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INTRA- AND INTER-POPULATION VARIABILITY OF FOOD PREFERENCES OF TWO *NATRIX* SPECIES ON THE BALKAN PENINSULA

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***Abstract*.—In aquatic and surrounding terrestrial ecosystems, snakes of the genus *Natrix* are among the top predators, feeding predominantly on fishes and amphibians, but also on other reptiles and small mammals. In the diets of *Natrix natrix* and *N. tessellata*, preferred food items vary geographically and during ontogeny. To understand these variations, we collected data on their diet composition in several habitats (river, wetlands, and two types of lakes), some of which are under severe anthropogenic pressures. Both *Natrix* species were able to quickly adapt to changes in available prey, and to feed even on non-indigenous, invasive, and potentially hazardous fish. Disturbed ecosystems are particularly susceptible to invasions. Therefore, if alien fishes become dominant, they may threaten populations of native snakes. On the other hand, semi-aquatic snakes can contribute to natural regulation of alien fish species abundance. The preliminary results presented herein emphasize the urgent need for integrative studies of natricine snakes and their prey ecology under various and/or dynamic circumstances. Better understanding of the functioning of different aquatic ecosystems may enable proper conservation and restoration for these snake species and their habitats.**

***Sažetak*.—U akvatičnim i okolnim terestričnim ekosistemima, zmije iz roda *Natrix* često su pri vrhu lanaca ishrane. Hrane se pretežno ribom i vodozemcima, ali i drugim gmizavcima i sitnim sisarima. Omiljeni plijen *Natrix natrix* i *N. tessellata* varira, kako geografski tako i tokom ontogenije. Kako bismo mogli razumjeti navedene razlike, prikupili smo podatke o sastavu ishrane ovih zmija u nekoliko staništa (rijeka, močvarna staništa i dva tipa jezera); neka od navedenih područja pod intenzivnim su antropogenim pritiscima. Obje vrste roda *Natrix* sposobne su se brzo prilagoditi promjenama u dostupnom plijenu, i hraniti se čak i alohtonim, invazivnim i potencijalno opasnim vrstama riba. Narušeni ekosistemi naročito su podložni naseljavanju invazivnim vrstama. U tom smislu, ukoliko bi strane vrste riba postale dominantne, mogle bi ugroziti populacije autohtonih vrsta zmija. Sa druge strane, semiakvatične vrste zmija mogu doprinijeti prirodnoj regulaciji brojnosti alohtonih vrsta riba. Preliminarni rezultati koje ovdje prikazujemo naglašavaju potrebu da se u najskorije vrijeme sprovedu integrativne studije ekologije akvatičnih zmija i njihovog plijena pod različitim i/ili promijenljivim okolnostima. Bolje poznavanje funkcionisanja različitih akvatičnih ekosistema može omogućiti adekvatnu zaštitu i oporavak navedenih vrsta zmija i njihovih staništa.**

Key Words.—Dice Snakes; diet shifts; disturbed habitats; Grass Snakes; invasive fish; *Natrix natrix*; *Natrix tessellata*; semi-aquatic snakes

INTRODUCTION

Grass Snakes (*Natrix natrix*) feed mostly on amphibians (Bruno and Maugeri 1990; Arnold and Ovenden 2002; Gregory and Isaac 2004). However, prey differences among populations, between the sexes, and among age classes within populations have been found in this species (Luiselli et al. 1997, 2005, 2007; Gregory and Isaac 2004; Bilcke et al. 2007). We are not aware of any publication regarding the consumption of allochthonous fish species by *N. natrix*. Another natricine species, the Dice Snake (*Natrix tessellata*), feeds predominately on fish. As with the Grass Snake, inter-population differences in diet of this species exist. These depend on numerous biotic and abiotic factors such as the differences between males and females and among age (i.e., size) categories (Luiselli et al. 2007). Nevertheless, very few comparative records exist on the consumption of non-native/invasive fishes by this snake (Acipinar et al. 2006).

