to estimate the potential dispersal of *T. dobrogicus* was based on Geographic Information Systems (GIS) cost distance analysis methodology, using species' known records and landscape features (altitudes <300 m ASL and flat terrain) that represent suitable topographical characteristics for the species. We employed a cost distance model to test the landscape permeability to the species' dispersal out of known population locations. The general assumption of the cost distance model is that the landscape friction increases with the geographical distance traveled and is dependent on the surface type (Adriaensen et al., 2003). Corridors and least cost dispersal paths were tested by running multiple analyses from western source populations to eastern target populations, and from eastern source populations to western target populations. All analyses were processed in ArcGIS 10 using Spatial Analyst Tools package (ESRI, 2011a).

The cost distance analysis tool in ArcGIS calculates resistance of different landscape features to species' movement (i.e., dispersal) from source points (species' occurrences) to the edge of the studied area based on a resistance raster (ESRI, 2011b). In our case, the resistance raster represented the elevation and slope of the terrain, the latter having a direct impact on formation of ponds used by newts in reproduction (Arntzen, 2003). Slope was derived from a digital elevation model (DEM) at 1 km resolution, downloaded from WorldClim database (Hijmans et al., 2005). Our goal was to produce a general cost distance model based on terrain features only, since vegetation features are highly dynamic and the Danube river floodplain changed dramatically in the past century, mostly due to anthropogenic factors.

Based on expert opinion (I.G.; Strugariu, Sahlean, Zamfirescu pers. com.) and published information (Arntzen, 2003; Arntzen et al., 1997) regarding suitable factors for the studied species, the elevation variable was reclassified in four categories (-5 – 300 m ASL, 301 – 1000 m ASL, 1001 – 2000 m ASL, and above 2000 m ASL) and the slope variable in three categories (flat, medium, and steep inclination). We considered these two variables as limiting the distribution of the Danube Crested Newt because the interaction between the two determines the species' suitable habitats (Arntzen, 2003; Arntzen et al., 1997). After reclassification, we merged the topography and slope in a resistance raster to use in our subsequent analysis.

2.4. Cost-distance and corridor analyses

Prior to computing the cost distance analysis, we randomly selected 10% of the occurrence points for thresholding the cost distance model. After we generated the cost distance model with 90% of occurrence data, we sampled the model using the remaining occurrence data and categorized the landscape in three dispersal categories: 1) low resistance to dispersal (below maximum value of cost raster associated with the testing points), 2) moderate resistance to dispersal (equal to maximum value of cost raster associated with the testing points) and 3) potentially impermeable to dispersal (above maximum value of cost raster associated with the testing points). These thresholds allowed us to make predictions about the dispersal ability of Danube Crested Newt within the landscape. All analyses were computed for the entire species and for the western and eastern regions separately.

To identify corridors most likely to be used by the Danube Crested Newt to cross the Carpathian Mountains, we used the Corridor function in ArcGIS Toolbox to calculate the sum of the accumulative cost values (see ESRI, 2011b for details) of cost rasters of eastern and western species' ranges. These cost values represented the least cost path of dispersal over the Carpathians from the eastern and western regions. After generating the corridor model, we used all occurrence points of Danube Crested Newt to extract the corresponding corridor model values and classified the model output in one of three categories: high corridor probability (lowest corridor model value to the third quartile associated with occurrence points), moderate corridor probability (third quartile to maximum value) and low corridor probability (maximum value of the corridor model associated with occurrence points). These corridors approximate the permeability between east and west ranges, according to landscape resistance and distance between known occurrences.

Finally, we identified potential routes that linked each occurrence in the western range and eastern range by running the analysis in both directions (west-east and east-west). For this purpose, we used the cost raster and the direction of movement (the backlink raster) in Cost Path tool in ArcGIS Toolbox and we ran 221 path analyses, for each available occurrence point. The cost paths were summed in order to indicate the major dispersal routes between ranges and within a range.

3. Results

We created a dispersal model to evaluate the potential landscape resistance for the Danube Crested Newt (Fig. 2). We found that in the western range, the landscape would permit connectivity between 91% of the occurrences, the rest of them being potentially separated by areas that are moderately difficult to disperse through (shown in green, Fig. 2). In the eastern part of the species range, the least resistance to dispersal between most of the occurrences (77%) is along the Lower Danube, Bărăgan Plain, and Lower Siret Plain, to Danube Delta. However, 23% of the occurrences are potentially isolated from the rest of the range, most notably the occurrences west of Olt river, Dnieper Delta, and Durankulak Lake. All these occurrences are separated by areas that, according to our model, are potentially impermeable to dispersal (shown in white and gray, Fig. 2).

