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

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.

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 km², 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

Table 1
Vertebrate species observed in Golem Grad and in the surrounding water (<100 m offshore), which present potential predators or prey to dice snakes (Potential status). Some species are endemic to the area (E), others have been introduced (A). The abundance index refers to the fact that the species was easily observed, not to real population size estimates. "High" means that the species (or evidence of its presence, e.g. faeces, tracks etc.) can be observed at any time during the active season, sometimes in large numbers. "Common" means that the species was observed several times per week. "Rare" means that the species was not observed every year, and was always in small numbers ($N < 5$).

Potential status	Broad taxon	Species	Endemic/allochtonous	Abundance
Prey	Fish	*Barbus prespensis*	E	Unknown
		Alburnus belvica	E	High
		Chondrostoma prespensis	E	Unknown
		Cobitis meridionalis	E	Unknown
		Alburnoides bipunctatus prespensis	E	Unknown
		Paraphoxinus epiroticus prespensis	E	Unknown
		Rhutilus ohridanus prespensis	E	Unknown
		Carassius auratus	A	Unknown
		Pseudorasbora parva	A	Unknown
		Lepomis gibbosus	A	Common
		Leuciscus cephalus		Unknown
		Rhodeus amarus		Unknown
	Amphibian	*Bufo viridis*		Rare
		Rana ridibunda		Rare
Predator	Reptile	*Vipera ammodytes*		High
	Bird	*Bubo bubo*		2 pairs
		Accipiter gentilis		Common
		Buteo buteo		Common
		Ardea cinerea		Common
		Larus sp.		High
	Mammal	*Lutra lutra*		High

amphibian species occur on the shores. These vertebrates represent potential prey to the dice snakes (Table 1). Golem Grad also shelters various avian, mammalian and reptilian species that might potentially feed on dice snakes (Table 1).

2.3. Field procedures

In spring 2008, we set up a capture-mark-recapture study. The population was monitored in spring and summer during four years 2008, 2009, 2010 and 2011. We spent a total of 89 days in the field (3–14 people). The snakes were captured by hand and they were kept in calico bags until measurements. Individuals were rapidly processed and released at the place of capture (±50 m). We recorded total and snout-to-vent lengths (TL, SVL, to the nearest 0.5 m), body mass (BM, to the nearest g), sex (based on the shape of the tail or hemipenis eversion when necessary, e.g. in juveniles), colour pattern, feeding status (palpation, spontaneous regurgitation, field observations of snakes swallowing prey, examination of faeces), reproductive status in females (palpation or dissection of dead individuals), presence of injuries, scars, and any other peculiarities. In addition, when possible, we recorded behavioural information at capture (e.g. snake hidden under stones, escaping, into the water, mating, fishing) and during measurements. Each individual was permanently marked using a modified technique of scale-clipping (Bonnet et al., 2002). We also collected dead animals irrespective of their preservation status. Fresh carcasses were dissected. Evidence of predation (e.g. examination of recently killed snakes, presence of snake remains in the faeces of mammals, and/or regurgitation pellets of avian predators) was systematically recorded. The presence of potential predators was noted, using direct (visual observations) and indirect clues (predator's tracks, shelters, faeces).

We considered females larger than 55 cm in SVL (smallest females with enlarged follicles) and males larger than 48 cm (smallest male observed mating) as adult (Luiselli and Rugiero, 2005). We also considered that the cohort of the smallest snakes (SVL < 32.5 cm, see Section 3) observed after hatching in late summer belonged to the neonate age class. Snakes intermediate in size were considered as sub-adults. As we individually marked almost all captured individuals, we discarded pseudo-replicate

effects from analyses when necessary. The statistical analyses were performed using Statistica 7.1 (®StatSoft Inc. 1984–2005).

3. Results

3.1. Population age structure

A total of 5796 snakes were observed; 5045 of them were individually marked, the others were found dead or observed but not marked. We recaptured 513 marked snakes. The sex ratio was biased towards females, both in captures (60% of females; $\chi^2 = 115.5$, df = 1, $P < 0.001$) and recaptures (79% of females, $\chi^2 = 96.5$, df = 1, $P < 0.001$). Adults represented 88.0% of the captures ($N = 4433$) whereas neonates (10.4%, $N = 524$) and especially sub-adults (1.6% of the total, $N = 81$) were markedly under-represented.

3.2. Body size, body mass and sexual size dimorphism

The main morphological characteristics of the different age and sex classes are presented in Table 2. Females were larger than males considering adult and sub-adult categories, but such sexual size dimorphism was not observed in the neonate age class (Table 2, Fig. 1). Body size distribution followed a multimodal pattern (Fig. 1): the first peak corresponded to the mean body size of the neonates (sexes mixed); then two partly overlapping but distinct peaks were associated with the mean body size of adult male and female categories respectively.

3.3. Colour morphs

Three main dorsal colour morphs were found ($N = 5045$ colour patterns recorded). The classical pattern with dots on the back was the most abundant (58%, $N = 2878$). The concolor, uniformly grey/olive-grey pattern was represented by 29% of the snakes ($N = 1435$). Melanistic snakes represented 13% of the total ($N = 656$).

3.4. Activity period and hibernation

During sunny days in late April – early May, large numbers of snakes were easily observed in heliotheria (i.e. *sun basking to*

Table 2
Descriptive statistics of the main morphological traits of dice snakes from Golem Grad Island. Mean values are presented with SD (ranges indicated in brackets). Age categories were based on body size for maturity, either using published values (A) or using the specific and more accurate data collected in Golem Grad (B); for comparison both are provided here (see text). ANOVA was performed with sex as factor. Note that very low values for minimal BM correspond to a few extremely skinny individuals.