The variable composition of the prey of natricine snakes implies that these species are quite capable of

surviving in areas where their usual prey decreases dramatically, by shifting to alternative diets, and including non-indigenous species (Gregory and Isaac 2004; Luiselli et al. 2005; Acipinar et al. 2006; King et al. 2006). Inter-population differences in snake diet can be related to climate or habitat characteristics (e.g., Capula and Luiselli 2002; Luiselli et al. 2007). How quickly a shift in diet occurs still remains to be investigated. Diet shifts in the same cohort within a single population, caused by habitat and prey alterations, have seldom been studied.

In general, interactions between non-native prey species and native predators have rarely been addressed (Bulte and Blouin-Demers 2008; Carlsson et al. 2009; Ward-Fear et al. 2009; Li et al. 2011; Robbins et al. 2013). The notable exceptions have been studies regarding the influence of introduced toads to indigenous snake species in Australia (e.g., Shine 2012 and references therein). However, the majority of these studies concern invasive species with chemical "weaponry"; invaders capable of inflicting physical damage are rarely considered.

Analyses and comparisons of Grass and Dice snake diets and their flexibility have not been performed in the Balkans. Our primary aim was to analyze diet composition and its geographic variability (i.e., possible relatedness to the type of habitat) in Grass and Dice snakes. Additional aim of our study was to assess the ratios of prey types (amphibians vs. fish, and native vs. non-native fish species) in the diets of these two snake species under different circumstances.

MATERIALS AND METHODS

Grass Snakes occur on three continents: Europe, Asia, and Africa (Arnold and Ovenden 2002; Gregory and Isaac 2004). They feed in both aquatic and terrestrial environments. Predominant prey types are amphibians; however, they regularly consume fish (Capula et al. 1994; Filippi et al. 1996; Filippi and Luiselli 2002). Dice Snakes rely almost exclusively on aquatic habitats and their primary prey is fish (Filippi et al. 1996; Bilcke et al. 2007; Capula et al. 2011). Both snakes are common throughout the Palearctic region (Mebert et al. 2011; Shehab et al. 2011).

Study sites.—Our first study site, the Bardača Protected Area (Important Bird Area [IBA] and Ramsar site), is a typical marshland. It is located ~50 km north-east of Banja Luka in northern Bosnia and Herzegovina (45°06′ N, 17°26′ E, Fig. 1). The site is at 85–95 m elevation. Its total area before the massive draining that occurred in 2012 was ~3,500 ha. This complex includes fish ponds, floodplain meadows and forests, arable land,

FIGURE 1. Localities on the Balkan Peninsula where we studied food preferences of the Grass Snake (*Natrix natrix*) and the Dice Snake (*Natrix tessellata*). In Bosnia and Herzegovina: Bardača Protected Area and Vrbanja River; in Serbia: Pančevački rit wetland; in Montenegro: Skadar Lake; in FYR of Macedonia: Prespa Lake.

and settlements. The ichthyofauna of Bardača comprises 24 species (17% non-native), with two invasive species (Goldfish, *Carassius auratus*, and Brown Bullhead, *Ameiurus nebulosus*) dominating in terms of density and biomass (Vuković et al. 2008; see Appendix). Destructive human activities that have lasted for many decades (Mihajlo Marković, unpubl. report) are continuing. In early 2012, eight of 11 lakes, including our study site, were completely dried out. In the Bardača wetland, we performed the capture-mark-recapture (CMR) surveys of Grass Snakes from March until June in 2011 and 2012 (13 days of fieldwork in total).

Another study site in Bosnia and Herzegovina, in the surroundings of Banja Luka, was the Vrbanja River, a tributary to the Vrbas River (44°47′ N, 17°14′ E, Fig. 1; ~200 m elevation). According to the available literature (Radević 2000; Golub et al. 2012), 21 native fish species are present in this river (see Appendix). Along the river stretch where we conducted our study, strong anthropogenic influences, such as industrial and wastewater discharge and riverbed modifications are evident (Radević 2000; Goran Šukalo, pers. obs.). We performed CMR field studies on Dice Snakes from May to September in 2011 and 2012 (a total of 67 days), along a 2.4 km river stretch. In addition to general population data, we recorded information related to the diet of this species.

