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The prey spectrum of *Natrix natrix* (LINNAEUS, 1758) and *Natrix tessellata* (LAURENTI, 1768) in sympatric populations
(Squamata: Serpentes: Colubridae)

Das Beutespektrum von *Natrix natrix* (LINNAEUS, 1758) und *Natrix tessellata* (LAURENTI, 1768) in sympatrischen Populationen
(Squamata: Serpentes: Colubridae)

ERNESTO FILIPPI & MASSIMO CAPULA & LUCA LUISELLI & UMBERTO AGRIMI

KURZFASSUNG

Das Beutespektrum von Ringelnatter, *Natrix natrix* (LINNAEUS, 1758), und Würfelnatter, *Natrix tessellata* (LAURENTI, 1768), wurde an starken sympatrischen Populationen eines hügeligen Gebietes in Mittelitalien ("Rota", Tolfa Berge, etwa 150 m ü. N. N., 42° 08' N, 12° 00' E) untersucht. Beide Arten waren in einem Fluß und in dessen Nähe häufig, doch wurde die Ringelnatter auch weiter entfernt vom Wasser angetroffen und ernährte sich von einem vergleichsweise breiten Spektrum kleiner Wirbeltierarten. Im Gegensatz dazu waren die Würfelnattern strikt an das Wasser und dessen unmittelbare Nähe gebunden und ernährten sich fast ausschließlich von Fischen. Würfelnattern zeigten im Laufe ihrer Ontogenese keine anderen signifikanten Veränderungen in der Zusammensetzung ihrer Beute, als daß größere Nattern eher größere Futtertiere zu sich nahmen. Demgegenüber fand sich bei Ringelnattern im Lauf der Individualentwicklung ein bemerkenswerter Wandel hinsichtlich der Beutezusammensetzung, indem große Weibchen vermehrt adulte Erdkröten (*Bufo bufo*), adulte Männchen häufig „Grünfrösche" fraßen. Kröten wurden gewöhnlich in einiger Entfernung vom Wasser erbeutet (mittlerer Gewässerabstand einer Natter mit einer Kröte im Magen: 256,7 ±115,03 m, Medianwert: 233 m). Etwa 91% der erbeuteten Kröten waren Männchen. Es wird vermutet, daß die Nattern beim Fressen männliche Kröten gegenüber ihren größeren Weibchen bevorzugen.

ABSTRACT

The prey spectrum of the Grass Snake, *Natrix natrix* (LINNAEUS, 1758), and Dice Snake, *N. tessellata* (LAURENTI, 1768) was studied in rich sympatric populations in the vicinity of a stream located in a hilly area of central Italy ('Rota', Tolfa mountains, about 150 m a.s.l., 42° 08' N, 12° 00' E). Both species were frequently present in the water of the stream or close to it. Grass Snakes were also found far from the stream, and preyed on a variety of small vertebrate species. Conversely, Dice Snakes were strictly bound to the water and its vicinity, and preyed almost exclusively on fish. Dice Snakes did not show significant ontogenetic changes in their dietary spectrum other than that larger individuals tended to feed on larger prey. Conversely, in the Grass Snakes, there was a remarkable ontogenetic change in diet composition, and larger females tended to prey frequently upon adult toads (*Bufo bufo*), while adult males frequently fed upon 'green frogs'. The toads were usually preyed at a distance far from the water (average distance from the closest water body of a snake found with a toad in its stomach: 256.7 ±115.03 m, median: 233 m). About 91% of these toads were males. It is suggested that male toads were preyed more frequently than female toads because of their smaller size.

KEYWORDS

Natrix natrix, Natrix tessellata; feeding ecology, prey spectrum, niche partitioning, toad-eating; Mediterranean habitat; Italy.

INTRODUCTION

Remarkable dietary differences among populations of a snake species can be expected if their respective habitats vary significantly (LUISELLI & ANIBALDI 1991; LUISELLI & al. 1995). Furthermore, microgeographical and historical differences in species composition of a snake population's diet may reflect microgeographical and historical changes in prey availability (KING 1993).

