

RESEARCH ARTICLE

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A global overview on the diet of the dice snake (*Natrix tessellata*) from a geographical perspective: foraging in atypical habitats and feeding spectrum widening helps colonisation and survival under suboptimal conditions for a piscivorous snake

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Abstract

Background: The dice snake (*Natrix tessellata* Laurenti, 1768) is generally considered to be a fully or partially piscivorous freshwater snake species. The aim of the study was to make the first global overview on the taxonomy and geographical distribution of the species based on own observations, available databases and the special literature.

Results: Besides freshwaters, *N. tessellata* turned out to hunt also in marine and terrestrial habitats preying on at least 29 and 15 species, respectively. On the basis of our data and the literature altogether, 113 prey taxa, mostly fish, were listed but 20% of them were invertebrates, amphibians, reptiles and mammals. The importance of non-fish species in the diet was especially pronounced in deserts, high mountains and in dry Mediterranean areas. In spite of the wide feeding spectrum, only fish and amphibians were found to be predominant food items over the whole species' range. Fish dominated the catch of the dice snake in most quantitative studies, except one survey in Turkey, where the ratio of non-fish prey items was over 50%.

Conclusions: The global analysis of the diet of the dice snake revealed a feeding spectrum characteristically changing over the broad distribution area including non-fish prey as well as taxa from marine and terrestrial habitats. The analysis of the feeding spectrum separated four large geographical units with further distinctions in Central and Eastern Europe. Such diversity helps explain why this species was able to colonise a large and diverse Eurasian range.

Keywords: *Natrix tessellata*; Reptilia; Diet; Feeding spectrum

Background

The dice snake (*Natrix tessellata* Laurenti, 1768) is a Eurasian snake species ranging from Germany and Switzerland to China, Pakistan and Egypt (Gasc et al. 1997; Ibrahim 2012; Mebert et al. 2013) and is well adapted to the aquatic environment (Lahav and Dmi'el

1996; Nekrasova et al. 2013). It occurs in aquatic or marshy habitats, including brackish water (Gruschwitz et al. 1999; Khonjakina 1969; Tuniyev et al. 2011) occasionally even inhabiting cities such as Rome and Prague (Velenský et al. 2011; Vignoli et al. 2009). The distribution area of the dice snake is partly overlapped with two other aquatic *Natrix* species. The grass snake (*Natrix natrix*) lives in Eurasian habitats, often inhabiting similar areas with the dice snake (Gasc et al. 1997) while the viperine snake (*Natrix maura*) has sympatric populations in Switzerland

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and Italy with the dice snake (Metzger et al. 2011; Scali 2011). It is listed in Annex II of the Bern Convention (1999) and it also appears in Annex IV of the Habitat Directive of the European Union (1992) but due to its wide distribution and presumably large population size, it is categorised as least concern by IUCN (2012). However, it is considered to be threatened in a number of western and central European states, with low genetic variation in some populations (Gautschi et al. 2002; Guicking et al. 2004) and its world population was also assessed as declining (IUCN 2012). As such, conservation measures should still be undertaken for this species as habitat destruction, pollution, road traffic, collection and persecution are listed as possible threats.

The dice snake has a large distribution and it occurs in different habitats, which would imply the species can adapt well to local conditions presumably by adopting a wide feeding spectrum. However, it is generally considered to be a diurnal piscivorous snake (Gasc et al. 1997) despite information that shows the species also eats non-fish prey items such as amphibians and reptiles (see e.g. Beshkov and Dushkov 1981). A number of publications contain information on the food of the dice snake, with several focusing on local areas (e.g. Luiselli et al. 2007 on Central Italy), but no global overview of the species' dietary preferences has been published.

The aim of this paper is to review the feeding spectrum of the dice snake over its global distribution by comparing the species' prey items in different countries and offer reasons for potential differences in prey item preference based on geography and habitat conditions.