The second locality where population (CMR) data on Dice Snakes has been gathered since 2011 is Skadar Lake in Montenegro (40°10′ N, 19°15′ E, Fig. 1; 5 m elevation). This lake, shared between Montenegro and Albania, has the largest surface area in the Balkan Peninsula (391 km^2), but its average depth is only 6 m. It represents one of the most important centers of biodiversity in southeastern Europe; it has the status of National Park, Ramsar site, and IBA (Radović et al.

2008). There are 47 fish species, mostly cyprinids (see Appendix), of which 14 (29%) are introduced (Cakić and Hristić 1987; Talevski et al. 2009). We made 21 field trips to this site from April to October in 2011 and 2012.

The third locality from which we collected data on the diet of Dice Snakes is Golem Grad Island in Prespa Lake, which, in part, is in the Former Yugoslav Republic of Macedonia (FYROM: 40°52′ N, 20°59′ E; Fig. 1). This site is ~850 m in elevation and the surface area of the lake is ~250 km^2 with a maximum depth of 55 m (Hollis and Stevenson 1997). The lake and the island are strictly protected within the Galičica National Park. Nevertheless, numerous allochthonous fish species (12 of 23, 52%: see Appendix) have been recorded in the lake (Talevski et al. 2009). Illegal fishing is widespread and common. This particular activity affects Dice Snakes in several ways: it leads to a shortage of food, and many snakes drown entangled in fishing nets set in the shallow waters around the island (Sterijovski et al. 2011). We started a long-term CMR study in 2008 with fieldwork occurring from April to August each year.

The fifth population study on snakes was conducted in the Pančevački rit, an area inundated by the Danube and Tamiš rivers, near Belgrade, Serbia (44°50′ N, 20°29′ E, Fig. 1; 76 m elevation). This wetland area is under various anthropogenic pressures: amelioration, pollution, construction projects, gravel extraction, burning of dry vegetation, intensive fishing, and introduction of non-native fish species (Cakić and Hristić 1987; Marko Anđelković, pers. obs.). Due to gravel extraction and illegal waste dumping, small water bodies continuously form and disappear; therefore, the composition of the terrain constantly changes. In Pančevački rit, we have studied both species of *Natrix* since 2011; we spent approximately 20 days in the field altogether. In this complex habitat, 35 fish species have been recorded; eight (23%; see Appendix) are introduced (Cakić and Hristić 1987).

Field procedures.—At all study sites, we captured snakes by hand and kept them in canvas bags until processing. After measuring and marking, we released them at the exact places of capture. For all individuals we recorded standard measurements: snout-to-vent length (SVL) with a tape measure to 1 mm, and body weight (BM) using an electronic scale, to 1 g. We marked all animals with a standard method of clipping ventral scales (Bonnet et al. 2002; Dorcas and Willson 2009). During this procedure, animals would often regurgitate the ingested prey. Also, we palpated some snakes to make them regurgitate the swallowed food. We used this method only with snakes that had obviously swallowed the prey a short time before capture (i.e., the prey was palpable in the upper portions of the digestive tract); hence, we were sure to obtain an intact food item. This procedure does not harm the snake (Fauvel et al. 2012).

RESULTS

We processed between 86 and 5,376 snakes in the five study sites. Sex ratios (M/F) were between 0.28 (Vrbanja River) and 2.77 (Pančevački rit). Percentages of adult animals that we found with prey ranged from 3.51 to 75.00; among juvenile and sub-adult snakes, these percentages varied between 0.63 and 50.00 (Table 1). We calculated the number and percentages of animals with food items in any condition (intact or half-digested, tangible in the stomach and abdomen, or regurgitated) from the total encounter numbers. In all samples, except Grass Snakes from Pančevački rit, there were more females than males that had eaten. This relation was obtained even in populations with male-biased sex ratios. Percentages of sub-adult and juvenile snakes with food were lower than in adults in all samples (Table 1). We obtained identifiable food items from 27 snakes in the wetland complex of Bardača, 19 from the Vrbanja River, eight from the Skadar Lake, and 80 from the Prespa Lake. In the Pančevački rit, we obtained identifiable food items from 18 Grass Snakes and 14 Dice Snakes.

