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Broad geographic, taxonomic and ecological patterns of interpopulation variation in the dietary habits of snakes

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Because of their unique morphological and ecological characteristics (i.e. being obligate carnivorous, solitary, and ingesting their prey whole), snakes are expected to show unusual dietary patterns compared to other ectothermic vertebrates, and the best way to explore this is to analyse the snake dietary patterns globally. Here I review and analyse the peer-reviewed snake diet literature available in order to explore whether there are broad patterns in the interpopulation variability of diet composition in these unique ectothermic predators. I collated data for 181 independent populations belonging to 58 species of snakes from some of the main families (1 Boidae, 2 Pythonidae, 27 Colubridae, 10 Elapidae, and 18 Viperidae) and from all the continents (4 from South and Central America, 13 from North America, 12 from Europe, 18 from Africa, 4 from Asia, and 7 from Australia). All these populations satisfied some precise criteria of inclusion, and were therefore re-analysed in a comparative perspective. I classified each literature entry according to 1) snake species, 2) snake family, 3) geographic position (continent) of the study areas, 4) climatic region (temperate versus tropical), 5) guild (if the species is aquatic, terrestrial, or arboreal), 6) hunting strategy (sit-and-wait versus active forager), and 7) venom (if the species is venomous or not). All these seven factors were analysed by GLM procedures to evaluate their effects on the interpopulation diet variation within snake species, that was assessed by using a univariate similarity index. The various taxonomical categories of snake prey were grouped according to two different levels of taxonomic affinity: a) general affinity, e.g. frogs and toads, salamanders, lizards, birds, etc., and b) close affinity, by grouping prey types belonging to a same genus. My study revealed that, within-species snake populations showed a very low variability in terms of diet composition. As for the general affinity criterion, there was no single factor that produced a significant effect on the interpopulation diet variation but, with regard to the interaction terms between factors, significant effects were determined by 1) continent × climatic region (with Asian, African and South-American tropical populations having significantly lesser similarity values), 2) continent × hunting strategy (diets being less diverse in ambush predators in Africa, Asia and South America), and 3) climatic region × guild (with arboreal tropical snakes showing less interpopulation similarity). As for the close affinity criterion, there was also no effect of single factors on interpopulation diet variability, but the interaction term hunting strategy × venom was significant, with sit-and-wait venomous species being less variable in their diet composition. Snake family was completely un-influent in determining any effect on snake interpopulation diet variation. The broad reasons that may explain these generalized patterns are discussed.

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The study of the feeding habits of animals has attracted much attention by ecologists, and thousands of contributions have appeared during the recent years, either theoretical (Schoener 1971, Stephens and Krebs 1986, Green 2006, Olsson and Brown 2006, etc.) or empirical (Ray and Sunquist 2001, Lekunze et al. 2001, and lots of other studies). As a result, we currently do know much more than just a few decades ago about the diet composition, and its ecological and behavioural determinants, of a number of living animals belonging to different taxonomic groups (for a case study, see Carretero 2004).

Snakes are unique among vertebrates because of some peculiar adaptations: they are exclusively carnivorous and solitary (but see Shine et al. 2002), and obligatorily ingest their prey whole (Greene 2001). Thus, they are gape-limited, and have evolved a suite of morphological and behavioural adaptations to kill their prey and ingest it whole, including sophisticated venom and the apparatus to inject it, extreme body strength and huge size to suffocate very large animals, and enormous skull distensibility (Greene 2001). Because of these unique characteristics, these animals can be expected to show unusual dietary patterns compared to other ectothermic vertebrates, and the best way to explore this is to analyse the snake dietary patterns globally, given that the use of specific study models may be partially inadequate to understand broader patterns. Up to the early 1990s, snakes remained relatively unstudied, but currently they have achieved the status of "model organisms" for ecological and evolutionary studies, and hence several broad studies have been published (Shine 1991, Shine and Bonnet 2000, Luiselli 2006a).