Methods

Information was gathered from literature sources and personal observations on the diet of the dice snake from its whole range, i.e. from Switzerland in the west to Pakistan and China in the east, and from Germany in the north to Iran in the south. Information from papers only mentioning large, collective groups such as 'insects', 'fish' or 'frogs' as food items without giving species (or genus) level information is discussed in the article (e.g. Brecko et al. 2011) but was not included in the database, even if their addition would have added new items to the list such as mice (Wang et al. 1987) or shrews (Radovanović 1951). No time limit was applied; reports available from the first half of the twentieth century were also used. Besides published records and our observations, citizen science data were also collected by approaching internet databases for photographic evidence of dice snake predation on a given taxa (e.g. <http://www.varangy.hu/>, <http://www.wuerfelnatter.de/>). The distribution of different prey classes among different habitats was calculated and information on their frequency in the diet of the dice snake was also

summarised. Species with no indication of frequency in the diet were listed under 'no quantitative data', whereas the following frequencies were listed when quantitative data was available: under 5% = rare; 5% to 20% = frequent; and >20% = common. Studies including quantitative data were also used for comparison after the relative abundance of prey taxa were calculated. Association analysis with the presence-absence data of the prey taxa of the dice snake were used in non-metric cluster analysis (Goodall 1953; Podani 1997, 2001; Williams and Lambert 1960) to elucidate geographical differences among 18 countries, where appropriate information could be collected. Statistical analysis was made using SYN-TAX 2000 (Podani 2001). Results were plotted by MS Office 2010 and SYN-TAX 2000 (Podani 2001).

Results

Species composition of prey taxa

Altogether, 113 animal taxa have been listed as prey for the dice snake belonging to three phyla: Mollusca, Arthropoda and Vertebrata. The ratio of classes among the taxa is 3% Gastropoda, 2% Insecta, 80% Pisces, 10% Amphibia, 3% Reptilia and 2% Mammalia. The complete list of prey species together with the indication of their frequency in the diet, country and habitat recorded is in Additional file 1.

Figure 1 contains the number of species from the different classes in different habitats and their frequency distribution. It shows that in marine habitats, only fish were predated; in freshwater and terrestrial habitats, the most frequently eaten prey items were fishes and amphibians, respectively. The quantitative data shows that fish and amphibians overall were the most frequently eaten prey items, with invertebrates, reptiles and mammals eaten only rarely.

Abundance of prey taxa in the diet of the dice snake

Detailed quantitative data on the diet of the dice snake were found in eight articles (Acipinar et al. 2006; Bakiev et al. 2011; Filippi et al. 1996; Göçmen et al. 2011; Hutinec and Mebert 2011; Luiselli et al. 2007; Sloboda et al. 2010; Zimmerman and Fachbach 1996) including 2,375 prey items from the investigation of more than 2,730 snakes. The relative abundance of the different fauna groups at six European and two Asian sites is summarised in Figure 2, which shows a relatively uniform pattern, fishes comprised the highest abundance of prey items in seven out of the eight studies (Acipinar et al. 2006; Bakiev et al. 2011; Filippi et al. 1996; Göçmen et al. 2011; Hutinec and Mebert 2011; Luiselli et al. 2007; Sloboda et al. 2010; Zimmerman and Fachbach 1996). In four surveys (Austria, Croatia, Northern Turkey, Romania), they were the only food items described, while in Italy, amphibians were also eaten in both cases.