Diet composition of Grass Snakes.—In 2011, in the Bardača wetland, we caught the majority of Grass Snakes along the shores of the Necik Lake. Green frogs (*Pelophylax* sp.) dominated (83%) their diet (Table 2). In 2012, Necik Lake was completely drained. Consequently, the snakes disappeared from this primary study area; instead, we searched for them around the adjacent Rakitovac Lake. A small pool formed along one of the Rakitovac Lake drainage canals, and a large number of fish were trapped in it (Fig. 2); the most common species was the Brown Bullhead. The other species present in this trap were the European Perch (*Perca fluviatilis*), the Prussian Carp (*Carassius gibelio*) and several other cyprinids.

In March and April 2012, we captured 70 Grass Snakes along the Rakitovac outlet canal. Of all the snakes we observed feeding or that had recently fed (21), 86% (18 individuals) had consumed Brown Bullhead, and we found three with Prussian Carp (100% of the diet were allochthonous fishes). This was despite the fact that snakes can be seriously injured or even killed by the stiff spines of the dorsal and pectoral fins of the Brown Bullhead (Fig. 3). Another significant observation was that among the 18 Grass Snakes that had caught catfish (*Ameiurus* spp.), 13 were large females (60.2–81.5 cm SVL) and five were males (50.1–58.2 cm SVL). We found one of the smaller females (65 cm SVL) and a small male (50.3 cm) with the spines of catfish

TABLE 1. Total numbers and numbers marked (in parentheses) – first three columns, adult sex ratio (M/F), and number and percentages (in parentheses; last three columns) of adult (A), subadult (SA), juvenile (J) Dice Snakes (*Natrix tessellata*) and Grass Snakes (*Natrix natrix*) with intact and half-digested food items (all encounters, captures and recaptures, are considered).

		Adults			Snakes with food		
	All Snakes	F	M	M/F	F	M	SA and J
Natrix tessellata							
Vrbanja River	374 (314)	131 (98)	30 (27)	0.28	20 (15.3%)	3 (10.0%)	31 (14.6%)
Lake Skadar	230 (227)	45 (45)	90 (87)	1.93	10 (22.2%)	16 (17.8%)	13 (13.8%)
Golem Grad Island	5960 (5376)	3369 (2906)	1939 (1826)	0.63	237 (7.03%)	68 (3.51%)	4 (0.63%)
Pančevački rit	162 (161)	14 (13)	36 (36)	2.77	7 (50.0%)	17 (47.2%)	10 (8.93%)
Natrix natrix							
Bardača	115 (108)	57 (53)	46 (43)	0.81	27 (47.4%)	15 (32.6%)	6 (50.0%)
Pančevački rit	86 (86)	20 (20)	12 (12)	0.60	11 (55.0%)	9 (75.0%)	22 (40.7%)

protruding from their bodies, but both snakes were alive and apparently well.

For comparison, Grass Snakes in Pančevački rit (two years pooled; Table 2) consumed mostly anurans: of 14 prey items, 12 (85.7%) were green frogs. One fish species eaten was native to the Balkans and another was the Brown Bullhead, native to eastern North America. In April 2013 we documented two prey species previously unreported for Grass Snakes: the Wall Lizard (*Podarcis muralis*) and the Green Toad (*Pseudepidalea viridis*). In fact, one Grass Snake had ingested both these species.