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Due to the secretive nature of most snake populations, the available data on prey composition is sketchy and little is known about the interpopulation variation in a given species' diet. Locally abundant snake species with a broad geographic distribution provide unique models for the study of microgeographic variation in dietary preferences (GREGORY 1978, 1984; KEPHART 1982; SHINE 1987; HASEGAWA & MORIGUCHI 1989; KING 1993). The European Grass Snake, *Natrix natrix* (LINNAEUS, 1758) and the Dice Snake, *Natrix tessellata* (LAURENTI, 1768) belong to this type of snake species. Both are widespread and extremely abundant in several regions of central Italy, both are frequently found sympatric (MAZZOTTI & STAGNI 1993) and their individual food preferences are known (BRUNO & MAUGERI 1990; LUISELLI & RUGIERO 1991; LUISELLI & al., 1996a).

In this paper we analyse the dietary habits of sympatric Grass and Dice Snakes inhabiting a stream environment in a Mediterranean hilly locality of central Italy. We compare our data with those obtained from a study which was conducted in a coastal plain environment situated about 30 km south-west of the present study site (LUISELLI & RUGIERO 1991).

MATERIALS AND METHODS

Study area

The field study was carried out in a hilly area in central Italy, located in the vicinity of the stream 'Fosso Verginese', situated about 60 km north-west of Rome ('Rota', Tolfa mountains, about 150 m a.s.l., 42° 08' N, 12° 00' E). The study, conducted from March 1991 to November 1994, is part of a larger research project on the ecology and population biology of snakes in the territory of Tolfa mountains (LUISELLI & AGRIMI 1991; LUISELLI & RUGIERO 1993; AGRIMI & LUISELLI 1994; FILIPPI 1995; RUGIERO & al. 1995). The field study was carried out primarily by one of the authors (E. F.) during his thesis research (see FILIPPI 1995).

The climate of this study area is Mediterranean-temperate with cold winters (without snow cover), rainy springs and autumns, and dry and hot summers (hypomesaxeric subregion type B, according to TOMASELLI & al. 1973). Compared to the site of LUISELLI & RUGIERO's (1991) study, the present locality has a more continental climate: the winter months are much colder, and there is slightly more rainfall. The extension of the surveyed area was 150 ha. The stream is sourronded by about 10 ha of riparian and wetland vegetation (mainly *Ulmus campestris*, but also *Salix* sp. and *Populus* sp.), while the rest of the area is characterized by bushy pastures (*Spartium, Cytisus, Pirus, Rubus, Crataegus*) and mesophilous forests (*Quercus cerris, Ostrya carpinifolia, Carpinetalia, Quercus pubescens*) (SPADA 1977). Typical sites of this area are shown in figures 1 and 2.

Grass Snakes were present in both wet and dry habitats. Adults, especially larger females, were found as far as 400 m from the river (FILIPPI 1995). Conversely, Dice Snakes were found only in the water of the stream or at its banks (FILIPPI 1995).

Methods

Throughout the study area, sampling of the snakes was done primarily between 7.00 a.m. and 3.30 p.m., sometimes later.

Snakes were captured by hand, identified (species and sex), measured (snout-vent length - SVL, to the nearest ±0.1 cm; total length - TL, to the nearest ±0.1 cm), weighed, scale-clipped for future identification, and then squeezed in the abdomen to obtain ingested food. No specimen was killed or damaged for this study.

Food niche breadth (*B*) was calculated using SIMPSON's (1949) diversity index, and food niche overlap (*O*) using PIANKA's (1973) symmetric equation which yielded values from 0 (no overlap) to 1 (total overlap).

Data were analyzed using a statistical analysis computer package (SAS version 6.0, 1985), all tests being two-tailed and

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Fig. 1: The study area, the stream 'Fosso Verginese' in the Tolfa mountains (province of Rome, central Italy), is inhabited by rich populations of *Natrix natrix* and *Natrix tessellata*. Photo: E. FILIPPI.

Abb. 1: Das Untersuchungsgebiet, der Fluß "Fosso Verginese" in den Tolfa Bergen (Provinz Rom, Mittelitalien), wird von starken *Natrix natrix* and *Natrix tessellata* Populationen bewohnt. Photo: E. FILIPPI.

Fig. 2: Area situated in about 250 m distance from the stream 'Fosso Verginese'. This is the typical habitat where adult female *Natrix natrix* were found to feed on adult toads (*Bufo bufo*). Photo: E. FILIPPI.

Abb. 2: Gebiet in etwa 250 m Entfernung vom Fluß "Fosso Verginese". Typischer Fundort weiblicher *Natrix natrix*, die Erdkröten (*Bufo bufo*) gefressen hatten. Photo: E. FILIPPI.