Trait	Age	Females	Males	F	df	P
Total length (cm)	Adult (A)	103.4 ± 10.6 (68.0–129.4)	84.4 ± 7.2 (59.5–103.1)	2375.3	1, 3465	<0.01
	Adult (B)	106.2 ± 7.8 (78.5–129.4)	85.1 ± 6.5 (59.5–113.5)	6086.5	1, 3093	<0.01
	Sub-adult (A)	61.4 ± 6.2 (41.1–69.4)	57.2 ± 5.6 (45.7–73.0)	8.6	1, 47	<0.01
	Sub-adult (B)	80.7 ± 10.1 (41.1–101.4)	62.4 ± 5.4 (45.7–73.0)	152.8	1, 319	<0.01
	Neonate (B)	30.2 ± 2.3 (22.6–38.0)	30.7 ± 2.5 (22.9–37.1)	3.2	1, 263	0.075
Snout vent length (cm)	Adult (A)	83.8 ± 9.1 (55.0–108.0)	66.3 ± 5.9 (48.0–80.9)	2907.1	1, 3464	<0.01
	Adult (B)	86.2 ± 6.7 (73.6–108.0)	66.9 ± 5.2 (53.2–80.9)	7404.3	1, 3180	<0.01
	Sub-adult (A)	49.0 ± 4.7 (32.9–54.5)	43.0 ± 3.6 (35.8–47.4)	23.9	1, 54	<0.01
	Sub-adult (B)	64.4 ± 8.0 (32.9–73.5)	48.2 ± 4.3 (35.8–52.7)	203.1	1, 334	<0.01
	Neonate (B)	24.0 ± 1.9 (18.7–29.6)	24.1 ± 2.0 (18.0–29.4)	0.6	1, 263	0.453
Body mass (g)	Adult (A)	263.7 ± 86.6 (53.2–583.0)	122.3 ± 37.1 (26.0–237.0)	2610.5	1, 3446	<0.01
	Adult (B)	281.6 ± 75.0 (65.0–583.0)	124.6 ± 34.4 (41.0–237.0)	4687.8	1, 3165	<0.01
	Sub-adult (A)	47.5 ± 12.0 (18.0–69.0)	31.2 ± 6.8 (19.7–40.8)	27.6	1, 52	<0.01
	Sub-adult (B)	122.3 ± 51.9 (28.0–284.2)	43.2 ± 12.8 (19.7–70.8)	123.6	1, 331	<0.01
	Neonate (B)	6.3 ± 1.6 (2.0–15.0)	6.0 ± 1.6 (2.0–10.6)	2.2	1, 260	0.141

increase body temperature; Bailly, 1894), courting, mating or fishing. However, during cloudy and rainy days, the snakes were inactive and were found hidden under stones. The snakes were also inactive and sheltered under large stones during cold climatic conditions in late September – early October. In summer, the snakes tended to bask in early morning and in the evening, but they remained sheltered during the hottest hours of the days. During hot summer nights (ambient temperature above 19 °C) the snakes were regularly observed fishing near the shore. We visited Golem Grad in searches for snakes in early November (only one dice snake observed), December, February and March (no snakes found, even under large rocks). Thus, we estimated that hibernation lasted approximately six to seven months.

3.5. Diet and proportion of fed snakes

Combining stomach palpation and spontaneous regurgitations, evidence of recently ingested prey items was obtained on 1611 occasions (32% of the total, including captures only). Among the identified prey (N = 130 snakes with one to eleven prey items in the stomach) we observed fish exclusively. Most of the prey were identified at a crude taxonomic level (N = 81 recently ingested fish

easily recognizable via palpation, 62.3%). Regurgitation of poorly digested (presumable recently swallowed) items provided more accurate information. Belvica (ray-finned fish) or closely related species were the most frequent prey: *Alburnus belvica* represented 35.6% of the total, 51.1% of the prey was identified as *Alburnus* sp. (all data combined = 86.7% of the prey belonged to *Alburnus* genus). Five specimens of the pumpkinseed sunfish (*Lepomis gibbosus*, 11.1%) and one other ray-finned fish (*Chondrostoma* sp., 2.2%) were also recorded. Dissections confirmed that the main prey was *A. belvica*. We also observed snakes capturing fish (mostly *A. belvica* and several sunfish) in the field. All the snakes observed fishing were in ambush position near the shore (<5 m offshore), sometimes in high density. Snakes were rarely observed swimming more than 100 m from the shore (N < 5).

The proportion of fed snakes varied across seasons (Fig. 2; χ^2 = 997.5, df = 8, P < 0.001). Dice snakes rarely foraged early in the active season in spring (late April to early May); only 15.4% of the snakes were observed with a prey in the stomach. This proportion increased markedly (44.1%) in summer (June–August) and the snakes ceased to fish in autumn (September–October). We found strong inter-annual differences in the proportion of snakes with a prey in the stomach (comparing the actual proportions observed
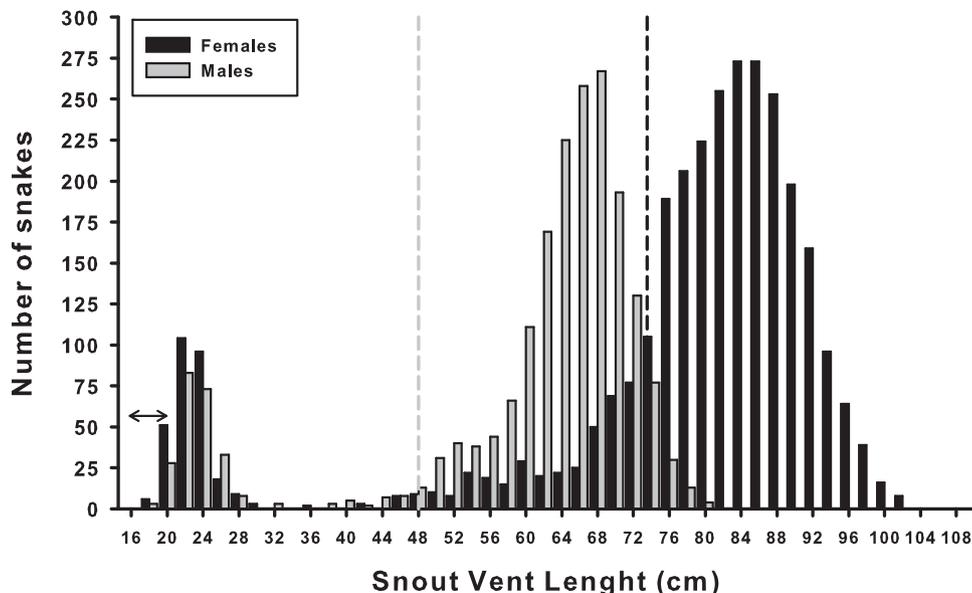

