Zoologischer Anzeiger 252 (2013) 350–358

Contents lists available at SciVerse ScienceDirect

Zoologischer Anzeiger

journal homepage: www.elsevier.de/jcz

Zoologischer Anzeiger

Unexpected life history traits in a very dense population of dice snakes

Rastko Ajtić[a], Ljiljana Tomović[b,c], Bogoljub Sterijovski[d], Jelka Crnobrnja-Isailović[c,e], Sonja Djordjević[b], Marko Djurakić[f], Ana Golubović[b], Aleksandar Simović[b], Dragan Arsovski[d], Marko Andjelković[b], Milivoj Krstić[b], Goran Šukalo[g], Sladjana Gvozdenović[h], Aurelie Aïdam[i], Catherine Louise Michel[i], Jean-Marie Ballouard[i,j], Xavier Bonnet[i,*]

[a] *Institute for Nature Conservation of Serbia, Dr Ivana Ribara 91, 11070 Belgrade, Serbia*
[b] *Institute of Zoology, Faculty of Biology, University of Belgrade, Studentski trg 16, 11000 Belgrade, Serbia*
[c] *Institute for Biological Research "Siniša Stanković", University of Belgrade, Bulevar Despota Stefana 142, 11000 Belgrade, Serbia*
[d] *Macedonian Ecological Society – herpetology group, Bulevar "Kuzman Josifovski-Pitu" 28/3-7 1000 Skopje, Macedonia*
[e] *Department of Biology and Ecology, Faculty of Natural Sciences, University of Niš, Višegradska 33, 18000 Niš, Serbia*
[f] *Department of Biology and Ecology, Faculty of Natural Sciences, University of Novi Sad, Trg Dositeja Obradovića 2, 21000 Novi Sad, Serbia*
[g] *Department of Ecology and Environmental Protection, Biology, Faculty of Science, University of Banja Luka, Mladena Stojanovića 2, Banja Luka, Bosnia and Herzegovina*
[h] *Department of Biology, Faculty of Natural Sciences and Mathematics, University of Montenegro, Džordža Vašingtona bb, Podgorica, Montenegro*
[i] *CEBC-CNRS, 79360, Villiers en Bois, France*
[j] *CRCC-SOPTOM, Center of Research and Conservation of Chelonians, 83590, Gonfaron, France*

ARTICLE INFO

Article history:
Received 13 April 2012
Received in revised form
27 September 2012
Accepted 4 October 2012
Available online 27 November 2012
Corresponding Editor: Julia A. Clarke.

Keywords:
Juveniles
Macedonia
Mark recapture study
Mortality
Natural history
Colour polymorphism
Population density
Predation
Reproduction
Sexual dimorphism
Snake

ABSTRACT

A population of dice snakes (*Natrix tessellata*) monitored since 2008 in a small island (18 ha, 850 m a.s.l., FYR of Macedonia) revealed unforeseen patterns for snakes living in temperate climates. More than 5000 individuals have been marked and the density is one of the highest ever recorded (>500 resident snakes per hectare). Reproductive and mortality rates are elevated, suggesting a high population turnover. These traits evoke a tropical rather than a temperate-climate ophidian demographic system. The population is highly polymorphic, three colour morphs (dotted, grey, and black) are observed in both sexes and each morph is represented by large numbers of individuals. This polymorphism pattern was not previously documented in snakes. Data obtained for other life history traits (e.g. body size, size at maturity, clutch size, diet, predation) markedly diverged in comparison to available information. Overall, our results reinforce the notion that the strong inter-population variability (often mediated by phenotypic plasticity) of snakes should be taken into account over large geographic scales; otherwise attempts to derive general patterns may well be strongly biased.

1. Introduction

The mechanisms underlying life history trait diversity among individuals and populations encompass a wide array of processes from morphological modifications occurring during early development to physiological and behavioural adjustments that take place after birth (Gerhardt and Kirschner, 1997; Dingemanse et al., 2010). These variations include both adaptive and non-adaptive responses: a phenotypic trait can be accidentally altered (e.g. due to a disease) or may result from the ability of an organism to change its phenotype to match environmental constraints (adaptive plasticity). These processes occupy a central place in evolutionary and applied ecology (Pigliucci, 2001; Reed et al., 2011). Therefore it is important to document phenotypic variations between individuals, across populations, and ultimately to disentangle the respective contributions of the different sources of phenotypic variations. This notion applies with force in highly polymorphic or plastic species where most life history traits respond to environmental conditions.