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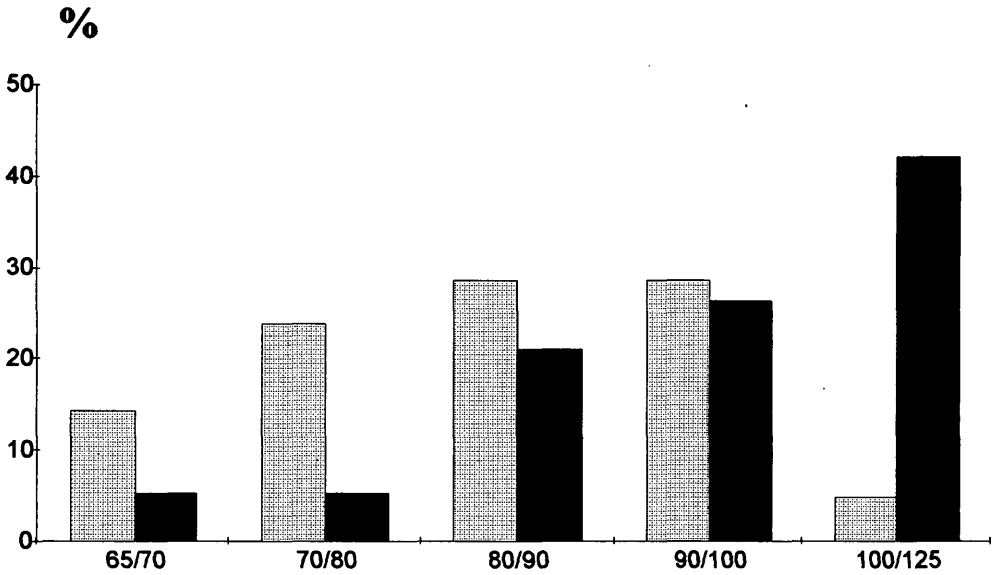

Fig. 3: Distribution of total length (abscissa, cm) in adult male (grey columns, $n = 21$) and adult female (black columns, $n = 19$) *Natrix natrix* in the study area.

Abb. 3: Verteilung der Gesamtlängen (Abszisse, cm) bei adulten männlichen (graue Balken, $n = 21$) und adulten weiblichen (schwarze Balken, $n = 19$) *Natrix natrix* im Untersuchungsgebiet.

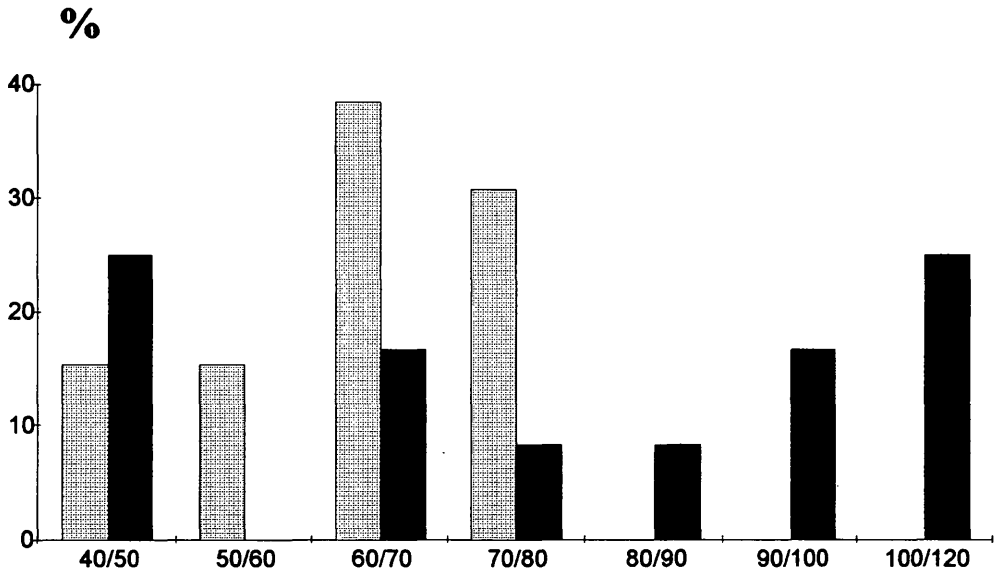

Fig. 4: Distribution of total length (abscissa, cm) in adult male (grey columns, $n = 13$) and adult female (black columns, $n = 12$) *Natrix tessellata* in the study area.