Although the study of the diet composition of free-ranging snakes has traditionally played a major argument of research for snake ecologists (Mushinsky 1987), nonetheless there is still no published attempt at identifying the broad patterns (geographic, taxonomic, and ecological) of the interpopulation variation within the snake species' dietary habits. This is a important shortcoming for our understanding of snake evolution and ecology, also in consideration of the fact that previous studies evidenced that dietary habits have crucial relevance in determining the morphological traits of snakes (for instance, the sexual size dimorphism and the head size and shape: Shine 1991, Shetty and Shine 2002), and that snakes are unusual among carnivorous vertebrates because they usually partition the food resource and not the spatial resource when in competition (Luiselli 2006a). The study of the interpopulation snake diet variation may be important to understand whether there are broad unifying patterns (at the taxonomical, geographical, or eco-ethological level) that may explain patterns and correlates of dietary variation, and this may in turn be useful also for comparisons with other carnivorous vertebrates in order to learn more of the evolution of the predatory behaviour in animals.

It therefore seems necessary to review recently published material on the interpopulation diet variation in snakes, and to respond to the following questions: 1) do the snakes species vary remarkably between populations in terms of their diet composition? 2) What factors are associated to the interpopulation variation in diet composition: systematic position (i.e. family), geographic origin (i.e. continent), climatic conditions (i.e. temperate versus tropical), ecological guild (i.e. terrestrial, aquatic or arboreal), hunting strategy (i.e. sit-and-wait versus active foraging), or presence/absence of venom apparatus? In this regard, it should however be noticed that several snakes exhibiting one of these factors also may exhibit the other one; i.e. several snakes that practice the sit-and-wait foraging strategy are also venomous (for instance, *Bitis gabonica* and *Bitis nasicornis*, see Luiselli 2006a). 3) Which reasons can explain the eventual observed patterns?

I will demonstrate that the impetuous advance of our understanding of snake ecology (Shine and Bonnet 2000) may prove useful to solve the above-mentioned issues, although many snake studies, because of the intrinsic elusiveness of the subject animals, still focus on just documenting small samples of food items taken from free-ranging snakes.

Materials and methods

I have reviewed through very extensive searches of the literature, the available data on the dietary habits of snake populations around the globe. Only those studies that furnished re-analysable raw data were selected for further inspection. I then considered for the proper statistical study only those bibliographic entries which met with the following conditions: 1) they should report precise diet data lists for distinct populations of snakes (Luiselli et al. 1996, 1997, Gregory and Isaac 2004), or diet data lists from snakes occurring in well-defined and habitat-homogenous geographically restricted regions (Shine 1987a, b, c, 1989, etc.); 2) they should report diet records gotten from at least 30 different snake specimens of each population. Studies reporting smaller sample sizes, albeit solid, were not considered for this study (e.g. some data in Shine 1981, 1982, Reynolds and Scott 1982). Although my search for appropriate literature datasets is likely not exhaustively complete, nonetheless it seems to be adequate for the scopes of this paper, given that it collates data from a wide range of different snake genera belonging to a wide range of families in a wide range of geographic and environmental contexts.

Only studies from peer-reviewed journals or, exceptionally, academic dissertations, were used. Every effort was made to avoid unbalanced coverage of the literature from the different regions of the world/snake family/snake genera, although where there is a difference in the amount of literature reviewed this reflects differences in the development of research on snake feeding ecology. For instance, some countries (e.g. USA, Italy, Nigeria, Australia) were disproportionately over-represented in my review. I confined my review only to the interpopulation variation in the taxonomic composition of the diet, as no adequate comparative dataset is available for other dietary aspects such as, e.g. prey-size, prey-size-predator-size relationships, etc.

The various taxonomical categories of snake prey were grouped according to two different levels of taxonomic affinity (defined affinity criteria in the following text): a) general affinity (e.g. frogs and toads, salamanders, lizards, birds, etc.), and b) close affinity, by grouping prey types belonging to a same genus (e.g. *Triturus* species, *Rattus* species, etc.). I avoided to consider also the interpopulation variation at the prey-species level because there are several cases in which snake populations may actually prey on a same type of prey (for instance, *Podarcis* species in the case of *Coronella girondica*), but on different species simply because different species may occur in the different areas where the snake diets were studied (for instance, *P. hispanica* in Spanish *Coronella girondica*, and *P. sicula* in the case of Italian *Coronella girondica*; Luiselli et al. 2001a). Hence, the actual interpopulation variation may be unrealistically overestimated by using species-level differences in prey type categories.