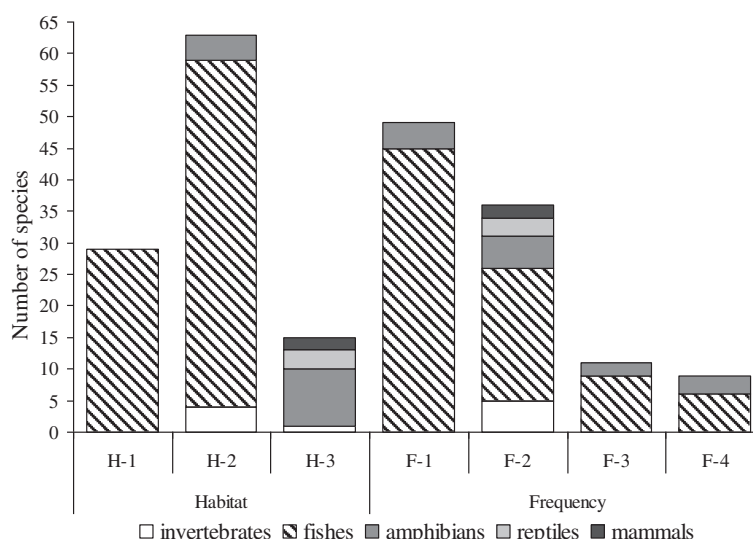


Figure 1 Number and frequency of prey species in the diet of *Natrix tessellata* in different habitats. Invertebrates were united into one group due to their low number and similar distribution. Code of categories: H-1: marine, H-2: freshwater, H-3: terrestrial, F-1: no quantitative data, F-2: rare, F-3: frequent, F-5: common.

Unlike these studies, fishes did not have an absolute dominance among the prey items in Central Turkey (Acipinar et al. 2006); dice snakes also consumed invertebrates (Bakiev et al. 2011; Göçmen et al. 2011), amphibians (Bakiev et al. 2011; Hutinec and Mebert 2011) and, to a moderate extent, reptiles (Bakiev et al. 2011; Filippi et al. 1996; Luiselli et al. 2007) and mammals (Göçmen et al. 2011).

Geographical differences in the feeding spectrum of the dice snake

Species (and, in some cases, genus) level data on the feeding spectrum of the dice snake was collected from 18 countries. Their similarity can be seen in Figure 3. The highest number of prey species eaten was found in studies conducted in Russia, Bulgaria and Switzerland, the lowest in Iran, Syria and Slovenia. Fish were

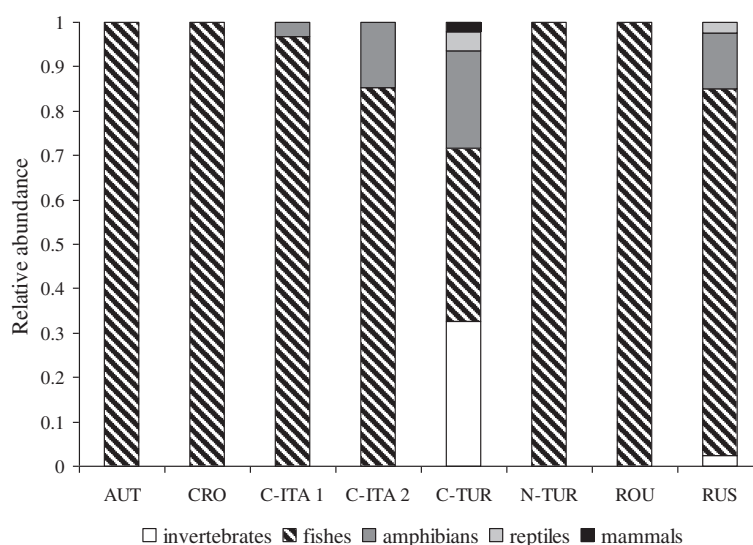


Figure 2 Relative abundance of prey items in the diet of *Natrix tessellata* in seven Eurasian studies. Invertebrates were united into one group due to their low number and similar distribution. Country codes: AUT: Austria, CRO: Croatia, C-ITA 1: Central Italy, C-ITA 2: Northern Italy, C-TUR: Central Turkey, N-TUR: Northern Turkey, ROU: Romania, RUS: Russia.

recorded in the diet of the dice snake in all countries and they comprised the highest number of species eaten in each of them. In spite of the high ratio of fishes among prey items investigated, in nearly 75% of the countries (Italy, Turkey, Switzerland, Slovenia, Czech Republic, Poland, Russia, Romania, Bulgaria, Georgia, Azerbaijan, Syria, Jordan), other prey groups were also found, amphibians in all these cases, invertebrates, reptiles and mammals in two or three countries. Invertebrates and mammals were only recorded in the diet of the dice snakes in Turkey and Russia and reptiles in those of Italy, Turkey and Russia. These results show the widest dietary niche of the dice snake is occurring in Turkey and Russia, with all five prey groups shown to be eaten in previous studies.