Abb. 4: Verteilung der Gesamtlängen (Abszisse, cm) bei adulten männlichen (graue Balken, $n = 13$) und adulten weiblichen (schwarze Balken, $n = 12$) *Natrix tessellata* im Untersuchungsgebiet.

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with α assessed at 5%. In the text, arithmetic means are followed by ± one standard deviation (S. D.). When calculating χ^2 values for $df = 1$, we used the correction factor of YATES as it permits to reduce the possible error in P calculations, which is true when the distribution in the χ^2 test is continuous while the series tested including all the eventual χ^2 values is not (GLANTZ 1988).

Data that refer to prey composition are based on the number of prey items, not on their weight or volume.

RESULTS AND DISCUSSION

General description of the diets

In *N. natrix* the adult males averaged 84.3 ± 12.8 cm TL ($n = 21$), the adult females 99.7 ± 18.2 cm TL ($n = 19$); intersexual TL differences were significant (STUDENT test: $t = 3.05$, $df = 38$, $P < 0.01$). In *N. tessellata* the adult males averaged 62.2 ± 9.9 cm TL ($n = 13$), adult females 78.5 ± 25.1 cm TL ($n = 12$); intersexual TL differences were significant (STUDENT test: $t = 4.90$, $df = 23$, $P < 0.01$). The body length distributions of both species are given in figures 3 and 4. Both male and female *N. natrix* were significantly longer than male and female *N. tessellata* (two-tailed STUDENT t-test: $P < 0.001$ in all comparisons). Immature individuals of both species were excluded from these measurements, as their TL depended on age rather than on sex.

For analysis of prey composition a sample (captures plus recaptures) of 114 *N. natrix* and 73 *N. tessellata* was examined. 42.1% of the Grass Snakes and 57.5% of the Dice Snakes contained prey in the stomach. Monthly variation in the frequency (%) of specimens containing prey is given in figures 5 (*N. natrix*) and 6 (*N. tessellata*).

The specific composition of the diet in the two species is given in figures 7 (*N. tessellata*), 8 and 9 (*N. natrix*). Often more than one prey item was obtained from a specimen (maximum: 17 small fish from a male *N. tessellata* 32.3 cm long) so that the overall number of prey items is higher than the total number of snakes caught.

In *N. tessellata* the prey consisted predominantly of fish (over 97% of the prey items), a newly metamorphosed *Bufo bufo* and an adult *Rana italica* were also found. There was no significant dietary difference between male and female snakes (χ^2 test with 1 df, $P > 0.5$). The value of the food niche breadth ($B = 1.90$) clearly indicates food specialization in this semi-aquatic snake. On a conservation perspective, conspicuous abundance of fish and fry has been said a primary factor affecting the potential distribution and the present status of Dice Snakes in different geographic regions (e. g., Austria see GRILLITSCH & CABELA 1992; ZIMMERMANN & KAMMEL 1994).

Conversely, in *N. natrix* fish constituted only about 17% of the males' and 9% of the females' prey (differences between sexes insignificant at χ^2 test with 1 df). 83% of the prey was formed by anurans (tadpoles, newly metamorphosed and adults), but lizards and rodents were also eaten. The dietary spectrum of male *N. natrix* was rather different from that of the females ($O = 0.65$), and niche breadth was significantly wider (non-parametric MANTEL test, $P < 0.05$) in males than in females ($B = 4.90$ versus 2.70).

The main differences observed between sexes were: (1) higher frequency of adult toads (*Bufo bufo*) in the prey of female *N. natrix* , and (2) higher frequency of adult frogs in the males' prey. Both observations above are explained by the fact that adult female *N. natrix* were frequently found far from the study stream (mean distance of capture: $\bar{x} = 144.96 \pm 152.55$ m, $n = 51$) where the toads migrated after their reproductive period, while the males were usually found in the vicinity of the water body (mean distance of capture: $\bar{x} = 24.03 \pm 60.23$ m, $n = 63$; difference between two samples: $z = 5.33$, $P < 0.01$). Toads were always eaten the head first, whil frogs were swallowed either the head or the rump first. Male toads seemed to be preyed more frequently than female toads (about 91% of the preyed toads were males, $n = 11$), but