Fig. 1. Body size distribution in female (black bars) and male (grey bars) dice snakes from Golem Grad (N = 5008). The arrow indicates the range of body sizes observed in 11 neonates immediately after hatching (data not displayed). Note the virtual absence of juveniles (32–40 cm gap).
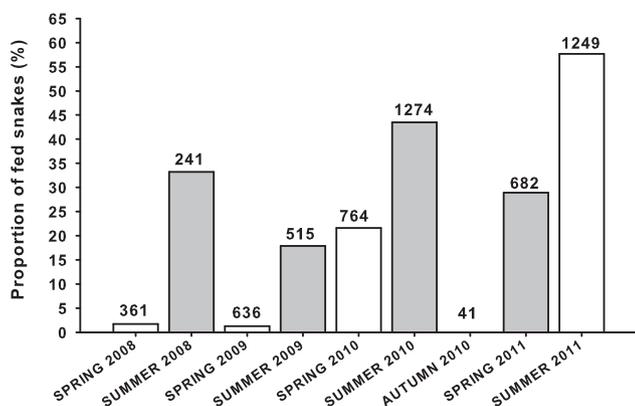
Fig. 2. Seasonal variation in the proportion of dice snakes observed with a prey in the stomach (e.g. 0% in autumn 2010).

Fig. 3. Seasonal variation in the proportion of neonate dice snakes compared to the rest of the observed population (sub-adults + adults).

over years respectively in spring versus summer against theoretical invariable proportions: $\chi^2 = 365.5$, df = 7, $P < 0.001$). For example, in 2009 feeding rate was very low in both spring and summer (Fig. 2).

3.6. Reproduction

Mating was observed immediately after spring emergence, in April until mid-May. Large numbers of snakes displayed intensive sexual behaviours. Several neighbouring groups of snakes (usually >5 males and one female per group) formed unstable mating balls: several males moving between groups. We never observed any ritual combat. The smallest male observed mating measured 48.0 cm (SVL).

Palpation of more than 3300 adult females during the study failed to detect growing follicles in spring. However, three females killed in early May by avian predators (deterred by our presence) exhibited obvious signs of early vitellogenesis (yellow turgescent follicles larger than 1 cm in length, but smaller than 1.5 cm). In late June–early July, enlarged follicles were easily detectable by palpation. We then assessed the proportion of gravid females and estimated fecundity in late June and at the beginning of July on a random subsample of females. Among 621 adult females examined, 336 were gravid (54.2%), 283 were not (45.5%), and 2 recently laid their eggs (as indicated by large distended skin folds, 0.3%). No females were gravid in August, suggesting that egg-laying occurred in July. The smallest gravid female measured 62.0 cm (SVL).

The mean clutch size was 9.1 ± 2.3 eggs ($N = 699$ females where the follicles could be counted by palpation, Table 3), ranging from 1 to 20 eggs. The clutch size distribution was not normal (Shapiro–Wilk $W = 0.97$, $P < 0.01$; Fig. 4): the number of clutches with less than 7 eggs was low but increased rapidly after this threshold-value (e.g. we counted 146 clutches of 8 eggs but only 94
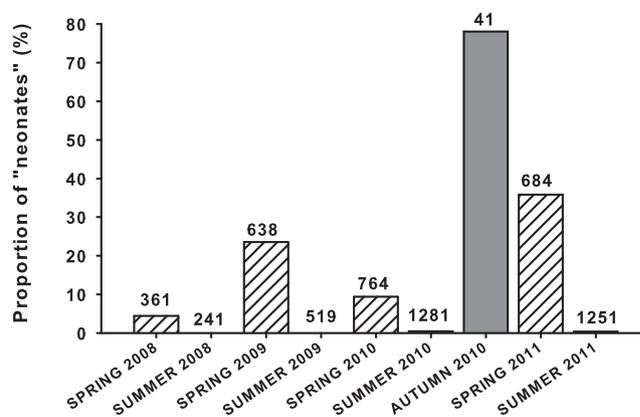
were expected under a theoretical normal distribution). Most of the clutches contained 6 to 13 eggs (87.3% of the data). We dissected 5 freshly dead gravid females found on the shore in 2009 and 17 others found drowned in a fishing net in June 2010 (among the latter 9 were gravid, 52.9%). In this subset of 14 dissected gravid females (Table 3), the mean clutch size was 10.1 ± 2.6 (7–16 eggs), suggesting that palpation of the 284 females correctly estimated the actual number of developing follicles (comparing the two means 9.1 versus 10.1: t-test $P = 0.109$).

In mid-September 2009 (15th) we witnessed hatching in the field. We recorded the main characteristics of 11 newborns immediately after they emerged from the eggs (Table 3). On average, these neonates were smaller than the individuals from the assumed neonate-cohort (Fig. 1). However, they were all within the range of body size distribution of this assumed age category, thereby validating our categorisation. The proportion of neonates and presumably very young snakes (i.e. snakes smaller than 32.5 cm SVL) compared to adults and sub-adults varied markedly between seasons (Fig. 3, $\chi^2 = 1329.1$, df = 16, $P < 0.01$). The highest value was recorded in autumn 2010, followed by the intermediate values recorded during the four spring sessions, whilst such proportion was close to zero during the four summer sessions. The proportion of sub-adults remained systematically very low (1.2% on average, and less than 2.4% at any time). We found numerous nests under stones and in crevices in various places of the island; in almost all cases the shells were empty suggesting a successful incubation.

3.7. Predation, anti-predatory behaviour and mortality

Various predators feed regularly on the dice snakes: European otter (*Lutra lutra*), different birds (e.g. *Bubo bubo*, *Ardea cinerea*,

Table 3

Reproductive traits obtained using different approaches (sources). Random sampling was performed by palpating more than 600 adult females in June (2008–2010): 336 were gravid and the eggs could be counted on 284 (see text). Dead albeit intact females (e.g. drowned in a net) were measured and dissected in June 2009 (a) and June 2010 (b). Eleven neonates were measured immediately after hatching in the field (body mass not recorded). SVL: snout-to-vent length (cm), BM: body mass (g), EL: egg (or follicle) length (cm), EM: egg (or follicle) mass (g).