The corridor model identified areas more likely to permit dispersal between eastern and western ranges, specifically Iron Gate Canyon and valleys of Timiş and Cerna rivers (Timiş - Cerna Gap; Figs. 1 and 3). When we employed route simulations through the Cost Path analysis, using each occurrence as an independent point, we found that 55% of them are most likely to be connected through the Iron Gate Canyon corridor and 45% of them through the Timiş – Cerna Gap. No other dispersal route across ranges was identified through simulations. Our results suggest that the Danube river is a dispersal corridor between eastern and western species' ranges for 91% of occurrences, with additional low resistance dispersal routes in the eastern range through Bărăgan and Romanian Plains. In the case of Dnieper Delta occurrences, our model identified western Black Sea coast and lagoons as the most likely corridors. In the western range we found no visible pattern west of the Carpathian Mountains. Most of the corridors are straight lines to the target population, suggesting low resistance to dispersal of the species across Pannonian Plain (Figs. 1 and 3).

4. Discussion

Geographical barriers break the connectivity between populations, however, individuals find dispersal corridors and occupy the available suitable habitat on the landscape. In the case of animals with low dispersal ability (like most reptiles and amphibians) or habitat specialists (like the Danube Crested Newt), finding these corridors can be challenging. Arntzen et al. (1997) suggested that exchanges between eastern and western ranges of Danube Crested Newt occurred via the Iron Gate Canyon, however, no evidence was provided to support this assumption. Recent genetic analyses (Voros and Arntzen, 2010; Wielstra et al., 2013) found very little or no difference between eastern and western range populations of Danube Crested Newt, supporting the hypothesis of a continuous gene flow between populations, despite the presence of the Carpathian Mountains as a barrier. However, the lack of further studies and evidence regarding dispersal routes precluded assessments of potential corridors used by Danube Crested Newts. Our study analyzed the landscape permeability to species' dispersal across the Carpathian Mountains and identified possible corridors among populations, both within and between the eastern and western ranges.

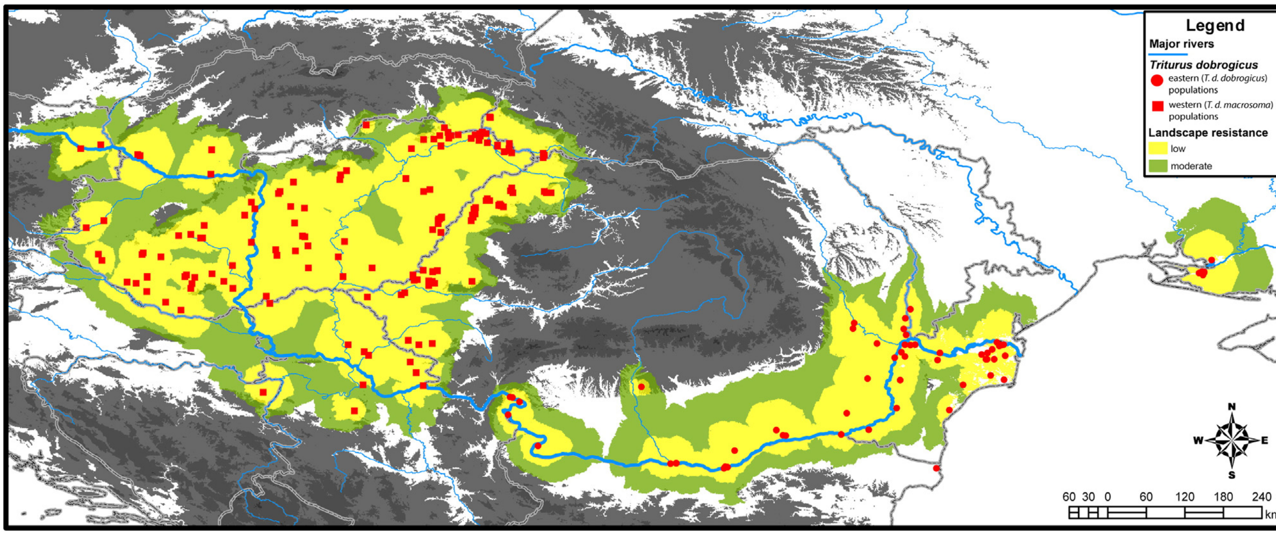

Fig. 2. Landscape resistance and population connectivity between Danube Crested Newt populations, with known records of the two populations (red) and the relief (gray) in the studied region; impermeable surfaces (white and gray) represent the remaining landscape.