The analysis of the results revealed zoogeographical differences in the feeding spectrum of the dice snake (Figure 4). In the Middle East, the number of species eaten was relatively low (under eight species in any country) with only fish and amphibians eaten. The same taxa characterise countries in the Ponto-Caspian group but different species are fed on and the number of species was also higher. The remaining two groups (Central and Eastern European, Mediterranean) are characterised by a wide feeding spectrum, characteristic differences among the countries and further division in the Central and Eastern European group e.g. according to altitude.

Discussion

Data from 18 countries proved that the dice snake feeds on at least 113 prey taxa from six classes. Fish were the

most important prey items; the importance of non-fish species in the diet was pronounced in deserts, high mountains and in dry Mediterranean areas. In spite of the wide feeding spectrum, only fish and amphibians were found to be predominant food items over the whole species' range.

Species composition of prey taxa

Due to its excellent swimming and diving abilities and fidelity to freshwater habitats, the dice snake is generally considered to be a piscivorous fish species (Gasc et al. 1997, Kreiner 2007). However, the global feeding spectrum of the dice snake is surprisingly wide; it also includes a reasonable number of marine and terrestrial species (Figure 1), both fast- and slow-moving animals. For example, reptiles, especially lizards, have been found in the diet of the dice snake for more than 60 years (Göçmen et al. 2011), and slow aquatic and terrestrial invertebrates, snails and insects were also repeatedly reported (Additional file 1) (Bakiev et al. 2011; Göçmen et al. 2011; Wang et al. 1987, 2005). A key factor determining the actual species composition is that according to current understanding of the species' habitat requirements over much of its range, the dice snake remains in the immediate vicinity of surface waters at a distance of less than 20 metres to the water edge during the active season (Conelli et al. 2011; Neumann and Mebert 2011; Velenský et al. 2011). As a result, the dice snake nearly exclusively feeds on aquatic and/or water-bound animals. The most important prey organisms are fish, especially in the European part of its distribution area, where over 75 species were recorded in the diet and 85% to 100%

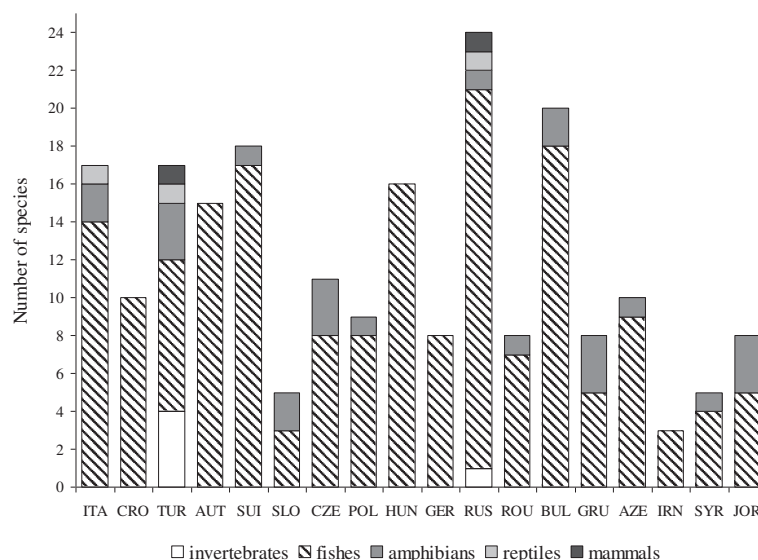


Figure 3 Geographical distribution of prey in the diet of *Natrix tessellata*. Invertebrates were united into one group due to their low number and similar distribution. Country codes: ITA: Italy, CRO: Croatia, TUR: Turkey, AUT: Austria, SUI: Switzerland, SLO: Slovenia, CZE: Czech Republic, POL: Poland, HUN: Hungary, GER: Germany, RUS: Russia, ROU: Romania, BUL: Bulgaria, GRU: Georgia, AZE: Azerbaijan, IRN: Iran, SYR: Syria, JOR: Jordan.