| Source	Item	Trait	Mean ± SD (range)
Random sampling	Gravid females ($N = 284$)	SVL	89.4 ± 7.7 (73.6–108.0)
		BM	245.2 ± 74.2 (78.0–454.0)
Dead females (a)	Gravid females ($N = 5$)	SVL	87.7 ± 5.6 (82.3–96.8)
		BM	334.6 ± 88.0 (199.0–418.0)
	Developing follicles ($N = 58$)	EL	3.6 ± 0.5 (2.2–4.6)
		EM	7.7 ± 1.4 (4.8–10.1)
Dead females (b)	Gravid females ($N = 9$)	SVL	79.2 ± 6.9 (68.8–86.5)
		BM	299.7 ± 60.1 (221.0–387.0)
	Developing follicles ($N = 83$)	EL	3.1 ± 0.5 (1.4–4.0)
		EM	2.8 ± 1.1 (0.3–4.4)
Hatchlings	Neonate ($N = 11$)	SVL	15.3 ± 1.1 (13.8–17.6)
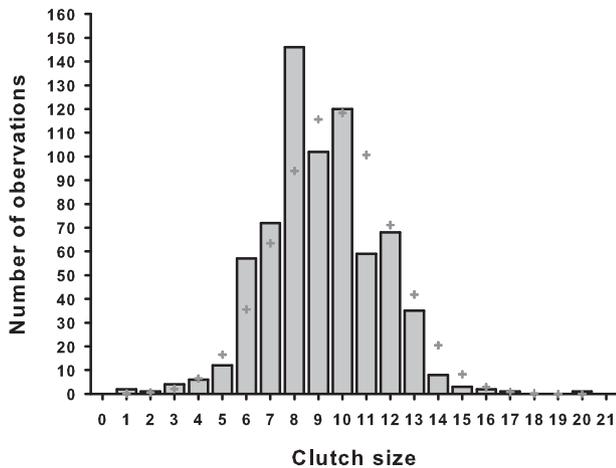
Fig. 4. Clutch size distribution observed in the dice snakes from Golem Grad. The grey crosses indicate the values expected under a normal distribution of the data.

Accipiter sp., *Buteo* sp., *Larus* sp.), and another snake species (*Vipera ammodytes*). For example, otter faeces (more than 50 items examined) systematically contained large amounts of snake scales and vertebrae. In addition, in the vicinity of the otter shelters where the faeces were observed, we found numerous remains of dice snakes, partly eaten and sliced: usually only the tail remained whereas the head was always absent (typical for mammalian predation, raptors tear snakes into pieces). All the eagle–owl pellets examined (*N* = 15) contained *N. tessellata* scales and vertebrae. We witnessed raptors (*Buteo* sp. and *Accipiter* sp.) predation on five dice snakes (two were still bleeding when examined): all were large adult females (total length range: 84.0–112.0 cm), and the birds selected only few organs (i.e. liver and/or gut). An adult nose-horned viper (*V. ammodytes*) was captured with a large adult dice snake in the stomach (regurgitated during manipulation); small dice snakes are commonly found in the stomach of the vipers. Overall, dice snakes are under strong predation, both by diurnal and nocturnal animals.

During field surveys, we found numerous dead snakes. In most cases, the cause of death remained obscure. To obtain a crude estimate of mortality over time, we recorded the number of dead snakes during five consecutive days in summer of 2009 (11–15 of August), and then during one additional day a month later (September 15th). All dead snakes were removed to prevent repeated counting. Fig. 5 shows that the number of dead snakes found in the field decreased rapidly over time, but such number
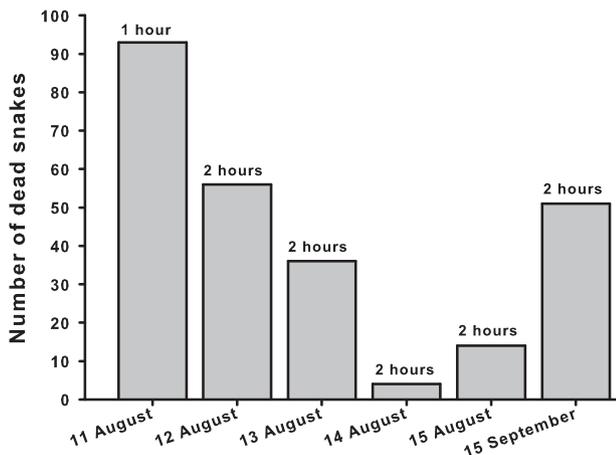
was again elevated one month later, suggesting that the number of new dead snakes was increasing rapidly in the study zone.

4. Discussion

Our data about the period of activity of the dice snakes show that hibernation extends over a long six to seven months period. At emergence the snakes were often inactive under stones as the ambient temperature was often low (e.g. <10 °C) whilst rainy and cloudy weather conditions precluded heliotheria. These data fit well with the notion that strong climatic constraints prevail in altitude (humid-cool-Mediterranean type; Hollis and Stevenson, 1997). Therefore the activity period was shorter in Golem Grad Island due to less favourable climatic conditions compared to those recorded at low altitude in central Italy for instance (Luiselli and Zimmermann, 1997); even 4° further north, in Romania, the activity season of the dice snake extends from March to October (Carlsson et al., 2011). As expected, we observed a massive shift for all the life history traits examined; the direction of the shift was unexpected however.

The dice snakes monitored on Golem Grad Island exhibit remarkable particularities. Firstly, the population density is extremely high: thousands (likely tens of thousands) of snakes are concentrated into a small area (18 ha). We emphasize that the snakes were permanent residents of the island, thus the very high population density is not comparable to transitory aggregations observed into hibernacula or during mating period (Graves and Duvall, 1995) where individuals rapidly disperse over large areas during the active season (e.g. garter snakes in Canada, Gregory, 1974; dice snakes in Romania, Carlsson et al., 2011).

In our study system, the snakes complete their entire life cycle on their home islet. Under the same stones, we found clutches, young snakes, gravid females and adult males mixed together; and dispersal was likely limited (see below). In a related amphibious species (*Nerodia sipedon*) that inhabits the islands spread out in the Lake Erie (North America), large numbers of individuals also complete their entire life cycle in coastal colonies and forage in the near-shore waters (King, 1986; King et al., 2006a). Our observations suggest that on Golem Grad Island, dice snakes alternate short foraging trips with longer periods on land for digestion, resting, or mating (unpublished data). We speculate that natricine snakes inhabiting small islands exhibit a typical central place foraging strategy and thus may display strong ecological similarities with the highly phylopatric piscivorous marine sea kraits (Brischoux et al., 2007, 2009a; Bonnet, 2012). Convergent foraging strategies exhibited by very different snakes' groups might be associated with similar population characteristics, notably a trend to form dense coastal colonies.