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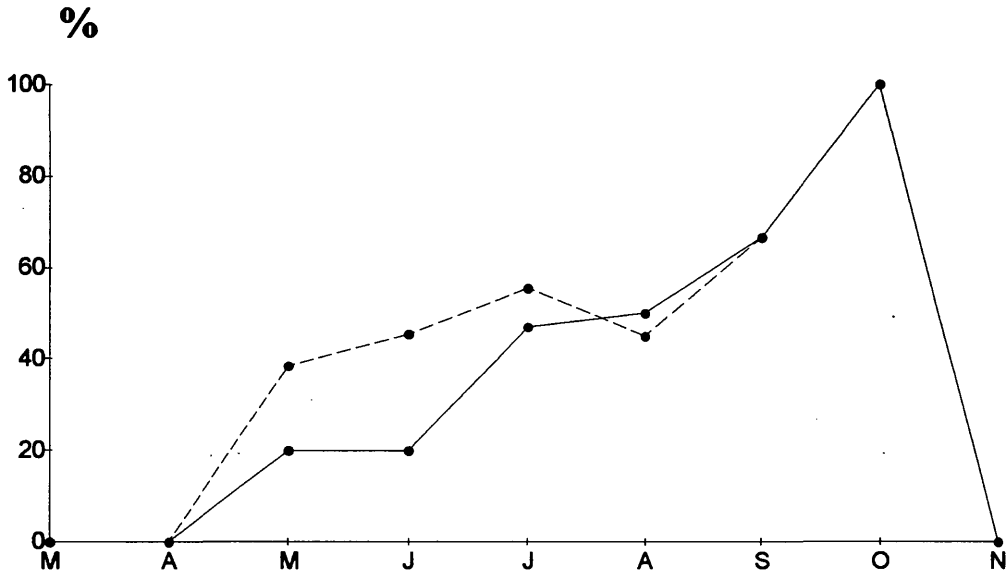

Fig. 5: Monthly variation in the percentage of Grass Snakes (*Natrix natrix*) with prey in the stomach. —— males (n = 63); - - - - - females (n = 51).

Abb 5: Prozentueller Anteil der in den Monaten April bis November im Untersuchungsgebiet gefangenen Ringelnattern (*Natrix natrix*) mit Beute im Magen. —— Männchen (n = 63); - - - - - Weibchen (n = 51).

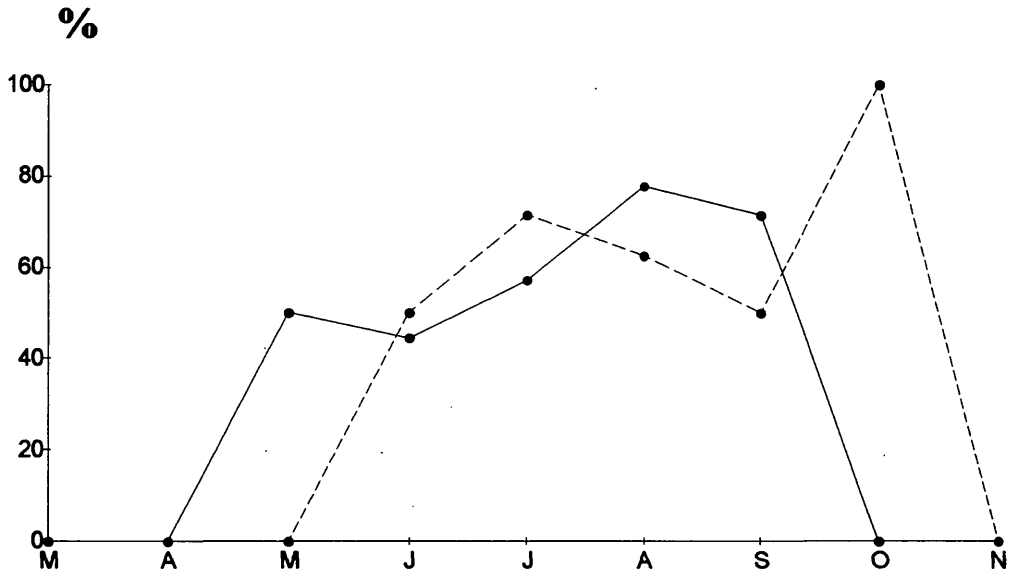

Fig. 6: Monthly variation in the percentage of Dice Snakes (*Natrix tessellata*) with prey in the stomach. —— males (n = 41); - - - - - females (n = 32).