Diet composition of Dice Snakes.—In the four localities where we studied Dice Snake diet, the composition of ichthyofauna differed substantially: from 100% autochthonous to 52% allochthonous species (see Appendix), and snakes' prey preferences differed in these circumstances (Table 3). In the Skadar Lake, although the native fish species are dominant (71%), as much as 62% of the diet of Dice Snakes was non-native fishes. In Prespa Lake, the percentages of native and non-native fish species are balanced (48% and 52%, respectively); however, Dice Snakes consumed considerably more autochthonous species (88%). In the Pančevački rit wetland, autochthonous fish species predominate (77%). We recorded 18 fish in the prey of the Dice Snakes from this ecosystem; 17 were European Weatherfish (*Misgurnus fossilis*), an autochthonous species, but we could not identify one species due to the degree of digestion by snake. On two occasions in April 2013, we found Smooth Newts (*Lissotriton vulgaris*) in the prey of Dice Snakes from Pančevački rit. We are not aware of any previous report of newts being consumed by these snakes. In the Vrbanja River, all fish species are autochthonous, and nothing but fish was found in the diet of Dice Snakes, in spite of the presence of huge numbers of green frogs.

FIGURE 2. A small pool along one of the Rakitovac Lake drainage canals with trapped fish Brown Bullhead, *Ameiurus nebulosus* dominating. (Photographed by Goran Šukalo).

DISCUSSION

Previous studies of European populations of Grass Snakes reported a wide spectrum of prey: amphibians (up to 93%), fish, small reptiles, birds, and rodents (Filippi et al. 1996; Gregory and Isaac 2004; Janev Hutinec and Mebert 2011). Luiselli et al. (2005) found substantial inter-population differences in the composition of the diet of the Grass Snake, dependent on the type of habitat, climate, altitude, and presence of congeneric competitors. The diet is determined by the abundance and availability (i.e., accessibility) of suitable prey (Willson and Hopkins 2011). Non-native species

TABLE 2. Grass Snake (*Natrix natrix*) intra-population variation in diet composition due to habitat change in Bardača in two consecutive years and intra-population diet variation in Pančevački rit.

Year	Total No. of prey items	Amphibian prey items	Autochthonous fish prey items	Allochthonous fish prey items
Natrix natrix, Bardača				
2011	6	5 (83%)	0	1 (17%)
2012	21	0%	0	21 (100%)
Pooled 2011 + 2012	27	5 (18.5%)	0	22 (81.5%)
Natrix natrix, Pančevački rit				
2011 spring	3	2 (66.7%)	0	1 (33.3%)
2011 summer	0	0	0	0
2012 spring	10	9 (90%)	1 (10%)	0
2012 summer	1	1 (100%)	0	0
Pooled 2011 +2012	14	12 (85.7%)	1 (7.1%)	1 (7.1%)

of amphibians and fish have been found in the prey of several *Natrix* species (Gregory and Isaac 2004; Santos and García-Cardenete 2005; Alarcos et al. 2009). During our two-year study, we recorded a dramatic change in the prey of the Grass Snake in the Bardača wetland, the habitat that suffered radical alteration. This wetland, although formally protected, is under heavy pressures, and the enormous concentration of alien fish species in its waters could be considered proof of the disturbed balance in this ecosystem (e.g., Cucherousset et al. 2006). After draining the majority of water bodies in Bardača, the snakes started feeding exclusively on allochthonous fishes instead of anurans.

The wide distribution of Grass and Dice snakes (Arnold and Ovenden 2002) illustrates their niche breadth and adaptability under challenging circumstances. Previous records and the findings presented herein demonstrate that snakes can find a way to feed even on fish that can inflict substantial damage or cause death, in some instances (Mills 2002; Santos and García-Cardenete 2005; Šukalo et al. 2012). One of these harmful fish is the Brown Bullhead, a species of North American origin, which is considered as invasive on other continents (Cakić and Hristić 1987; Declerck et al. 2002). In the native range of ictalurid catfish, there are records of natricine snakes (*Nerodia taxispilota*) that survived massive wounds inflicted by these fish, living for several years, and in some instances, growing considerably (Mills 2002). There are populations within this species in which adults feed almost exclusively on ictalurid catfish (Mills et al. 1995; Mills 2002).