* Corresponding author.
E-mail addresses: rastko.ajtic@zzps.rs (R. Ajtić), lili@bio.bg.ac.rs (L. Tomović), sterijovski@mes.org.mk (B. Sterijovski), jelka@ibiss.bg.ac.rs (J. Crnobrnja-Isailović), sonjadj@bio.bg.ac.rs (S. Djordjević), marko.djurakic@dbe.uns.ac.rs (M. Djurakić), lunja975@yahoo.com (A. Golubović), alexandar.simovic@gmail.com (A. Simović), andjelkovicmarkomare@gmail.com (M. Andjelković), sukalogoran@yahoo.com (G. Šukalo), sladjana87gvozdenovic@yahoo.com (S. Gvozdenović), jean-marie.ballouard@cebc.cnrs.fr (J.-M. Ballouard), bonnet@cebc.cnrs.fr (X. Bonnet).

0044-5231/$ – see front matter © 2012 Elsevier GmbH. All rights reserved.
http://dx.doi.org/10.1016/j.jcz.2012.10.001

Snakes exhibit considerable variations in response to environmental factors. For instance, within species, body size, sexual size dimorphism, head morphology, diet, and reproductive output are highly variable (Ford and Seigel, 1989; Madsen and Shine, 1993; Bronikowski and Arnold, 1999; Bonnet et al., 2001; Shine, 2003). Experimental investigations showed that a great part of these variations is expressed through phenotypic plasticity; however, underlying genetic components are also involved (Bronikowski, 2000; Aubret et al., 2004; Manier et al., 2007). Numerous field studies documented strong differences among nearby populations; in most cases, variations of prey abundance, prey size, and climatic conditions determined an important proportion of the variability in snake's life-history traits (e.g. Seigel and Ford, 1991; Madsen and Shine, 1993; Aubret and Shine, 2009; Tanaka, 2010). Overall, encompassing phenotypic diversity across disjunct populations is essential to accurately describe, and thus to better understand the ecology of snakes.

The present study focuses on the dice snake (*Natrix tessellata*), a species that offers several advantages to examine the issues exposed above. This amphibious species is distributed over an extremely extended geographic area, from Italy to China, and occupies a very wide variety of habitats (distribution range spreads over >5500 km east-west; Bannikow et al., 1977; Gruschwitz et al., 1999). However, current ecological information is limited to the most western parts of the species' range, notably Italy (Luiselli and Zimmermann, 1997; Luiselli and Rugiero, 2005; Luiselli et al., 2007, 2011), Switzerland (Metzger et al., 2009), and Germany (Lenz and Gruschwitz, 1993). Preliminary reports from other areas nonetheless suggest that this species might be polymorphic (Jelić and Lelo, 2011; Göçmen et al., 2011; Velensky et al., 2011). This study aimed to examine if a peculiar ecological situation is associated with a shift (if any?) of major life history traits. Intuition indeed suggests that peculiar habitats should shape individuals and population functioning in particular way. We targeted a very dense population that occupies a small island (Golem Grad) situated in an altitude lake (FYR of Macedonia; Sterijovski et al., 2011) where the habitat and the climatic conditions are strongly divergent compared to previous studies that were essentially performed in low altitude and/or river populations in Western Europe. In addition, insularity deeply influences a wide range of life history traits, notably through dietary, predation, and density dependent processes (Bonnet et al., 1999; Boback, 2003; Buckley and Jetz, 2007; Aubret and Shine, 2009). As our study population accumulates a set of unusual characteristics, cool climatic region, high population density, and insularity (Sterijovski et al., 2011), we expected strong shifts in morphological and ecological traits.