As dice snakes forage in the waters surrounding Golem Grad Island, the resulting increased home range should be taken into account to examine population density. However, evidence suggests that this effect does not markedly modify the high density pattern of Golem Grad dice snakes. We observed very few snakes more than 50 m offshore and foraging individuals were almost systematically found very near (<10 m) the shore. Interviewed fishermen reported that large numbers of snakes occur exclusively in the close vicinity of the island. In addition, focal observations of fishing snakes revealed that individuals return immediately to the shore after prey capture; accordingly, prey found in the stomach of the snakes coming back on land were almost undigested, indicating a very short offshore foraging distance (Brischoux et al., 2007). These observations are also convergent with those reported for the related water snake *N. sipedon* (King, 1986; Jones et al., 2009).

Although we marked more than 5000 snakes, we recaptured only 513 of them. Such a low recapture rate (~10% on average)

Fig. 5. Number of dead snakes found in Golem Grad during six successive days in August 2010, and then on the 15th of September. Dead snakes were removed from the field to avoid multiple counting.

means that our intensive capture effort was diluted. In 2011, despite the fact that thousands of marked snakes have been released in the three previous years, recapture rate remained low (14%, $N = 1936$). Dice snakes were observed in (very) large numbers almost everywhere on the shore and in many places on the plateau. In practice, we focused our searching effort on several sections of the island in an (unsuccessful) attempt to limit dilution and to improve recapture rates; indeed, amphibious snakes tend to exhibit a fine-scale fidelity for particular segments of the shore (Brischoux et al., 2009a; Bonnet et al., 2009). Each year we captured more than 1400 snakes on average, but most of them were unmarked and we did not prospect the whole island. Overall, we can prudently infer (the low annual recapture rate precludes precise estimates) that at least 10,000 snakes inhabit Golem Grad Island. This leads to a density estimate of more than 500 snakes per hectare. Considering an average body mass of 200 g, this roughly represents a total of 2 tonnes of snakes (95 kg of snakes per hectare).

The constant and marked deficit of sub-adults and the strong seasonal age structure variations due to the rapid disappearance of the neonate class every summer (2008, 2009, 2010 and 2011) were intriguing. Following the hatching period and winter emergence we observed many neonates, and this fits well with the high number of gravid females observed in summer along with the large numbers of empty shells found in many places. Apparently, large cohorts of neonates are produced every year in late summer, but following the emergence, few months later, most of them disappear or at least escape observation, generating the gap in the body size distribution pattern (Fig. 1). Several non-exclusive possibilities can be proposed. First, a rapid population turnover: many neonates might survive the first winter and rapidly reach adult size (in few months). Alternatively, most juveniles may not survive after winter emergence and/or they may massively disperse. The subadult age class is then represented by a limited number of individuals (i.e. several hundreds of subadults diluted in the very large number of adults). Whatever the case, this suggests a very fast recruitment rate rather typical for reptiles inhabiting warm and humid tropical regions (e.g. pythons and water snakes; Brown and Shine, 2002; Madsen and Shine, 2000), but unexpected in a relatively cool environment associated with a short activity period. Alternatively, a massive juvenile mortality might have occurred during the four years of observation of the population; a rapid decline would be the automatic consequence in the coming years. Finally, sub-adults might be abundant but owing to a secretive life style they may escape observation (Aubret and Bonnet, 2007; Pike et al., 2008). However, the smallest snakes (i.e. neonates) were easily observed in the field, notably sheltered under stones, rendering unlikely the possibility for very large numbers of subadults to remain invisible.

The co-occurrence of large numbers of individuals from both sexes exhibiting three distinct colour morphs in a single population of snakes has not been previously documented (to our knowledge). Anecdotic reports of melanic or concolor dice snakes suggest that this type of polymorphism sporadically occurs in other populations (Mebert, 2011). More generally, melanism and sexual dichromatism have been documented in different snake species (Luiselli, 1992; Forsman, 1995; Lorioux et al., 2008). But the Golem Grad dice snakes situation is particular: hundreds of snakes of the three colour morphs are found mixed together, this polymorphism is observed in both sexes and all combinations were observed during mating – a situation that partly reflects the complex case of the North American Lake Erie water snakes (King, 1987; King and Lawson, 1995, 1997). Discussing the evolutionary trade-offs (e.g. predation versus thermoregulation) that underlie the maintenance of polymorphism is out of scope of the current study (King, 1987; Forsman, 1995), melanic and concolor morphs must be under strong positive selection however.
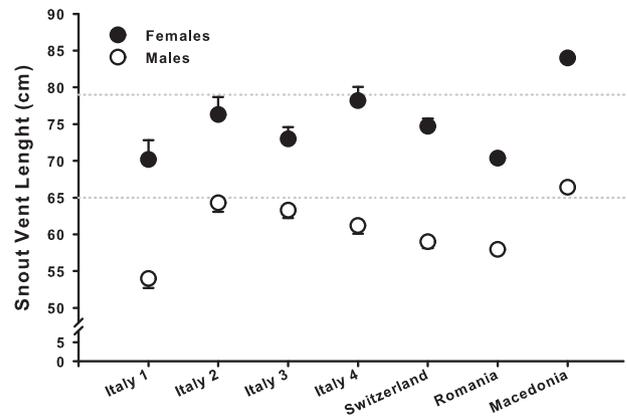

Fig. 6. Comparison of the mean body size between different populations (four countries) of dice snakes ($P < 0.01$ in all t-tests comparing Golem Grad snakes against other populations). Females are represented with open circles, males with black circles. Values are expressed as mean $\pm$ 1SE. The dashed lines facilitate comparisons, Golem Grad snakes are clearly the largest. Data were obtained from (Metzger et al., 2009; Capula et al., 2011; Carlsson et al., 2011).