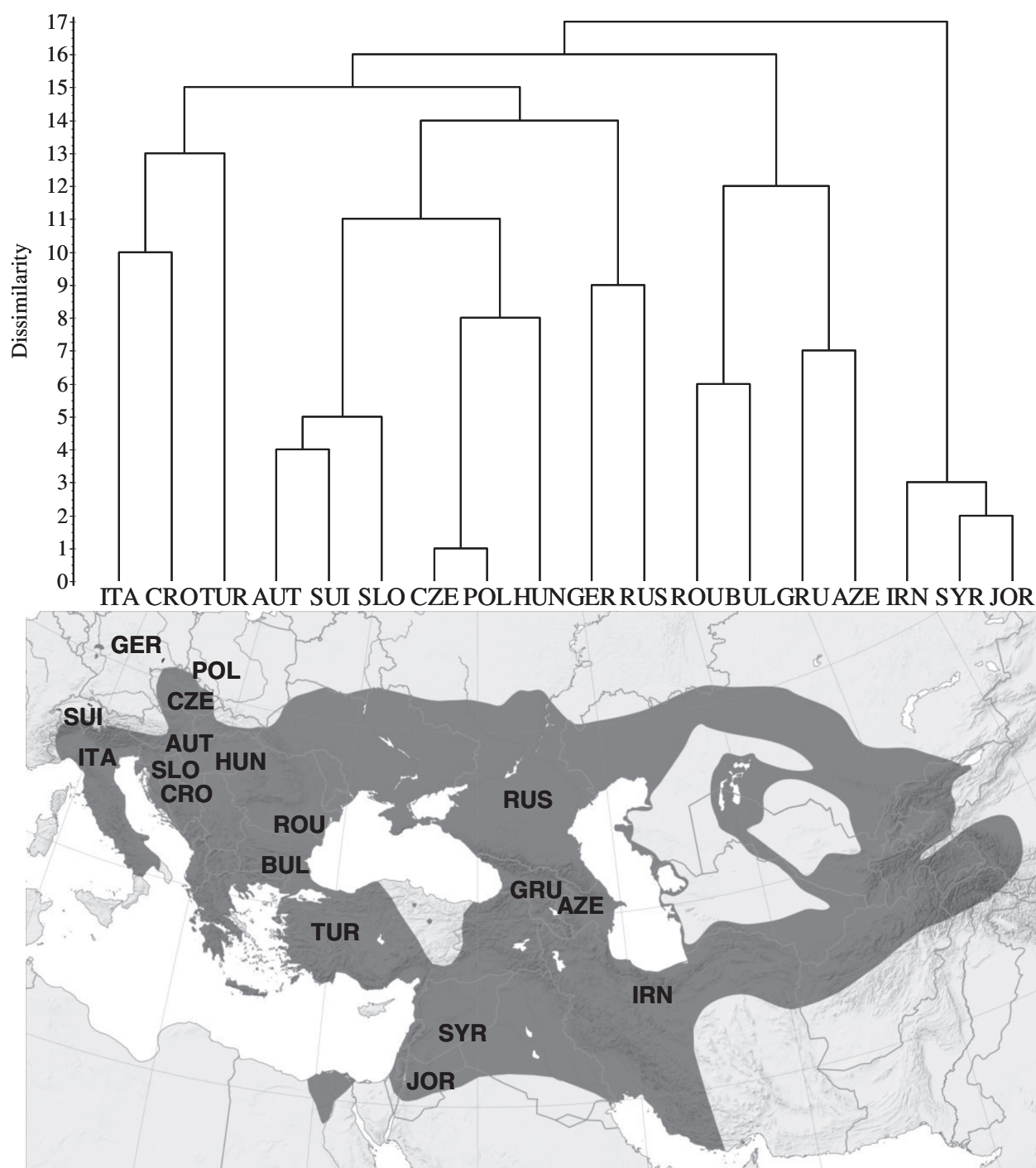


Figure 4 Similarity of the feeding spectrum of *Natrix tessellata* in 18 countries. Shading in the map indicates the species' range. Country codes: ITA: Italy, CRO: Croatia, TUR: Turkey, AUT: Austria, SUI: Switzerland, SLO: Slovenia, CZE: Czech Republic, POL: Poland, HUN: Hungary, GER: Germany, RUS: Russia, ROU: Romania, BUL: Bulgaria, GRU: Georgia, AZE: Azerbaijan, IRN: Iran, SYR: Syria, JOR: Jordan.

of food items belonged to this group. There is a clear relationship between fish species preyed upon and the size of water bodies. In seas, the dice snake may cover long distances up to several kilometres to hunt on benthic (*Neogobius* sp., *Parablennius* sp., *Ponticola* sp.) or open

water marine (*Clupeonella* sp., *Symphodus* sp.,) fish species as it has been observed in the Caspian Sea (Tuniyev et al. 2011). In large lakes such as Lake Baćina (Hutinec and Mebert 2011), Lake Balaton (own unpublished data), Lake Prespa (Sterijovski et al. 2011), Lake Sinoe (Sloboda et al.

2010) and Lake Geneva (Metzger et al. 2011), the dice snake mostly eats benthic fish (*Neogobius* sp., *Cottus gobio*) and/or fish species hidden in aquatic vegetation stands (*Cyprinidae* sp., and e.g. *Blennius fluviatilis*, *Lepomis gibbosus*, *Perca fluviatilis*). In large rivers, densely vegetated water courses and lakes, they hunt fish (mainly *Cyprinidae* sp.), amphibian larvae and adults (mainly *Pelophylax* and *Rana* sp.) near the bank (Acipinar et al. 2006; Filippi et al. 1996; Gaebeler et al. 2013; Luiselli et al. 2007; Vlček et al. 2010; Weiperth et al. 2014; Zimmerman and Fachbach 1996). In fishponds, the main prey species of the dice snake were juvenile fish from aquaculture and allochthonous fish species (Acipinar et al. 2006) with occasional predation on amphibians (tadpoles and froglets) such as in Jordanian fish ponds (Amr and Disi 1998) (Additional file 1). With decreasing waterbody size, the feeding spectrum of the dice snake considerably changes to include terrestrial species besides fish and amphibians common in the given area (Amr and Disi 1998, 2011; Bakiev et al. 2011; Göçmen et al. 2011; Luiselli et al. 2007; Žagar et al. 2011) (Additional file 1). Populations in high mountains (over 1,000 m a.s.l.) may specialise on eating larval and adult amphibians (Cafuta and Krofel 2007; Frotzler et al. 2011; Tuniyev et al. 2011; Žagar et al. 2011) as predominant food. It can also be considerable in arid regions, where the dice snake often lives along temporary water bodies or fish ponds, where only a limited number of fish species are present (Amr and Disi 2011; Amr et al. 2011; Göçmen et al. 2011; Laňka 1978; Gruschwitz et al. 1999; Shehab et al. 2011). As young fish produced in fish farms can become an important element in the diet of the dice snake besides natural conditions, human activity may also influence the spread and survival of this snake (Acipinar et al. 2006; Göçmen et al. 2011).