FIGURE 3. Grass Snake (*Natrix natrix*) along the Rakitovac outlet canal with half-swallowed Brown Bullhead (*Ameiurus nebulosus*). The fin spine of the fish is protruding from the ventral body wall of the snake. (Photographed by Goran Šukalo).

The majority of alien fishes present in the surveyed ecosystems were introduced into Europe and/or the former Yugoslavia 50 to 120 y ago (Cakić and Hristić 1987; Lenhardt et al. 2011; Rutkayová et al. 2013). Therefore, we assume that not all native predators have learned to cope with alien prey and many die trying to eat these fish (Šukalo et al. 2012; data presented herein); however, the potential for overcoming possible perils of feeding on some alien fish is evident. It was experimentally shown that the spines in another ictalurid species (Channel Catfish, *Ictalurus punctatus*) cannot prevent attacks, but they seriously complicate ingestion by gape-limited predators. However, such predators were proven capable of learning to avoid fish with intact spines (Bosher et al. 2006). In the Bardača wetland, the Brown Bullhead was caught mostly by large female Grass Snakes. Among the females that had caught Brown Bullheads, only one was pierced by its spines. This is in accord with the gape size limitations, and with the female-biased sexual dimorphism in body length and relative head size (Luiselli et al. 2007). Thus, it is possible that the snakes that are large enough to swallow a hazardous fish seized an opportunity to feast on the trapped prey. Our data also corroborate previous findings that snakes feed on prey species that are the most abundant, and therefore the easiest to catch under given circumstances (see also King et al. 2006).

Another potentially deadly fish species found in the study areas surveyed during the course of the present

TABLE 3. Ratios of autochthonous to allochthonous fish species in the diet of Dice Snakes (*Natrix tessellata*) from four study sites.

Site	Total No. prey items	Autochthonous fish as prey	Allochthonous fish as prey
Vrbanja River	19	19 (100%)	0 (0%)
Skadar Lake	8	3 (37.5%)	5 (62.5%)
Prespa Lake	80	71 (88.8%)	9 (11.25%)
Pančevački rit	18	18 (100%)	0 (0%)

study is the Pumpkinseed Sunfish (*Lepomis gibbosus*).

This fish also originated in North America and its success in colonizing some freshwater habitats in Europe results from high plasticity in crucial life-history traits (Fox et al. 2007). According to available information (Velikov 2011), there are no published data of Dice Snakes being killed by Pumpkinseed Sunfish. However, its congeners, Grass Snakes and Viperine Snake (*Natrix maura*) can die of the damage inflicted by the sharp fin rays of the Pumpkinseed Sunfish, Brown Bullhead, and other alien fish species (Santos and García-Cardenete 2005; Alarcos et al. 2009; this study). Even without directly damaging the snake, a Pumpkinseed can increase its vulnerability. An experiment with the Southern Watersnake (*Nerodia fasciata*) showed that after ingestion of a fish of inadequate shape (Fig. 4), the mobility of the snake was dramatically reduced (Willson and Hopkins 2011) making it more vulnerable to predators.