Similarity in prey types between different populations of each species were estimated by applying Pianka's (1986) symmetric equation of overlap. Although Pianka's overlap formula was originarily designed to assess niche overlap between two potential competitors, nonetheless it is merely a similarity index, and hence can be readily used as a univariate measure of similarity in dietary spectrum between two different populations of animals (Pianka 1986). By this formula, the values ranged from 0 (no similarity) to 1 (total identity). This formula is very appropriate for this study, because Pianka's index is similar to MacArthur and Levins (1967) index, with the denominator that has been normalized to make it symmetric, but the stability properties were unchanged (May 1975). For each species, I have built a data matrix in which each cell was the Pianka's similarity index between two populations (see Table 1 for an example), and the various matrices varied in size from a single cell (when data from just two populations of a single population are available) to 28 cells (when data from 8 different populations are available; Table 1). Then, I calculated the mean similarity index of each species by calculating the arithmetic mean of the pairwise similarity indexes.

Each literature entry was classified according to 1) snake species, 2) snake family, 3) geographic position of the study areas (at a continental level: Europe, North America, South and Central America, Africa, Asia, Australia), 4) climatic region (i.e. temperate versus tropical), 5)

Table 1. Example of a data matrix used for this study; the species used for this example is *Natrix natrix*. Each cell in this matrix represents the value of Pianka's (1986) similarity index between two populations of the study species; also the study areas and the original literature sources are given. Note that this dataset is relative to diet similarity expressed as "general affinity" (see the text for more details).

	England (Stebbings in Gregory and Isaac 2004)	England (Reading and Davies 1996)	Sweden (Madsen 1983)	Italy (Luiselli and Rugiero 1991)	Italy (Filippi et al. 1995)	Italy (Luiselli et al. 1997)	Italy (Luiselli et al. 2005)
England (Gregory and Isaac 2004)	0.9418	0.9299	0.9286	0.9321	0.9293	0.9351	0.9003
England (Stebbings in Gregory and Isaac 2004)		0.9981	0.9966	0.9983	0.9983	0.9956	0.7036
England (Reading and Davies 1996)			0.9961	0.9985	0.9874	0.9909	0.6797
Sweden (Madsen 1983)				0.9992	0.9969	0.9871	0.6771
Italy (Luiselli and Rugiero 1991)					0.9943	0.9897	0.6826
Italy (Filippi et al. 1995)						0.9794	0.6852
Italy (Luiselli et al. 1997)							0.7008

guild (i.e. if the species is aquatic, terrestrial, or arboreal, see Luiselli 2006a), 6) hunting strategy (i.e. if the species is a sit-and-wait or a active forager), and 7) venom (i.e. if the species is venomous and use its venom for killing its prey or not). All these seven factors were analysed to evaluate their effects on the interpopulation diet variation within snake species.

All statistics were done by a SPSS (ver. 11.0) PC package, with all tests being two-tailed and alpha set at 5%. The effects of the seven above-mentioned factors, entered singly in the analysis, on the snake interpopulation diet overlap values, were tested by means of one-way ANOVAs, since the assumptions of normality and homoscedasticity were met. To evaluate the effects of the interaction terms between the various factors on the snake interpopulation diet overlap values, I fitted a generalized linear model (McCullagh and Nelder 1989) using the general factorial design in SPSS, followed by Tukey's post-hoc test, since log-transformed data satisfied the normality and homoscedasticity assumptions. All possible two-way and three-way interactions among the seven factors were included as fixed-effect factors in the model (McCullagh and Searle 2002).

