available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/biocon

A multi-scale approach to facultative paedomorphosis of European newts (Salamandridae) in the Montenegrin karst: Distribution pattern, environmental variables, and conservation

Mathieu Denoël[a,*], *Gentile Francesco Ficetola*[b], *Ruža Ćirović*[c], *Dejan Radović*[d], *Georg Džukić*[e], *Miloš L. Kalezić*[d,e], *Tanja D. Vukov*[e]

[a]*Laboratory of Fish and Amphibian Ethology, Behavioural Biology Unit, University of Liège, 22 Quai van Beneden, 4020 Liège, Belgium*
[b]*Department of Environmental Sciences, University of Milano-Bicocca, Piazza della Scienza 1, 20126 Milano, Italy*
[c]*Republic Institute for the Protection of Nature, Trg Vojvode Bećir-Bega Osmanagića 16, 81000 Podgorica, Montenegro*
[d]*Institute of Zoology, Faculty of Biology, University of Belgrade, Studentski trg 16, 11000 Belgrade, Serbia*
[e]*Institute for Biological Research "Siniša Stanković", University of Belgrade, Bulevar despota Stefana 142, 11060 Belgrade, Serbia*

ARTICLE INFO

Article history:
Received 14 June 2008
Received in revised form
4 November 2008
Accepted 16 November 2008
Available online 1 January 2009

Keywords:
Amphibian decline
Conservation
Dimorphism
Ecological determinants
Invasive species
Landscape ecology

ABSTRACT

Facultative paedomorphosis, a process in which newt larvae can opt for reproduction before or after metamorphosis, is geographically heterogeneous. Despite numerous ecological studies and recent evidence of declines in paedomorphic populations, however, no attempt to model environmental variables that explain the presence of paedomorphs has been made at a multi-scale level. Our aim was to fill this gap in studying three newt species (*Lissotriton vulgaris*, *Mesotriton alpestris*, and *Triturus macedonicus*) of the Montenegrin karst as model species. To this end, we used multivariate analysis on three scales of habitat: the breeding pond, the land use and the climatologic features. Results show that the study area is both an important hotspot for paedomorphosis and where intraspecific diversity is quickly disappearing (20–47% extirpation) because of fish introductions. Other habitat variables (water permanency, pH or the habitat origin) were shown to act on paedomorphosis but not consistently across species, confirming complexity of the evolutionary and ecological processes. This study appeals for more long-term and detailed landscape studies of polyphenisms, a neglected but promising topic, to better understand and protect alternative modes of development. Particularly, measures should be taken to identify hotspots of intraspecific diversity at a global scale and stop fish introductions before we reach a point of no-return.

1. Introduction

Facultative paedomorphosis occurs in many tailed amphibian species; larvae either metamorphose into terrestrial adults or attain sexual maturity while retaining larval morphology (e.g. external gills and gill slits) (e.g. Semlitsch and Wilbur, 1989; Denoël et al., 2005a). The appearance and maintenance of alternative adult phenotypes is based on genotype

* *Corresponding author:* Tel.: +32 4 3665084; fax: +32 4 355113.
E-mail address: Mathieu.Denoel@ulg.ac.be (M. Denoël).
0006-3207/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2008.11.008

–environment interactions experienced by larvae and paedomorphs, which can retain the ability to metamorphose (for the most recent review, see: Denoël et al., 2005a). Particularly, mesocosm experiments showed that paedomorphosis was selected in permanent waters and at low density (Harris, 1987; Semlitsch, 1987).

Several field studies examined habitat characteristics of paedomorphic and metamorphic populations. Among possible determinants of developmental alternatives, streambed structures, and permanency of water (Semlitsch, 1987; Bennett and Chippindale, 2006) as well as the harshness of the terrestrial environment (Wilbur and Collins, 1973; Healy, 1974; Sprules, 1974a,b) were outlined. Paleontological studies also suggested the importance of global cooling for the success of paedomorphs (Roček, 1995). However, the presence of paedomorphs in a large variety of water bodies indicates a multifactorial nature of the environmental context of the expression of the polyphenism (Sprules, 1974b; Semlitsch, 1987; Breuil, 1992; Whiteman, 1994; Denoël et al., 2001). For instance, Collins (1981) did not find significant habitat variables to distinguish between alternative morphs for elevation or landscape traits and Denoël (2006) found often paedomorphs in semi-permanent waters.