We further emphasize that focusing on unusual ecological context is important for comparative studies. Indeed, in ectotherms, constraining environmental conditions such as cool climates and high population density limit prey availability, foraging activity, digestion, and reproduction. Consequently, it is expected that mean body size, fecundity and population turnover should exhibit lower values in dense populations from high latitudes in comparison to warmer areas (e.g. central Italy). More generally, there is a trend for increasing body size across populations and species with latitude (Ashton and Feldman, 2003). There is no simple climatic correspondence between elevation and longitude, however given the relatively high elevation of our study site (~850 m a.s.l.) we expected patterns that characterize populations living in cool climate. Although local adaptation and other factors (e.g. trophic resources) influence life history traits, we predicted that the environmental conditions that prevail at relatively high altitude would entail low growth rate, small average body size, low fecundity, and low reproductive rate, and possibly longer life span in comparison to populations living in less constraining climatic areas (Blouin-Demers et al., 2002).

Our main field objectives were to describe the main life history traits (e.g. population structure, mean body size, fecundity) of the dice snakes from Golem Grad, and to examine if they were divergent compared to previous ecological reports based on data gathered in different ecological situations.

2. Materials and methods

2.1. Study species

The dice snake (*Natrix tessellata*), a medium-sized oviparous species (Bruno and Maugieri, 1990), occupies an extremely wide distribution range from Italy towards the Middle East, the Nile Delta and extending to the east across central Asia to China (Bannikow et al., 1977; Gruschwitz et al., 1999). The diced-colouration of the species is typical: both vernacular and Latin names refer to the dorsal mosaic pattern formed by a network of dots (i.e. tesselles). This amphibious snake forages in water in search of different species of fish and amphibians, but comes on land for thermoregulation, digestion, reproduction, and skin sloughing. Populations are found near lakes, streams, rivers, and on small marine islands near estuaries.

Several genetic and narrow-focused morphological investigations (e.g. occurrence of abnormal scales; Herczeg et al., 2005) have been performed in different parts of its distribution range (Ioannidis and Bousbouras, 1997; Gautschi et al., 2002; Acipinar et al., 2006; Guicking et al., 2007). Field studies provided information on population size, diet, and on several other life history traits (e.g. mean body size, predation, reproduction; Metzger et al., 2009; Capula et al., 2011; Carlsson et al., 2011); however, variations of life history traits (morphology, ecology) among populations have not been assessed yet.

Previous research suggests that the mating season takes place from March to June and that clutch size varies from 4 to 29 eggs, with a mean value of 14 ± 8 (Luiselli and Rugiero, 2005; Carlsson et al., 2011). Laying period is virtually unknown. Inter-population differences in diet have been recorded (Luiselli et al., 2007), suggesting that other life history traits, notably those driven by food availability, may also diverge among populations, especially over larger geographic ranges.

2.2. Study area

Golem Grad Island (N 40°52′08″; E 20°59′23″) is located in the Prespa Lake (National Park Galičica, FYR of Macedonia). The other well studied population where ecological and morphological data are available (Luiselli et al., 2007) is situated in central Italy, less than 2.5° south and at a low altitude ~250 m a.s.l) whereas Prespa lake is situated at relatively high altitude (~850 m a.s.l., not an extreme elevation as snakes occur above 3500 m a.s.l. in Europe). The lake covers a large surface (~254 km^2, mean depth ~ 14 m [maximum 48 m]) and is surrounded by high mountains (above 2.000 m a.s.l; Matzinger et al., 2006). The climate of the area is classified as humid-cool-Mediterranean type (Hollis and Stevenson, 1997).

The island (~18 ha) is oval with narrow shores and a plateau delimited by vertical cliffs (10–30 m). The shores are mainly colonized by bushes (*Rosa dumalis*, *Rubus ulmifolius*, *Ephedra campylopoda*, *Asparagus acutifolius*) and small trees (*Prunus mahaleb*, *Prunus cerasifera*, *Ficus carica*, *Ostrya carpinifolia* and *Fraxinus ornus*). The plateau is dominated by a forest of large juniperus trees (*Pruno webbii-Juniperetum excelse* association; Em, 1965). Dice snakes are found everywhere on the island, although they are more abundant on the shores. The ichthyofauna of the waters surrounding Golem Grad consists of 23 species (Crivelli et al., 1997). Two