Confounding factors of the analysis

I identified the following confounding factors for my analysis: 1) different methods used to collect data (i.e. only stomach contents or stomach+gut contents; dissection of museum vouchers or examination of free-living specimens by abdominal palpation. Unfortunately, no study has examined the possible discrepancies in the description of snake diets by considering only stomach or stomach + gut food contents, thus it is impossible to determine whether this factor may have or may have not biased the analyses. 2) Unstandardized mean distance between study areas within- and among-species. It is possible that the species whose the study populations came from greater distances differed more than those whose study populations were geographically closer. However, given the still fragmentary knowledge on the study subject, it is impossible to assess properly whether or not this factor may have partially biased the analyses. 3) Many snakes show remarkable ontogenetic dietary changes (Saint Girons 1980, Luiselli and Agrimi 1991) and intersexual dietary divergence (Shine 1991). These changes may bias the comparative analyses, so I considered when possible 1) only the adults and 2) assumed that, on average, males and females contributed equally to the examination of the diet of a given snake composition, thus considering males + females data pooled. This latter point is certainly correct, given that all authors tended to present diet data well equilibrated between sexes. 4) In several cases, it was impossible to calculate the overlap values for the close affinity criterion from the original sources.

Results

General affinity

In total, I found re-analyzable data for 181 independent populations belonging to 58 species of snakes from all the main families (1 Boidae, 2 Pythonidae, 27 Colubridae, 10 Elapidae, and 18 Viperidae) and from all the continents (4 from South and Central America, 13 from North America, 12 from Europe, 18 from Africa, 4 from Asia, and 7 from Australia) (Table 2). The great majority of the species showed very high interpopulation diet similarity values when considering the general affinity criterion (mean ± SD = 0.885 ± 0.117, range = 0.432–0.999, n = 58; Fig. 1).

The means and dispersion measures of the interpopulation diet similarity values divided by continent, guild, and family are given in Fig. 2. Univariate Analysis of Variance models (i.e. 1-way ANOVAs for measuring the effects of single factors, and GLM – general factorial design for the effects of the interaction terms between factors) showed that (Table 3): 1) there was no single factor that produced a significant effect on the interpopulation diet variation; 2) with regard to the interaction terms between factors, the significant effects on the interpopulation diet similarity values were: a) continent × climatic region (Tukey HSD post-hoc test revealing that Asian, African and South-American tropical populations had significantly lesser similarity values; in all cases, $p < 0.01$), b) continent × hunting strategy (diets less different in ambush predators in Africa, Asia and South America), c) climatic region × guild (with arboreal tropical snakes showing less interpopulation similarity in prey composition).

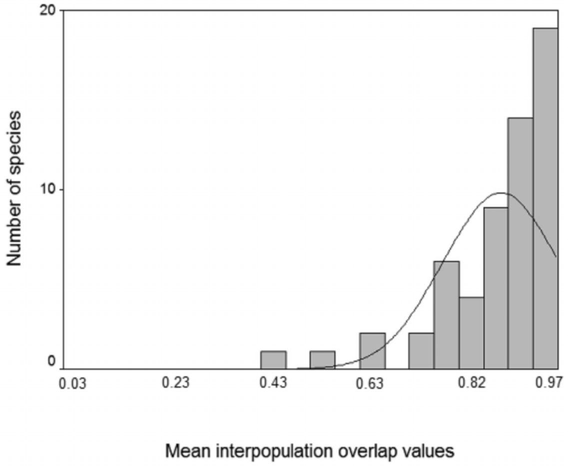

Fig. 1. Distribution of the number of snake species in terms of their interpopulation diet overlap values (calculated by Pianka's formula; all snake families included) as regards the general affinity criterion. The line indicates the normal curve. Note that the great majority of the species are distributed in the very high overlap values intervals (mean ± SD = 0.885 ± 0.117, n = 58).

Table 2. Summary of the interpopulation variation in snake dietary composition, assessed by Pianka's (1986) similarity equation. Symbols: r = range; x = mean; n = number of populations examined.