Abundance of prey taxa in the diet of the dice snake

Several publications include estimates on the frequency of different prey organisms of the dice snake, including estimates for various habitats. Wang et al. (1987, 2005), for example, investigated 200 individuals and listed fish as the main food item in large, reed covered water bodies, insects, tadpoles and adult amphibians in temporarily water-covered rice paddies and connecting canals among them, and fish, tadpoles, insects and rodents (primarily mice) along streams in other agricultural areas in north-eastern China.

From the summary of detailed quantitative studies at half the sites only fish species were found in the dice snake (Figure 2); this result is characteristic for the species inhabiting permanent streams and large water bodies or rivers in Austria, Croatia, Romania and northern Turkey (Acipinar et al. 2006; Hutinec and Mebert 2011; Sloboda et al. 2010; Zimmerman and Fachbach 1996). Contradictory results were found on prey selection. For example, in Styrian waters, there was no complete

overlap between the abundance of the different species in fish communities and in the diet of the dice snake (Zimmerman and Fachbach 1996), while in the Danube Delta, the number of snake-caught gobiid species was reflective of the abundance of the respective species in bottom habitats (Sloboda et al. 2010). Though the feeding spectrum of the studies was wide, fish were also the most abundant prey species at the other sites including the Mediterranean (Bakiev et al. 2011; Filippi et al. 1996; Luiselli et al. 2007). In one case, however, other food items (insects, amphibians, reptiles and mammals) in total were more numerous than fish (Göçmen et al. 2011). Though the number of these studies is limited, they support the general conclusion that over much of its range, the dice snake primarily feeds on fish, while in arid areas (see also Frotzler et al. 2011) and, according to Cafuta and Krofel (2007), also in high mountains, its diet may shift towards amphibians and other prey items.

Geographical differences in the feeding spectrum of the dice snake

The feeding spectrum of the dice snake differs among different regions, the analysis of the results revealed four main groups (Figure 4). The group separated most from other branches includes Asian countries with dice snake populations in highly arid regions (Iran, Syria, Jordan). The list of prey species in these countries is short, with snakes predominantly feeding on fish and amphibians from permanent rivers and alien fish species kept in fish farms (Amr and Disi 2011; Amr et al. 2011; Shehab et al. 2011). Fish ponds also function as refugia over the driest periods but at the same time the dice snake is under great predation pressure there due to the large number of aquatic birds present (Amr and Disi 2011; Bakaloudis et al. 1998; Shehab et al. 2011).

The second group in the cluster includes countries with the highest number of Ponto-Caspian gobiid species (e.g. *Neogobius*, *Parablennius*, *Ponticola*). Marine fish species are also common and amphibian predation was recorded in all countries of the Romanian-Bulgarian-Georgian-Azerbaijani branch (Additional file 1) as well (Fautz 1986; Schülter 2006; Sloboda et al. 2010; Tuniyev et al. 2011).

Central and Eastern European countries formed a common group with Russia. There are several fish with very large distribution areas among the prey species there such as *Alburnus alburnus*, *Squalius cephalus*, *Rutilus rutilus*, *Cyprinus carpio*, *Gobio gobio*, *Perca fluviatilis* (Additional file 1). The Czech - Polish branch include countries with limited amphibian consumption (Rehak 1992; Švab 2003; Vlček et al. 2010), while high mountain populations (Austria, Switzerland, Slovenia) feeding on locally characteristic fish species and also on amphibians are on another sub-branch.

Countries with Mediterranean climate (Croatia, Italy, Turkey) form the final group with freshwater tolerating marine fish species and cosmopolitan fish species in the diet of the dice snake. This area is characterised with the most diverse feeding spectrum including snails, insects, reptiles and mammals (Additional file 1, Figure 3) related to the drying out of many water bodies during summer. During extremely hot summers, the dice snake was also observed to hunt at night, also far away from surface waters, which furthers the potential feeding spectrum of this snake (see e.g. Moller 1990, who observed over a period of several weeks a large dice snake which 'unusually' hunted geckos at night).