Although other results about body size and diet were less unexpected, our large data set nonetheless revealed important peculiarities that offer a fulcrum to investigate geographical variability. For instance, the dice snakes from Golem Grad Island were markedly larger than in all the other studied populations (the reverse was expected), extending the maximal body size of the species by 18% and 22% in females (108 cm SVL) and males (81 cm SVL), respectively (Fig. 6). Palpation suggested that body size for maturity is considerably greater in Golem Grad island (62.5 cm SVL) compared to the published value (55.0 cm SVL) for females; this notion applies to males as well (53.0 cm versus 48.0 cm in SVL for the smallest male observed mating). The mean clutch size on Golem Grad (~9) is considerably lower than the value reported in Italy (~15; Luiselli and Rugiero, 2005); similarly, the maximal clutch size determined by palpation was 20 eggs on Golem Grad island (note that this exceptional value was extracted from more than 600 clutch sizes, see Fig. 4) versus 29 eggs in Italy. As Golem Grad females are larger, the maternal body size/fecundity relationship diverged markedly compared to Italian snakes (using Luiselli and Rugiero (2005) data; ANCOVA with clutch size as the dependent variable, country as the factor and maternal SVL as the independent variable: difference between the slopes, $F_{1, 716} = 525.39$, $P < 0.01$; Fig. 7). Consequently, the mean adjusted clutch sizes were also
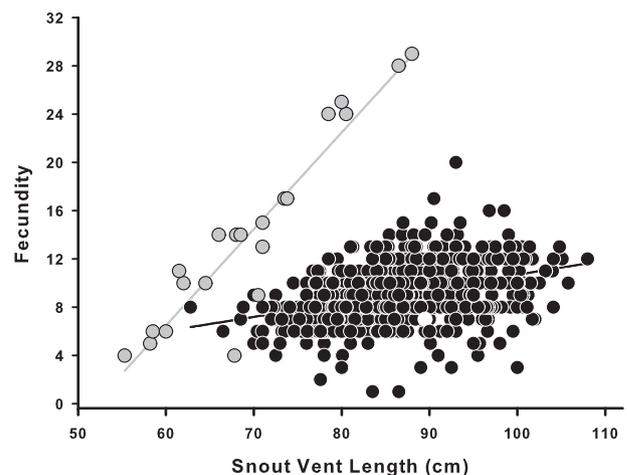

Fig. 7. Comparison of the relationship between body size (SVL) and fecundity between Italian (grey symbols and grey regression line) and Golem Grad snakes (black symbols and black regression line). See text for statistics.

very different 15.5 ± 7.8 in Italy versus 7.9 ± 2.3 in Macedonia. The respective allometric coefficients (exponent b, Log transformed data; King, 2000) that provide scale-independent descriptors of the body size versus fecundity relationship were also markedly divergent: 1.137 for Golem Grad females (a very low value) and 4.161 for Italian females (a high value). This magnitude of variation is greater than previously documented among populations in other snake species (Ford and Seigel, 1989; Bonnet et al., 2000, 2003; Sun et al., 2002; Zuffi et al., 2008, 2009). The low fecundity of the Golem Grad females might be the result of density dependent processes (e.g. food depletion, competition among neonates), or may promote female's mobility through a reduction of the clutch load. The relatively low proportion of gravid females and the 7-eggs threshold value suggests a biennial capital-breeding tactic (Bonnet et al., 2000, 2003).

Our data confirmed the piscivorous diet of the dice snake (e.g. Luiselli et al., 2007). Uniquely, however, Golem Grad snakes feed exclusively on fish despite the presence of amphibians; other populations of dice snakes display a more eclectic diet as amphibians are (albeit sometimes rarely) consumed (Luiselli et al., 2007; Bakiev et al., 2011; Tuniyev et al., 2011; Velensky et al., 2011). Golem Grad dice snakes were remarkably selective by targeting a single endemic fish species (A. belvica); such degree of specialization was surprising considering the great dietary flexibility of many snakes (Aubret et al., 2006; King et al., 2006b; Luiselli et al., 2007; Brischoux et al., 2009b). Perhaps the predominance of the belvica fish (48% of the total weight of the fish sampled in the Prespa Lake; Crivelli et al., 1997) favoured the most efficient foraging tactic that ultimately resulted into a strong specialization. Finally, the exceptionally high density of dice snakes suggests that this predator not only exerts a significant role on the fish communities of Prespa Lake (Ineich et al., 2007), but also represents an important prey item for various mammalian and avian top predators; and thus occupy a key position in the Golem Grad ecosystem.

Acknowledgements

References

Acipinar, H., Gaygusuz, O., Tarkan, A.S., Gursoy, C., Al, Z., 2006. Presence of an invasive fish species Carassius gibelio (Bloch, 1782) in the diet of the dice snake, Natrix tessellata (Laurenti, 1768). Journal of Fisheries and Aquatic Science 1, 213–217.

Ashton, K.G., Feldman, C.R., 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. Evolution 571, 151–1163.

Aubret, F., Shine, R., Bonnet, X., 2004. Adaptive developmental plasticity in snakes. Nature 431, 261–262.

Aubret, F., Burghardt, G., Maumelat, S., Bonnet, X., Bradshaw, S.D., 2006. Feeding preferences in two disjunct populations of tiger snakes, Notechis scutatus (Elapidae). Behavioral Ecology 17, 716–725.

Aubret, F., Bonnet, X., 2007. Food versus risk: foraging decision in young tiger snakes Notechis scutatus. Amphibia-Reptilia 28, 304–308.

Aubret, F., Shine, R., 2009. Genetic assimilation and the postcolonization erosion of phenotypic plasticity in island tiger snakes. Current Biology 19, 1932–1936.

Bailly, A., 1894. Dictionnaire Grec-français. Eds Librairie-Hachette, Paris.

Bakiev, A., Kirillov, A., Mebert, K., 2011. Diet and parasitic helminths of dice snakes from the Volga Basin, Russia. Mertensiella 18, 325–329.

Bannikow, A.G., Darewskij, I.S., Ishenko, V.G., Scerbak, N.N., 1977. Opredelitelj zemnowodrych i presmykajuscichsja fauny SSSR. [Identification of amphibians and reptiles of the SSSR]. Proswesenije, Moscow.

Blouin-Demers, G., Prior, K.A., Weatherhead, P.J., 2002. Comparative demography of black rat snakes (Elaphe obsoleta) in Ontario and Maryland. Journal of Zoology 256, 1–10.

Boback, S.M., 2003. Body size evolution in snakes: evidence from island populations. Copeia 2003, 81–94.

Bonnet, X., 2012. Long term field study of sea kraits in New Caledonia: fundamental and conservation issues. Integrative and Comparative Biology, 1–15, http://dx.doi.org/10.1093/icb/ics069

Bonnet, X., Bradshaw, S.D., Shine, R., Pearson, D., 1999. Why do snakes have eyes? The (non-) effect of blindness in island tiger snakes. Behavioral Ecology and Sociobiology 46, 267–272.

Bonnet, X., Naulleau, G., Shine, R., Lourdais, O., 2000. Reproductive versus ecological advantages to larger body size in female Vipera aspis. Oikos 89, 509–518.