4.1. Landscape resistance and connectivity

According to our models, the eastern part of Danube Crested Newt's range is fragmented in three clusters that contain most of the known occurrences. The largest cluster, comprising most of the occurrences, is located in the Danube river floodplain, between Olt river and Danube Delta. The rest of the Romanian Plain was indicated by our model as having high levels of landscape resistance due to the mid-high slopes that make dispersal difficult for the Danube Crested Newt. In addition, the Northern Crested Newt (*T. cristatus*) is also present in the Romanian Plain (Cogălniceanu et al., 2013) and complicates the dispersal of the Danube Crested Newt due to competition (Arntzen, 2003; Arntzen et al., 1997). However, in the Bărăgan Plain, our dispersal resistance model suggests little landscape resistance to the Danube Crested Newt dispersal. Our models also suggest that, west of Olt river (in the southern part of the Olteniei Plain), the landscape resistance is very high. Consequently, the connectivity between the occurrences is low, creating a second cluster, between the Olt river and the Carpathian Mountains (Figs. 1 and 2). Moreover, no records of Danube Crested Newts are known from that region, on either side of the Danube (Cogălniceanu et al., 2013; Tzankov and Stoyanov, 2008), lending support to our findings. The third cluster of occurrences is located around Dnieper Delta and appears to be completely isolated from the rest of the species range. Our dispersal resistance model suggests significant gaps and little connectivity between these occurrences and the rest of the species' eastern range (Fig. 2).

In the western range of the species we observed different patterns compared to the eastern range: we did not identify large gaps, as only a few occurrences were separated by moderate landscape resistance from the cluster that comprises most of the occurrence points (Fig. 2). The less fragmented distribution patterns in the western range can be explained by lower slope values than in the eastern range, thus lower landscape resistance.

4.2. Dispersal corridors and route patterns

Our results clearly support Arntzen et al. (1997) hypothesis that the Danube Crested Newt used the Iron Gate Canyon to cross the Carpathian