Advancements of statistical tools, specifically multivariate modeling and complex spatial procedures (see e.g. Mazerolle, 2006), have allowed a large number of studies that focused on the landscape and other habitat determinants of amphibians (e.g. Joly et al., 2001; Van Buskirk, 2005; Denoël and Ficetola, 2007) to emerge. Multiple spatial scales can be particularly important to understand the ecological determinants of amphibian distribution (Denoël and Lehmann, 2006; Murray et al., 2008). Despite this, studies have all focused on interspecific diversity. It is thus unknown whether polyphenisms such as facultative paedomorphosis could be affected at various scales by climate, landscape and breeding site features. Such determination is of primary importance to understand the success of alternative developmental pathways in the field.

Understanding distribution of different alternative morphs and their relationship with environmental features is an essential pre-requisite to determine their status and provide efficient conservation measures. Although amphibian conservation has been the target of many studies (Collins and Storfer, 2003; Stuart et al., 2004), paedomorph conservation remains little explored (Whiteman and Howard, 1998; Ćirović, 2005; Denoël et al., 2005b; Denoël, 2007). Much remains to be done, such as identifying hotspots for paedomorphosis, as well as proximate and ultimate causes of this process. The Montenegrin karst area, a restricted part of the Dinaric Alps is already appreciated as a recognizable center of facultative paedomorphosis with populations composed of metamorphs and paedomorphs of three different species (Džukić et al., 1990; Breuil, 1992; Denoël et al., 2001; Ćirović, 2004).

The objective of this study was to survey the water bodies of Montenegro to determine the occurrence and distribution of alternative developmental morphs and to seek environmental characteristics related to paedomorphosis in three newt species at three scales: the breeding aquatic site, the land use and the local climatic characteristics, using analytical tools allowing to take into account the complex spatial structure of data. Moreover, distribution of paedomorphic populations have changed in time (i.e., some populations disappeared). We therefore evaluated environmental features affecting changes in distribution of paedomorphic populations. This allowed testing the effect of environmental change on the distribution of morphs.

2. Materials and methods

2.1. *Sampling procedure*

The research was carried out between 1970 and 2005 (mainly 2000–2005) at 145 breeding sites in the Montenegrin karst (Fig. 1). Our surveys covered an area of about 10 080 km^2. Most of the breeding sites (90%) were visited for at least two breeding seasons. Visual Encounter Survey (VES; Crump & Scott, 1994) was the most frequently used technique throughout the study. VES are effective in most habitats and for the study species, which breed in lentic water. Each aquatic site was surveyed for at least 45 min. Most newts were identified by sight (*Triturus macedonicus*, *Lissotriton vulgaris*, and *Mesotriton alpestris*; these newts were previously named *T. carnifex*

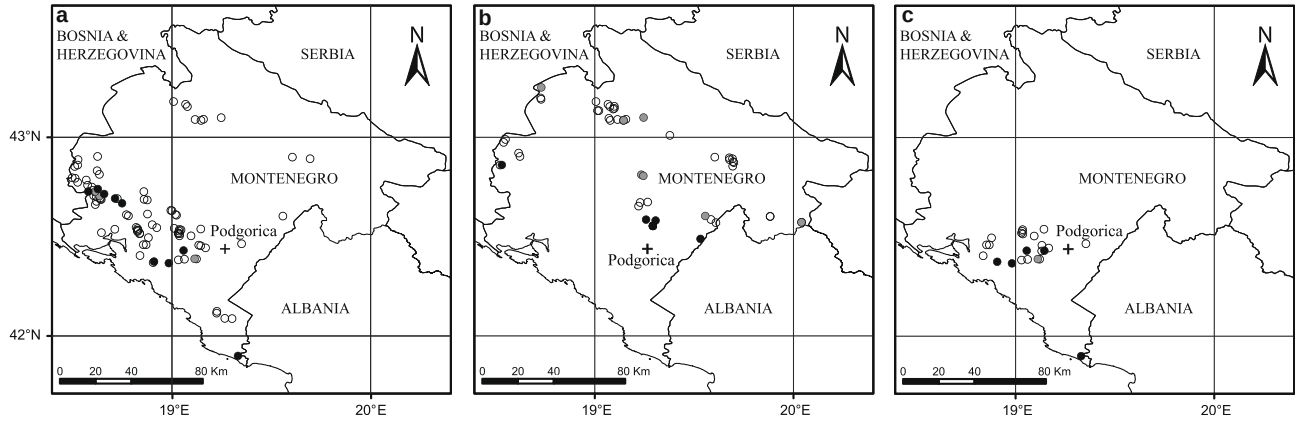

Fig. 1 – Distribution of populations with facultative paedomorphosis and only metamorphosis in the Montenegrin karst in (a) *Lissotriton vulgaris*, (b) *Mesotriton alpestris*, (c) *Triturus macedonicus*. Full circles: presence of paedomorphs; grey circles: extirpation of paedomorphs after fish introduction; open circles: absence of paedomorphs, presence of metamorphs.