Bonnet, X., Shine, R., Naulleau, G., Thiburce, C., 2001. Plastic vipers: influence of food intake on the size and shape of Gaboon vipers (Bitis gabonica). Journal of Zoology 255, 341–351.

Bonnet, X., Pearson, D., Ladyman, M., Lourdais, L., Bradshaw, D., 2002. Heaven" for serpents? A mark-recapture study of tiger snakes (Notechis scutatus) on Carnac Island, Western Australia. Australian Ecology 27, 442–450.

Bonnet, X., Shine, R., Lourdais, O., Naulleau, G., 2003. Measures of reproductive allometry are sensitive to sampling bias. Functional Ecology 17, 39–49.

Bonnet, X., Brischoux, F., Pearson, D., Rivalan, P., 2009. Beach-rock as a keystone habitat for sea kraits. Environmental Conservation 36, 62–70.

Brischoux, F., Bonnet, X., Shine, R., 2007. Foraging ecology of sea kraits (Laticauda spp.) in the Neo-Caledonian Lagoon. Marine Ecology Progress Series 350, 145–151.

Brischoux, F., Bonnet, X., Pinaud, D., 2009a. Fine scale site fidelity in sea kraits: implications for conservation. Biodiversity and Conservation 18, 2473–2481.

Brischoux, F., Bonnet, X., Shine, R., 2009b. Determinants of dietary specialization: a comparison of two sympatric species of sea snakes. Oikos 118, 145–151.

Bronikowski, A.M., 2000. Experimental evidence for the adaptive evolution of growth rate in the garter snake (Thamnophis elegans). Evolution 54, 1760–1767.

Bronikowski, A.M., Arnold, S.J., 1999. The evolutionary life-history variation in the garter snake Thamnophis elegans. Ecology 80, 2314–2325.

Brown, G.P., Shine, R., 2002. Reproductive ecology of a tropical natricine snake Tropidonophis mairii (Colubridae). Journal of Zoology 258, 63–72.

Bruno, S., Maugieri, S., 1990. Serpenti d'Italia e d'Europa. Editoriale Giorgio Mondatori, Milano.

Buckley, L.B., Jetz, W., 2007. Insularity and the determinants of lizard population density. Ecology Letters 10, 481–489.

Capula, M., Filippi, E., Rugiero, L., Luiselli, L., 2011. Dietary, thermal and reproductive ecology of Natrix tessellata in central Italy: a synthesis. Mertensiella 18, 147–153.

Carlsson, M., Kärvemo, S., Tudor, M., Sloboda, M., Mihalca, A.D., Ghira, I., Bel, L., Modry, D., 2011. Monitoring a large population of dice snakes at lake Sinoe in Dobrogea, Romania. Mertensiella 18, 237–244.

Crivelli, A.J., Catsadorakis, G., Malakou, M., Rosecchi, E., 1997. Fish and fisheries of the Prespa Lakes. Hydrobiologia 351, 107–125.

Dingemanse, N.J., Kazem, A.J., Réale, D., Wright, J., 2010. Behavioural reaction norms: animal personality meets individual plasticity. Trends in Ecology and Evolution 25, 81–89.

Em, H., 1965. Šumske zajednice četinara u NR Makedoniji. Bioloki Glasnik Zagreb 15, 1–38.

Ford, N.B., Seigel, R.A., 1989. Phenotypic plasticity in reproductive traits: evidence from a viviparous snake. Ecology 70, 1768–1774.

Forsman, A., 1995. Opposing fitness consequences of colour pattern in male and female snakes. Journal of Evolutionary Biology 8, 53–70.

Gautschi, B., Widmer, A., Joshi, J., Koella, J.C., 2002. Increased frequency of scale anomalies and loss of genetic variation in serially bottlenecked populations of the dice snake Natrix tessellata. Conservation Genetics 3, 235–245.

Gerhardt, J., Kirschner, M., 1997. Cells, Embryos, and Evolution. Blackwell Scientific, Malden.

Göçmen, B., Çiçek, K., Yildiz, M.Z., Atatür, M.K., Dinçaslan, Y.E., Mebert, K., 2011. A preliminary study on the feeding biology of the dice snake, Natrix tessellata, in Turkey. Mertensiella 18, 365–369.

Graves, B.M., Duvall, D., 1995. Aggregation of squamate reptiles associated with gestation, oviposition, and parturition. Herpetological Monographs 9, 102–119.

Gregory, P.T., 1974. Patterns of spring emergence of the red-sided garter snake (Thamnophis sirtalis parietalis) in the Interlake region of Manitoba. Canadian Journal of Zoology 52, 1063–1069.

Gruschwitz, M., Lenz, S., Mebert, K., Lanka, V., 1999. Natrix tessellata (Laurenti, 1768) – Würfelnatter. In: Böhme, W. (Ed.), Handbuch der Reptilien und Amphibien Europas, vol. 3(2). AULA-Verlag GmbH, Wiesbaden, pp. 581–644.

Guicking, D., Lawson, R., Joger, U., Wink, M., 2007. Evolution and phylogeny of the genus Natrix (Serpentes: Colubridae). Biological Journal of the Linnean Society 87, 127–143.

Herczeg, G., Szabó, K., Korsós, Z., 2005. Asymmetry and population characteristics in dice snakes (Natrix tessellata): an interpopulation comparison. Amphibia-Reptilia 26, 422–426.

Hollis, G.E., Stevenson, A.C., 1997. The physical basis of the Lake Mikri Prespa systems: geology, climate, hydrology and water quality. Hydrobiologia 351, 1–19.

Ineich, I., Bonnet, X., Brischoux, F., Kulbicki, M., Séret, B., Shine, R., 2007. Anguilliform fishes and sea-kraits: neglected predators in coral-reef ecosystems. Marine Biology 151, 793–802.

Ioannidis, Y., Bousbouras, D., 1997. The space utilization by the reptiles in Prespa National Park. Hydrobiologia 351, 135–142.

Jelić, D., Lelo, S., 2011. Distribution and status quo of *Natrix tessellata* in Croatia, Bosnia and Herzegovina. Mertensiella 18, 217–224.

Jones, P.C., King, R.B., Stanford, K.M., Lawson, T.D., Thomas, M., 2009. Frequent consumption and rapid digestion and prey by the Lake Erie watersnake with implications for an invasive prey species. Copeia, 437–445.