Snakes have strikingly different feeding spectra ranging from strictly egg-eating species with limited distribution (see e.g. Dandge 2008) to generalist species living over large areas (Gregory and Isaac 2004). The dice snake is present in over 20 countries on three continents, which is, unlike what has been suggested earlier on the basis of observations from the western-central part of its distribution area, partly the result of its generalist feeding strategy leading to a good adaptive ability if the potential prey spectrum changes (Acipinar et al. 2006; Reshetnikov et al. 2013). It is also supported by its anatomy enabling this snake to hunt effectively in both aquatic and terrestrial environments (Bilcke et al. 2006, 2007; Brecko et al. 2011; Ghira et al. 2009; Wassenbergh et al. 2010). As such, a wide feeding spectrum had been expected as a result of this study. On the one hand, the global comparison supported the assumption that the dice snake is a piscivorous snake; it stressed the importance of fish in the diet. On the other hand, it revealed the complexity of the feeding spectrum including invertebrates, amphibians, reptiles and mammals and good adaptability to the effect of climate, altitude and even human activity, which explains why this species could colonise a large and diverse Eurasian range. Also, it elucidated the ability of this snake to survive under suboptimal conditions at the edge of its distribution, enter atypical habitats in natural areas such as high mountains as well as in human-dominated landscapes, such as rice paddies by shifting its diet even towards terrestrial or marine prey species.

Abiotic environmental parameters are known to have an important, but limited power in determining reptile distributions on a larger scale; other factors such as resources are also important (Guisan and Hofer 2003). As far as feeding spectra are concerned, the dice snake was considered to be in an intermediate position among the three *Natrix* species inhabiting the Palearctic. In a comparative study with the closely related grass snake (*Natrix natrix*), Luiselli and Rugiero (1991) found the dice snake to have a narrower feeding spectrum than the grass snake, which also has a broader distribution (Gasc et al. 1997). The latter species more plastically changing its diet and populations near to each other within relatively

short distances may specialise on different food (Luiselli et al. 2005). What is more, the presence of the dice snake did not have any apparent effect on the food types eaten by grass snakes because grass snakes consumed fish when sympatric with *N. tessellata* (Luiselli et al. 2005). The diet of the third species, the viperine snake, *Natrix maura*, shows a considerable overlap with that of the dice snake but with some exceptions (see e.g. the observations of Scali, 2011), and due to other factors as fertility and size, the dice snake is able to outcompete the viperine snake (Metzger et al. 2011).

Conclusions

This study altered the hypothesis that the diet of the dice snake consists of fish from freshwater habitats as indicated by several authors. While this is still the majority of the diet, the feeding spectrum characteristically changed over the broad distribution of the species including non-fish prey as well as taxa from marine and terrestrial habitats as well. The dice snake is rather opportunistic in preying on fish, in total it was proved to eat at least 87 fish taxa, but it also takes other prey, primarily amphibians, when fishes are regionally not constantly available. The analysis of the feeding spectrum separated four large geographical units with further distinctions in Central and Eastern Europe. Such diversity helps explain why this species was able to colonise a large and diverse Eurasian range.

Additional file

Additional file 1: Global prey spectrum of the dice snake (*Natrix tessellata*). The file contains detailed information on each prey taxa of *Natrix tessellata*, countries they were recorded, their frequency, the habitat type they were found and the source of the information (Ahmadzadeh et al. 2011; Bressi 1995; Carlsson et al. 2011; Kammel and Mebert 2011; Karvemo et al. 2011; Kireev 1983; Krasawtzev 1934; Mårtson et al. 2001; Mebert et al. 2011; Musilová and Zavadiš 2011; Schiemenz 1987; Velikov 2011).

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

WA, GT, PI and PM participated in field sampling and overviewed the online databases, WA, PI and PM designed and prepared the additional file and processed the multi-lingual literature, WA and GT prepared the cluster analysis of country-based data presented in Figure 4, and PM finalized the manuscript with WA. All authors read and approved the final manuscript.

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