Species	Geographic origin of the study populations	Main preys	Similarity (general affinity)	Similarity (close affinity)	References
Boidae					
Boa constrictor	Argentina, West Indies	Mammals and birds (all populations)	0.795; n = 2	0.206; n = 2	Sironi et al. 2000, Quick et al. 2005
Pythonidae					
Python regius	Benin, Nigeria	Mammals (all populations)	0.798; n = 2	0.463; n = 2	Politano 1985, Luiselli and Angelici 1998
Python sebae	Nigeria	Mammals (all populations)	0.776; n = 2	0.346 ; n = 2	Luiselli et al. 2001b
Colubridae					
Afronatrix anoscopus	Benin, Nigeria	Frogs, tadpoles and fish (all populations)	r = 0.864–0.998; x = 0.931; n = 4	Not calculable from the original datasets	Politano 1985, 1998, Luiselli et al. 1998b, Luiselli 2006b
Coluber constrictor	USA	Insects and rodents (all populations)	r = 0.988–0.998; x = 0.992; n = 3	Not calculable from the original datasets	Brown and Parker 1982, Fitch 1982, Cooper et al. 2000
Coronella austriaca	Italy	Lizards (all populations)	0.999; n = 2	0.163; n = 2	Rugiero et al. 1995, Luiselli et al. 1996
Coronella girondica	Italy, Spain	Lizards (all populations)	0.939; n = 2	0.382; n = 2	Luiselli et al. 2001a
Elaphe quadrivirgata	Japan	Lizards or frogs (variable depending on the populations)	r = 0.243–0.723; x = 0.436; n = 4	Not calculable from the original datasets	Fukada 1959, 1992, Kadowaki 1992, 1996, Tanaka and Ota 2002
Elaphe quatuorlineata	Italy	Birds, rodents (all populations)	r = 0.715–0.973; x = 0.863; n = 5	r = 0.209–0.864; x = 0.563; n = 5	Filippi et al. 2005
Gastropyxis smaragdina	Nigeria	Lizards and frogs (all populations)	0.913, n = 2	0.663; n = 2	Luiselli et al. 2000, Inyang 2005
Grayia smythii (= *smithii*)	Nigeria	Frogs and fish (all populations)	0.848; n = 2	0.863, n = 2	Akani and Luiselli 2001 + unpubl., Luiselli 2006b
Hemorrhois hippocrepis	Morocco, Spain	Rodents, lizards (all populations)	0.940; n = 2	0.708; n = 2	Pleguezuelos and Moreno 1990, Pleguezuelos and Fahd 2004)
Hierophis viridiflavus	Italy	Lizards, and rodents as secondary prey (all populations)	r = 0.942–0.977; x = 0.960; n = 3	r = 0.747–0.957; x = 0.841; n = 3	Rugiero and Luiselli 1995, Capizzi and Luiselli 1996, Rugiero et al. 2002
Lamprophis fuliginosus	Benin, Nigeria	Rodents (all populations)	r = 0.732–0.981; x = 0.848; n = 4	r = 0.399–0.901; x = 0.624; n = 4	Politano 1985, 1998, Inyang 2005
Natriciteres fuliginoides	Nigeria	Earthworms and anuran larvae or anuran larvae and metamorphs (depending on the populations)	r = 0.580–0.988; x = 0.787; n = 4	r = 0.457–0.936; x = 0.644; n = 4	Luiselli 2003
Natriciteres variegata	Nigeria	Amphibian larvae and metamorphs (all populations)	0.965; n = 2	0.965; n = 2	Luiselli 2003

Table 2. Continued.