King, R.B., 1986. Population ecology of the Lake Erie water snake *Nerodia sipedon insularum*. Copeia, 757–772.

King, R.B., 1987. Color pattern polymorphism in the lake Erie water snake, *Nerodia sipedon insularium*. Evolution 41, 241–255.

King, R.B., 2000. Analyzing the relationship between clutch size and female body size in reptiles. Journal of Herpetology 34, 148–150.

King, R.B., Lawson, R., 1995. Color pattern variation in Lake Erie water snakes: the role of gene flow. Evolution 49, 885–896.

King, R.B., Lawson, R., 1997. Microevolution in island water snakes. BioScience 47, 279–286.

King, R.B., Ray, J.M., Stanford, K.M., 2006a. Gorging on gobies: beneficial effects of alien prey on a threatened vertebrate. Canadian Journal of Zoology 84, 108–115.

King, R.B., Queral-Regil, A., Stanford, K.M., 2006b. Population size and recovery criteria of the threatened Lake Erie watersnake: integrating multiple methods of population estimation. Herpetological Monographs 20, 83–104.

Lenz, S., Gruschwitz, M., 1993. Zur Autökologie der Würfelnatter, *Natrix t. tessellata* (Laurenti, 1978) (Reptilia: Serpentes: Colubridae) in Deutschland. Mertensiella 3, 235–252.

Lorioux, S., Bonnet, X., Brischoux, F., De Crignis, M., 2008. Is melanism adaptive in sea kraits? Amphibia-Reptilia 29, 1–5.

Luiselli, L., 1992. Reproductive success in melanistic adders: a new hypothesis and some considerations on Andren and Nilson's (1981) suggestions. Oikos 64, 601–604.

Luiselli, L., Zimmermann, P., 1997. Thermal ecology and reproductive cyclicity of the snake *Natrix tessellata* in south-eastern Austria and central Italy: a comparative study. Amphibia-Reptilia 18, 383–396.

Luiselli, L., Rugiero, L., 2005. Individual reproductive success and clutch size of a population of the semi-aquatic snake *Natrix tessellata* from central Italy: are smaller males and larger females advantaged? Revue de Ecologie (Terre Vie) 60, 77–81.

Luiselli, L., Capizzi, D., Filippi, E., Anibaldi, C., Rugiero, L., Capula, M., 2007. Comparative diets of three populations of an aquatic snake (*Natrix tessellata*, Colubridae) from Mediterranean streams with different hydric regimes. Copeia 2007, 426–435.

Luiselli, L., Madsen, T., Capizzi, D., Rugiero, L., Pacini, N., Capula, M., 2011. Long-term population dynamics in a Mediterranean aquatic snake. Ecological Research 26, 745–753.

Madsen, T., Shine, R., 1993. Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. Evolution 47, 321–325.

Madsen, T., Shine, R., 2000. Rain, fish and snakes: climatically driven population dynamics of Arafura filesnakes in tropical Australia. Oecologia 124, 208–215.

Manier, M.K., Seyler, C.M., Arnold, S.J., 2007. Adaptive divergence within and between ecotypes of the terrestrial garter snake, *Thamnophis elegans*, assessed with FST–QST comparisons. Journal of Evolutionary Biology 20, 1705–1719.

Matzinger, A., Jordanoski, M., Veljanoska-Sarafiloska, E., Sturm, M., Müller, M., Wüest, A., 2006. Is Lake Prespa jeopardizing the ecosystem of ancient Lake Ohrid? Hydrobiologia 553, 89–109.

Mebert, K., 2011. Geographic variation of morphological characters in the dice snake (*Natrix tessellata*). Mertensiella 18, 11–19.

Metzger, C., Ursenbacher, S., Christe, P., 2009. Testing the competitive exclusion principle using various niche parameters in a native (*Natrix maura*) and an introduced (*N. tessellata*) colubrid. Amphibia-Reptilia 30, 523–531.

Pigliucci, M., 2001. Phenotypic Plasticity: Beyond Nature and Nurture. John Hopkins University Press, Baltimore.

Pike, D.A., Pizzatto, L., Pike, B.A., Shine, R., 2008. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. Ecology 89, 607–611.

Reed, T.E., Schindler, D.E., Waples, R.S., 2011. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. Conservation Biology 25, 56–63.

Seigel, R.A., Ford, N.B., 1991. Phenotypic plasticity in the reproductive characteristics of an oviparous snake, *Elaphe guttata*: implications for life history studies. Herpetologica 47, 301–307.

Shine, R., 2003. Reproductive strategies in snakes. Proceedings of Royal Society B 270, 995–1004.

Sterijovski, B., Ajtić, R., Tomović, L., Djordjević, S., Djurakić, M., Golubović, A., Crnobrnja-Isailović, J., Ballouard, J.M., Groumpf, F., Desmonts, D., Bonnet, X., 2011. *Natrix tessellata* on Golem Grad, FYR of Macedonia: a natural fortress shelters a prosperous snake population. Mertensiella 18, 298–301.

Sun, L.X., Shine, R., Zhao, D.B., Tang, Z.R., 2002. Low costs, high output: reproduction in an insular pit-viper (*Gloydius shedaoensis*, Viperidae) from north-eastern China. Journal of Zoology 256, 511–521.

Tanaka, K., 2010. Phenotypic plasticity of body size in an insular population of a snake. Herpetologica 67, 46–57.

Tuniyev, B., Tuniyev, S., Kirschey, T., Mebert, K., 2011. Notes on the dice snake, *Natrix tessellata*, from the Caucasian isthmus. Mertensiella 18, 343–356.

Velensky, P., Velensky, M., Mebert, K., 2011. Ecology and ethology of dice snakes (*Natrix tessellata*) in the city district Troja, Prague. Mertensiella 18, 157–176.

Zuffi, M.A.L., Fornasiero, S., Bonnet, X., 2008. Geographic variation of reproductive output in female European whip snake (*Hierophis viridiflavus*). Herpetology Journal 17, 219–224.

Zuffi, M.A.L., Gentilli, A., Cecchinelli, E., Pupin, F., Bonnet, X., Filippi, E., Luiselli, L.M., Barbanera, F., Dini, F., Fasola, M., 2009. Geographic variation of life-history traits and reproductive patterns in Continental and Mediterranean asp vipers, *Vipera aspis*. Biological Journal of the Linnean Society 96, 383–391.