Abb 6: Prozentueller Anteil der in den Monaten April bis November im Untersuchungsgebiet gefangenen Würfelnattern (*Natrix tessellata*) mit Beute im Magen. —— Männchen (n = 41); - - - - - Weibchen (n = 32).

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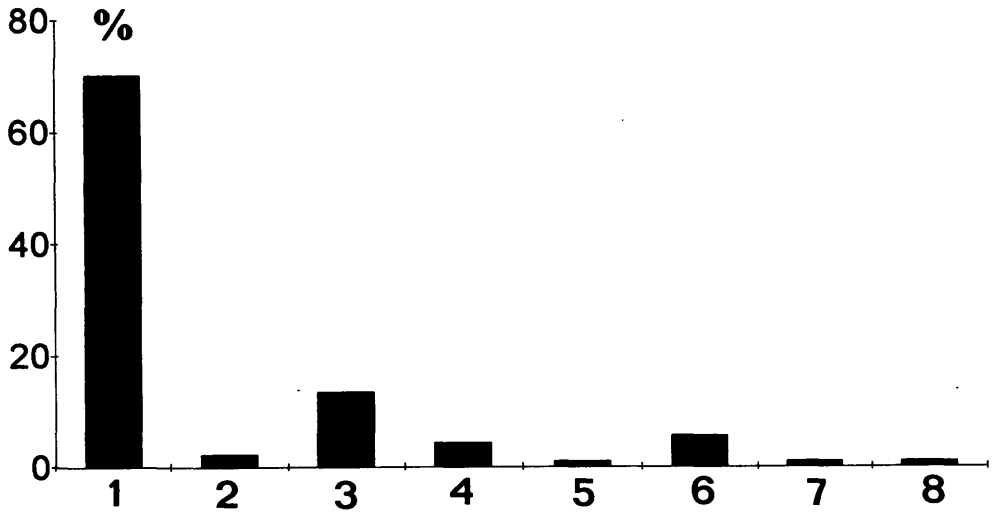

Fig. 7: Specific dietary composition of *Natrix tessellata* (42 individuals) in the study area. Data for males and females (88 prey items) pooled because of lack of significant difference between sexes in food composition.
1- undetermined Cyprinidae; 2 - *Leuciscus cephalus*; 3 - *Scardinius erythrophtalmus*; 4 - undetermined Gobiidae; 5 - *Cobitis thaenia*; 6 - undetermined fish; 7 - *Rana italica*; 8 - newly metamorphosed of *Bufo bufo*.

Abb. 7: Artliche Zusammensetzung der Beute von *Natrix tessellata* (42 Individuen) im Untersuchungsgebiet. Daten für Männchen und Weibchen (88 Futtertiere) gepoolt, da keine signifikanten geschlechtsspezifischen Unterschiede in der Beutetierzusammensetzung bestanden. 1- unbestimmte Cypriniden; 2 - *Leuciscus cephalus*; 3 - *Scardinius erythrophtalmus*; 4 - unbestimmte Gobiiden; 5 - *Cobitis thaenia*; 6 - unbestimmte Fische; 7 - *Rana italica*; 8 - frisch metamorphosierte *Bufo bufo*.