In a long-term sense, aquatic snakes can contribute to restoring the previous balance in a disturbed ecosystem, by participating in regulation of the dynamics of invasive fish species populations (Alarcos et al. 2009; Carlsson et al. 2009; Kornis et al. 2012). However, if these fish become the prevalent prey, too many snakes may die struggling to feed. Comparisons of two of our wetland habitats showed that in an ever-changing, polluted, but not drained, wetland (Pančevački rit), Grass Snakes fed mostly on anurans, which is their normal diet. In Bardača, a wetland that had been drained and of which only a small portion remained, the snakes switched to invasive fish. Comparisons of the diets of Dice Snakes showed that in three of four study sites (Vrbanja River, Prespa Lake, and Pančevački rit), Dice Snakes fed predominately on native fish but in Skadar Lake they ate more alien species. Native fish were prevalent in Vrbanja River, Skadar Lake, and Pančevački rit. The discrepancy was found in the Prespa and Skadar lakes. Despite a high proportion of alien fish species, in Prespa the snakes fed mostly on native fish species but in Skadar Lake, despite the prevalence of natives, snakes feed on alien fish species. At present, this result must be considered cautiously, due to the small prey sample size from Skadar Lake. Nevertheless, it can be supposed that in an ancient, deep, and comparatively well preserved Prespa Lake, the food web is more stable than in other surveyed habitats. This includes Skadar Lake, which is large but shallow, and presumably more prone to variations in abiotic and biotic constituents. Certainly, wider-scope studies are necessary to determine the link between the type and state of a water body, presence of non-native fish species, and relations between various kinds of predators, prey, and their parasites (see Reshetnikov et al. 2013).

FIGURE 4. Dice Snake (*Natrix tessellata*) starting to swallow a Pumpkinseed Sunfish (*Lepomis gibbosus*) in a small artificial pool near the village Bački Brestovac. (Photographed by Aleksandar Popović).

Invasions into aquatic ecosystems by various organisms are most likely to take place in disturbed, unstable habitats (Cucherousset et al. 2006, and references therein; Gherardi 2007). Alien fish species can and often do seriously disturb and threaten native ichthyofauna and herpetofauna; their numerous direct and indirect influences have been recorded, but not all are fully understood and explained (Declerck et al. 2002; Kreutzenberger et al. 2008; Copp et al. 2010; Li et al. 2011; Rutkayová et al. 2013). Some snake species have successfully included allochthonous fish and amphibians in their food spectrum (Mullin et al. 2004, Li et al. 2011; Kornis et al. 2012). Further studies of the biology of aquatic snakes would be beneficial in numerous ways. To understand piscivorous snakes, it is necessary to understand native and non-native fish and their biology. Comprehension of the food web and the effects of numerous abiotic and anthropogenic influences on it can lead to the prescription of appropriate preservation and restoration measures for entire aquatic ecosystems (see Matthews et al. 2002; Cucherousset et al. 2006; Phillips and Shine 2006; Carlsson et al. 2009; Shine 2012). Additionally, being the top predators, (semi-)aquatic snakes were long ago recognized as good indicators of the contamination levels of aquatic habitats (Stafford et al. 1976; Ohlendorf et al. 1988; Fontenot et al. 2000). Nevertheless, few studies of contamination of water

bodies have been done with snakes as the main target organism. Future ecological and conservation studies and programs for the restoration of wetlands should consider the feeding habits and behavioral traits of aquatic snakes.

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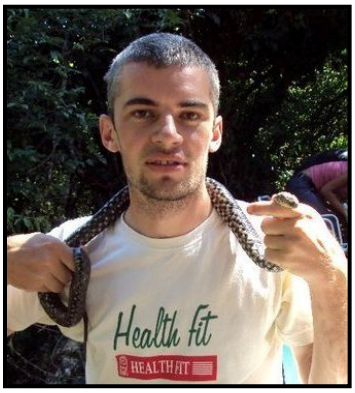

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APPENDIX. Ichthyofauna of the five surveyed localities on the Balkan Penisula that are potential prey of the Grass Snake (*Natrix natrix*) and the Dice Snake (*Natrix tessellata*). Under each locality: Aut. = autochthonous fish species and All. = allochthonous fish species.