Species	Geographic origin of the study populations	Main preys	Similarity (general affinity)	Similarity (close affinity)	References
Natrix maura	Italy, Spain	Frogs, or fish and frogs (depending on the population)	r = 0.140–0.918; x = 0.525; n = 3	r = 0.006–0.206; x = 0.125; n = 3	Santos and Llorente 1998, Rugiero et al. 2000
Natrix natrix	England, Italy, Sweden	Frogs and toads (all populations)	r = 0.677–0.999; x = 0.872; n = 8	r = 0.188–0.812; x = 0.472; n = 7	Madsen 1983, Luiselli and Rugiero 1991, Reading and Davies 1996, Luiselli et al. 1997, 2005, Gregory and Isaac 2004
Natrix tessellata	Austria, Italy	Fish (all populations)	r = 0.961–0.998; x = 0.987; n = 3	r = 0.921–0.967; x = 0.947; n = 3	Luiselli and Rugiero 1991, Filippi 1995, Zimmermann and Fachbach 1996
Nerodia sipedon	USA	Fish (all populations)	0.985, n = 2	0.155, n = 2	King 1993
Nerodia taxispilota	USA	Fish (all populations)	r = 0.912–0.990; x = 0.954; n = 3	r = 0.548–0.913; x = 0.689; n = 3	Camp et al. 1980, Gibbons and Dorcas 2004
Pituophis catenifer	USA	Mammals (all populations)	r = 0.489–0.951; x = 0.783; n = 4	Not calculable from the original datasets	Rodriguez-Robles 2002
Pituophis melanoleucus	USA	Rodents (all populations)	0.933; n = 2	Not calculable from the original datasets	Brown and Parker 1982, Fitch 1999
Psammophis phillipsii	Nigeria	Lizards (all populations)	r = 0.833–0.975; x = 0.891; n = 3	r = 0.439–0.811; x = 0.695; n = 3	Politano 1985, Akani et al. 2003, Luiselli et al. 2004a
Rhabdophis tigrinum	Japan	Amphibians	r = 0.865–0.967; x = 0.921; n = 3	Not calculable from the original datasets	Fukada 1959, 1992, Kadowaki 1992, Hirai 2004
Rhamnophis aethiopissa	Cameroon, Nigeria	Frogs, or lizards and birds (depending on the populations)	r = 0.667–0.811; x = 0.745; n = 3	r = 0.339–0.611; x = 0.498; n = 3	Luiselli et al. 1999–2000, Inyang 2005
Thamnophis elegans	Canada, USA	Slugs, fish and amphibians (depending on the populations)	r = 0.645–0.838; x = 0.739; n = 4	Not calculable from the original datasets	Fitch 1940, Fox 1952, Gregory 1978, Gregory and Nelson 1991
Thamnophis sirtalis	Canada, USA	Amphibians and earthworms (all populations)	0.919; n = 2	Not calculable from the original datasets	Fitch 1965, 1982, Gregory 1978
Toxicodryas blandingii	Benin, Nigeria	Birds and lizards (all populations)	r = 0.793–0.988; x = 0.902; n = 3	r = 0.441–0.776; x = 0.612; n = 3	Politano 1985, Luiselli et al. 1998a, Inyang 2005
Zamenis longissimus	Italy	Rodents (all populations)	r = 0.858–0.998; x = 0.907; n = 4	r = 0.761–0.937; x = 0.818; n = 4	Capula and Luiselli 2002, Rugiero et al. 2002
Elapidae					
Cryptophis nigrescens	Australia	Lizards (all populations)	0.998; n = 2	0.975; n = 2	Shine 1984
Demansia psammophis	Australia	Lizards (all populations)	0.997; n = 2	0.776; n = 2	Shine 1980
Dendroaspis jamesoni	Nigeria	Birds and rodents (all populations)	0.986; n = 2	0.776; n = 2	Luiselli et al. 2000b, Inyang 2005
Hemiaspis signata	Australia	Frogs and lizards (all populations)	0.989; n = 2	0.870; n = 2	Shine 1987a

Table 2. Continued.