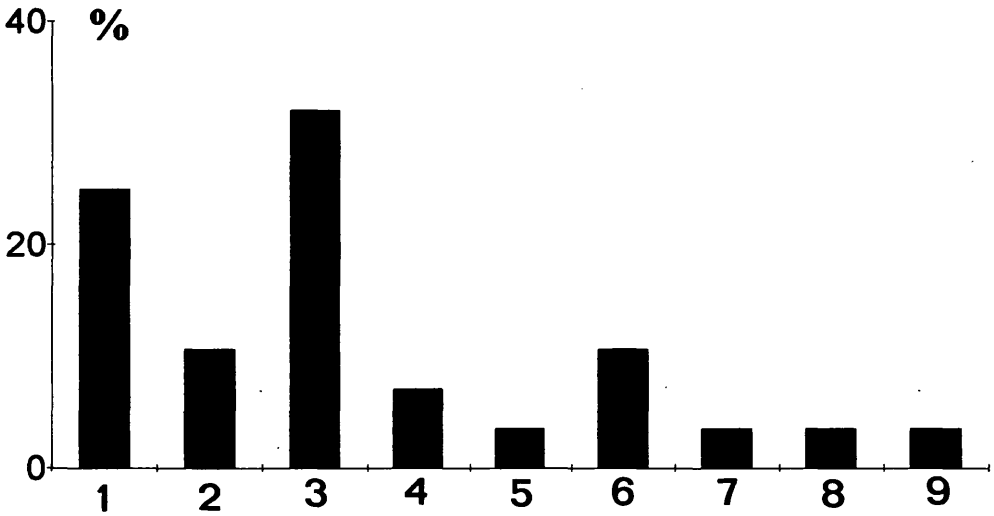

Fig. 8: Specific dietary composition (28 prey items) of male *Natrix natrix* (23 individuals) in the study area.
1 - newly metamorphosed *Bufo bufo*; 2 - *Rana italica*; 3 - 'Green Frogs'; 4 - anuran tadpoles; 5 - undetermined Cyprinidae; 6 - undetermined Gobiidae; 7 - *Anguilla anguilla*; 8 - *Podarcis muralis*; 9 - *Apodemus sylvaticus*.

Abb. 8: Artliche Zusammensetzung der Beute (28 Futtertiere) männlicher *Natrix natrix* (23 Individuen) im Untersuchungsgebiet.
1 - frisch metamorphosierte *Bufo bufo*; 2 - *Rana italica*; 3 - "Grünfrösche "; 4 -Anurenlarven; 5 - unbestimmte Cypriniden; 6 - unbestimmte Gobiiden; 7 - *Anguilla anguilla*; 8 - *Podarcis muralis*; 9 - *Apodemus sylvaticus*.

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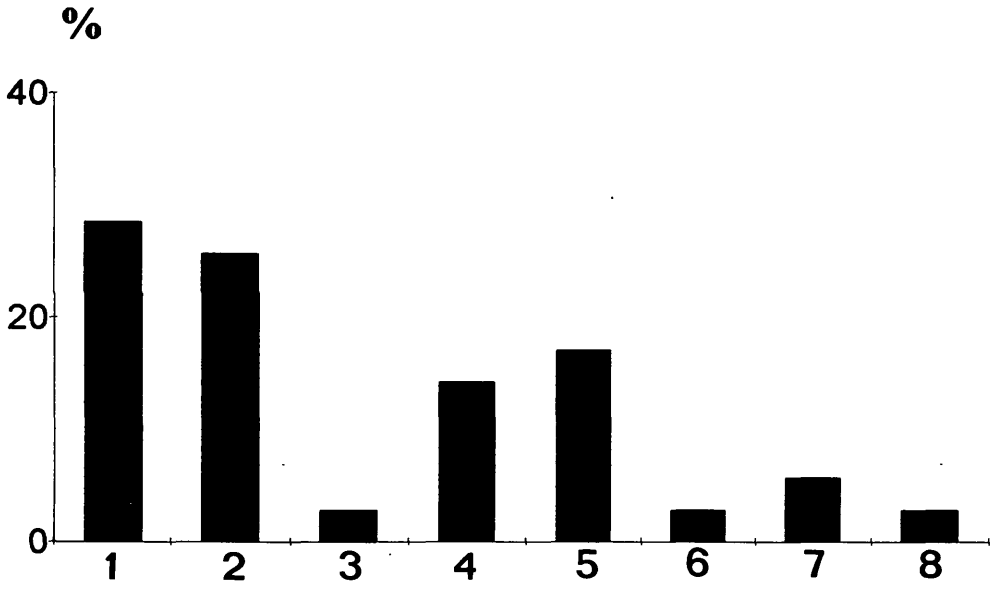

Fig. 9: Specific dietary composition (35 prey items) of female *Natrix natrix* (25 individuals) in the study area. 1 - *Bufo bufo*, adult; 2 - *Bufo bufo*, newly metamorphosed; 3 - *Rana italica*; 4 - 'Green Frogs'; 5 - anuran tadpoles; 6 - undetermined Cyprinidae; 7 - undetermined Gobiidae; 8 - *Podarcis muralis*.