Species	Bardača		Vrbanja		Lake Skadar		Lake Prespa		Pančevački rit	
	Aut.	All.	Aut.	All.	Aut.	All.	Aut.	All.	Aut.	All.
Abramis ballerus									+	
Abramis brama	+		+						+	
Abramis sapa									+	
Acerina cernua	+								+	
Acerina schraetser									+	
Acipenser naccarii					+					
Acipenser ruthenus									+	
Acipenser sturi					+					
Alburnoides bipunctatus			+							
Alburnoides ohridanus					+					
Alburnoides prespensis							+			
Alburnus alburnus	+		+						+	
Alburnus belvica							+			

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Species	Bardača		Vrbanja		Lake Skadar		Lake Prespa		Pančevački rit	
	Aut.	All.	Aut.	All.	Aut.	All.	Aut.	All.	Aut.	All.
Alburnus scoranza					+					
Alosa falax					+					
Ameiurus nebulosus						+				+
Anguilla anguilla					+		+			
Aspius aspius									+	
Barbatula zetensis					+					
Barbus balcanicus			+							
Barbus barbus			+							
Barbus prespensis							+			
Barbus rebeli					+					
Blicca bjoerkna	+								+	
Carassius carassius									+	
Carassius gibelio		+				+		+		+
Chalcalburnus chalcoides	+								+	
Chondrostoma nasus	+		+						+	
Chondrostoma prespense							+			
Chondrostoma scodrensis					+					
Citharus linguatulus					+					
Cobitis elongatoides		+								
Cobitis ohridana				+						
Cobitis meridionalis						+				
Cobitis taenia	+							+		
Cottus gobio		+								
Ctenopharyngodon idella					+			+		+
Cyprinus carpio	+	+		+		+		+		
Dicentrarchus labrax				+						
Esox lucius	+							+		
Gambusia holbrooki					+			+		
Gasterosteus gymnurus				+						
Gobio gobio		+								
Gobio obtusirostris	+	+								
Gobio skadrensis				+						
Hucho hucho		+								

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Species	Bardača		Vrbanja		Lake Skadar		Lake Prespa		Pančevački rit	
	Aut.	All.	Aut.	All.	Aut.	All.	Aut.	All.	Aut.	All.
Hypophthalmichthys molitrix					+		+		+	
Hypophthalmichthys nobilis					+				+	
Ictalurus nebulosus	+				+				+	
Lampetra fluviatilis								+		
Lepomis gibbosus	+						+		+	
Leuciscus idus		+						+		
Leuciscus leuciscus				+						
Liza ramada										
Megalobrama terminalis					+					
Misgurnus fossilis								+		
Mugil cephalus				+						
Mylopharyngodon piceus					+					
Oncorhynchus mykiss					+		+			
Pachychilon pictum				+						
Parabramis pekinensis							+			
Pelasgus minutus				+						
Pelasgus prespensis						+				
Perca fluviatilis				+				+		
Pleuronectes flessus			+							
Phoxinus phoxinus	+									
Pleuronectes flessus			+							
Pomatoschistus montenegrensis			+							
Pseudorasbora parva		+		+		+		+		
Rhodeus amarus	+		+		+		+			
Rhodeus sericeus										
Romanogobio kesslerii	+									
Rutilus ohridanus			+							
Rutilus prespensis					+					
Rutilus pigus	+									
Rutilus rutilus	+									
Salaria fluviatilis			+							
Salmo farioides			+							

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Species			Bardača		Vrbanja		Lake Skadar		Lake Prespa		Pančevački rit	
			Aut.	All.	Aut.	All.	Aut.	All.	Aut.	All.	Aut.	All.
Salmo letnica							+					
Salmo marmoratus					+							
Salmo peristericus						+						
Salmo trutta, m. *fario*			+									
Salmothymus zetensis					+							
Salvelinus fontinalis						+						
Scardinius erythrophtalmus	+							+				
Scardinius knezevici					+							
Silurus glanis	+						+	+				
Squalius cephalus	+		+									
Squalius prespensis						+						
Squalius squalus					+							
Stizostedion lucioperca	+							+				
Telestes montenegrinus					+							
Thymallus thymalus			+			+						
Tinca tinca	+					+		+	+			
Umbra krameri									+			
Vimba vimba			+						+			
Total Number	20	4	21	0	34	14	11	12	27	8		
Percentage Auto. and Allo.	83	17	100	0	71	29	48	52	77	23		