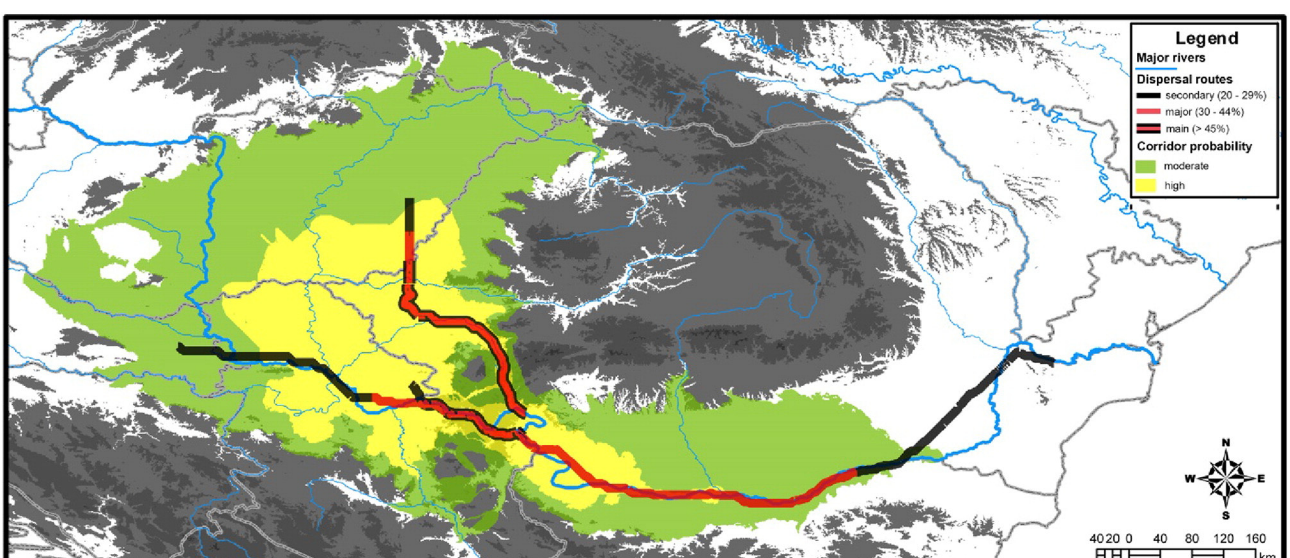

Fig. 3. Possible dispersal corridors used by the Danube Crested Newt to cross the Carpathian Mountains and main routes connecting known occurrences. The relief of the study area is shown in grey. Route classes (secondary, major, main) are based on the percent of occurrences that are connected via routes identified.

Mountains from Lower Danube floodplain to Pannonian Plain and/or vice versa. In fact, our models suggested that 55% of all populations are connected through the Iron Gate Canyon. However, the Iron Gates Canyon is the site of a reservoir with the same name, built over four decades ago, which makes the region unsuitable for the Danube Crested Newt due to its topography that does not support formation of reproduction ponds. The landscape of the reservoir area does not comprise suitable topography and habitat for the Danube Crested Newt. The slopes are very steep and this prohibits floodplain formation, the suitable habitat for this newt species; within the reservoir itself, the species has never been reported, and we presume it absent or probably exposed to high fish predation. In addition, we found that from a coarse landscape perspective, Timiş – Cerna Gap could also represent a suitable dispersal route over the mountains to or from the northern part of the Pannonian Plain for 45% of the occurrences (Fig. 3). However, despite the very high amphibian sampling effort in the areas suggested by our models as corridors for Danube Crested Newt, neither this nor its sister species, the Northern Crested Newt, have been found (Cogălniceanu et al., 2013). Moreover, in the broader region of Banat Mountains, the Northern Crested Newt has been recorded only in four locations (Cogălniceanu et al., 2013). This might suggest that the competition between Northern Crested Newts and Danube Crested Newt is very low in the region, and even currently, the latter could use this migration corridor (Fig. 3).

4.3. Alternative dispersal hypothesis

Besides active dispersal, some species are dispersed passively, commonly by water transportation (rivers, streams) of seeds, eggs or larvae (Leuven et al., 2009; Rempel and Smith, 1998; Säumel and Kowarik, 2010). This passive dispersal could also be possible for the Danube Crested Newt since individuals remain in reproduction ponds for up to 6 months, sometimes until winter (Litvinchuk et al., 1997), and their larvae metamorphosis can occur as late as September or October (Jehle et al., 1997). This time span coincides with the Danube river water level peak and seasonal floods, especially in spring and summer (e.g. Peršić and Horvatić, 2011; Tockner et al., 1999; Zehetner et al., 2008). Consequently, when the Danube river experiences its highest water levels, it floods the wetlands in which the Danube Crested Newts reproduce, thus eggs, larvae or adults could be carried from western to eastern ranges, in the direction of Danube river flow.

4.4. Concluding remarks

Our models clearly show that even when a species' distribution is separated in two ranges by a geographical barrier (presumably allopatric), corridors between populations still exist, hence, possibly allowing gene flow. We also show that, even at a coarse resolution, corridors can be estimated and dispersal resistance of the landscape measured, especially if the model species has ecological limitations highly correlated with distribution (such as Danube Crested Newt, e.g. Arntzen, 2003; Arntzen et al., 1997). We suggest using these coarse landscape features (elevation and slope) as variables in studies of similar species. However, as a limitation of our analysis, if the models overlap with a river, it is very difficult to assess whether the species uses the corridor in a passive or active way, as we discussed in the case of the Danube Crested Newt that most likely used both strategies. We suggest that future sampling efforts could concentrate along the two corridors identified through our analysis (Iron Gate Canyon and Timiş – Cerna Gap), in habitats specific for the Danube Crested Newt (swamps, marshes, flooded riparian areas, and plains). In addition, these models can be extrapolated to other species, such as the Fire-bellied Toad (*Bombina bombina*), that use the same reproduction ponds as the Danube Crested Newt, assuming there are similar dispersal scenarios between the species (as was suggested by Arntzen et al., 1997).

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Appendix 1. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.ecoinf.2015.03.005.

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