Abb. 9: Artliche Zusammensetzung der Beute (35 Futtertiere) weiblicher *Natrix natrix* (25 Individuen) im Untersuchungsgebiet.
1 - *Bufo bufo*, adult; 2 - *Bufo bufo*, frisch metamorphosiert; 3 - *Rana italica*; 4 - "Günfrösche"; 5 -Anurenlarven; 6 - unbestimmte Cypriniden; 7 - unbestimmte Gobiiden; 8 - *Podarcis muralis*.

the small sample size prevented us from obtaining a statistically significant difference (YATES' $\chi^2 = 2.91$, $df = 1$, $P > 0.05$). We suggest that the Grass Snakes' preference of male toads is caused by their small size (ARNOLD & BURTON 1978). Considering that the snakes are very stationary during the digestive process (especially when a big prey item like a toad was eaten), the locality of capture of the snake should be indicative of the place where the toad was ingested. Toads eaten by *N. natrix* came from snakes that were captured at an average distance of 256.7 ± 115.03 m (median: 233 m) from the closest water body, thus, corroborating the suggestion that toad-eating by *N. natrix* occurs primarily far from water bodies. A higher incidence of toad predation by female rather than male *N. natrix* was also reported from populations in southern Sweden (MADSEN 1983) and the Italian Alps (LUISELLI & al. 1996a).

A shift towards larger prey (usually accompanied by reduced feeding frequency) in female snakes has already been reported for several snake species in temperate regions (e. g., *Coronella austriaca*, LUISELLI & al. 1996b), and may be necessary to reconstruct the fat reserves essential for clutch production (KLAUBER 1936; SAINT GIRONS 1957; SAINT GIRONS & KRAMER 1963), since reproduction may be very costly in terms of both energy and survival (LUISELLI & al. 1996a, 1996b).

Comparing the specific diet composition of male and female *N. tessellata* to that of male *N. natrix* ($O = 0.03$) as well as female *N. natrix* ($O = 0.02$), food niche overlap is extremely low. This indicates clear food niche partitioning between these coexisting snake species, and suggests that their trophic competition is definitely low. Equivalent observations were made in an-

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other place in central Italy (LUISELLI & RUGIERO 1991), although the dietary similarity between these two taxa was higher than in the present study.

With regard to Mediterranean snake communities it should be noted that, whilst the sympatric semi-aquatic *Natrix* species usually partition the available food resource (LUISELLI & RUGIERO 1991; this study), the terrestrial snake species frequently do not, thus, resulting in strong interspecific competition when the food resource tends to decline (CAPIZZI & al. 1995).

Ontogenetic changes in the diet

No apparent ontogenetic change in the diet composition of *N. tessellata* was found, except that the immature individuals of this species preyed on fry and small fish, while the adults tended to prey on larger fish (relationship between *log* of prey length and *log* of predator length, $P < 0.001$). Thus, *N. tessellata* is a piscivorous snake at all ages.

Conversely, in *N. natrix* the taxonomical composition of the prey proved to change with age. The prey of young individuals (i. e., shorter than 65 cm TL) consisted of tadpoles (30.8 % of the diet), newly methamorphosed anurans (53.8 %), small green frogs (3.8 %), and adult *Rana italica* (11.6%), whereas the adults preyed on adult anurans (frogs and toads), fish, lizards and rodents. There was a positive correlation between prey size and predator size (log-transformed) in this species ($P < 0.001$). In comparison to the adults, a remarkable excess of tadpoles and newly metamorphosed anurans was found in the diet of the young (χ^2 test with 1 *df*, $P < 0.005$). Thus, in *N. natrix* there was not only an ontogenetic shift in prey size (as in *N. tessellata*) but also in taxonomical dietary composition.

Generally speaking, the pattern of ontogenetic food change in *N. natrix* described in this study is very similar to that of a population of another freshwater environment in central Italy (LUISELLI & RUGIERO 1991) and also resembles that shown by a mountainous population in the Italian Alps (LUISELLI & al. 1996a). The present study is largely in accordance with results of previous studies on dietary preferences, food niche breadth and overlap of sympatric *N. natrix* and *N. tessellata* (e. g., LUISELLI & RUGIERO 1991). This suggests that a true food niche partitioning does exist between these species.

Food niche partitioning between *N. natrix* and *N. tessellata* follows a general pattern in reptile communities wherever size differences occur between potential competitors (RICKLEFS 1973; CAPULA & LUISELLI 1994). However, BESHKOV & DUSHKOV (1981) observed that the individuals of mixed populations of *N. natrix* and *N. tessellata* were primarily batrachophagous in southwestern Bulgaria. This indicates some remarkable geographic variation in the food preferences of *N. tessellata*, which possibly occurs where availability of fish is reduced (BESHKOV & DUSHKOV 1981).

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