Species	Geographic origin of the study populations	Main preys	Similarity (general affinity)	Similarity (close affinity)	References
Naja melanoleuca	Nigeria	Mammals, amphibians, fish	0.819; n = 2	0.624; n = 2	Luiselli et al. 2002
Naja nigricollis	Nigeria	Lizards and mammals	0.929; n = 2	0.588; n = 2	Luiselli et al. 2002
Notechis scutatus	Australia	Frogs, or frogs and lizards, or small mammals (depending on the populations)	r = 0.468–0.831; x = 0.601; n = 3	r = 0.294–0.335; x = 0.316; n = 3	Shine 1987b
Pseudechis australis	Australia	Lizards, frogs and small mammals	r = 0.807–0.981; x = 0.874; n = 3	r = 0.475–0.713; x = 0.568; n = 3	Shine 1987c
Pseudonaja nuchalis	Australia	Small mammals and reptiles (all populations)	r = 0.891–0.988; x = 0.942; n = 3	r = 0.627–0.915; x = 0.785; n = 3	Shine 1989
Pseudonaja textilis	Australia	Reptiles and small mammals (all populations)	r = 0.952–0.994; x = 0.972; n = 3	r = 0.109–0.711; x = 0.387; n = 3	Shine 1989
Viperidae					
Agkistrodon piscivorus	USA	Fish, frogs, snakes (all populations)	0.942; n = 2	0.576; n = 2	Himes 2003, Vincent et al. 2004
Bitis caudalis	South Africa	Lizards (all populations)	r = 0.906–0.989; x = 0.946; n = 3	r = 0.579–0.776; x = 0.708; n = 3	Shine et al. 1998
Bitis gabonica	Nigeria	Mammals (all populations)	r = 0.997–0.999; x = 0.998; n = 6	r = 0.779–0.975; x = 0.862; n = 6	Luiselli (unpubl.)
Bitis nasicornis	Nigeria	Mammals and frogs (all populations)	r = 0.906–0.989; x = 0.965; n = 6	r = 0.593–0.976; x = 0.778; n = 6	Luiselli (unpubl.)
Bothrops atrox complex	Ecuador, Peru, Brazil	Mammals, lizards, frogs (all populations)	r = 0.836–0.939; x = 0.892; n = 4	Not calculable from the original datasets	Duellmann 1978, Cunha and Nascimento 1993, Duellmann and Mendelson 1995, Nogueira et al. 2003
Bothrops neuwiedi complex	Brazil	Mammals, lizards, amphibians	0.870; n = 2	0.451; n = 2	Valdujo et al. 2002, Hartmann et al. 2005
Calloselasma rhodostoma	Malaysia and south Thailand, Java	Mammals, birds and reptiles (all populations)	0.892; n = 2	Not calculable from the original datasets	Daltry et al. 1998
Causus maculatus	Nigeria	Frogs and toads (all populations)	0.893, n = 2	0.883, n = 2	Luiselli et al. 2004b, Inyang 2005
Crotalus atrox	USA, Mexico	Rodents (all populations)	r = 0.901–0.978; x = 0.956; n = 3	r = 0.726–0.903; x = 0.822; n = 3	Beavers 1976, Reynolds and Scott 1982, Pisani and Stephenson 1991
Crotalus horridus	USA	Rodents (all populations)	0.989, n = 2	0.776, n = 2	Uhler et al. 1939, Fitch 1982, 1999
Crotalus lepidus	USA	Mammals, lizards, arthropods (all populations)	r = 0.683–0.967; x = 0.776; n = 3	r = 0.248–0.339; x = 0.294; n = 3	Beaupre 1995, Holycross et al. 2002

Table 2. Continued.

Species	Geographic origin of the study populations	Main preys	Similarity (general affinity)	Similarity (close affinity)	References
Crotalus oreganus	USA	Mammals and lizards (all populations)	r = 0.726–0.908; x = 0.842; n = 5	Not calculable from the original datasets	Fitch and Twining 1946, Cunningham 1959, Diller and Johnson 1988, Macartney 1989, Wallace and Diller 1990
Porthidium godmani	Guatemala	Arthropods and mammals (all populations)	0.979, n = 2	Not calculable from the original datasets	Campbell and Solorzano 1992
Sistrurus catenatus	USA	Mammals, lizards, snakes, and invertebrates (variable depending on the populations)	r = 0.214–0.987; x = 0.650; n = 6	Not calculable from the original datasets	Greene and Oliver 1965, Keenlyne and Beer 1973, Hallock 1991, Holycross and Mackessy 2002
Trimeresurus stejnegeri	Taiwan	Frogs (all populations)	0.997, n = 2	Not calculable from the original datasets	Creer et al. 2002
Vipera aspis	Italy, Switzerland	Rodents (all populations)	r = 0.926–0.996; x = 0.948; n = 4	r = 0.382–0.843; x = 0.678; n = 4	Monney 1996, Luiselli and Agrimi 1991, Capizzi and Luiselli 1996
Vipera berus	England, Denmark, Poland, Czech Republic, Russia, Italy	Rodents (all populations)	r = 0.796–0.998; x = 0.874; n = 7	r = 0.087–0.877; x = 0.480; n = 7	Pielowski 1962, Prestt 1971, Pomianowska-Pilipiuk 1974, Kjaergaard 1981, Luiselli and Anibaldi 1991, Drobenkov 1995
Vipera ursinii	France, Italy	Orthoptera (all populations)	r = 0.936–0.998; x = 0.963; n = 4	r = 0.792–0.923; x = 0.867; n = 4	Agrimi and Luiselli 1992, Baron 1992, Filippi and Luiselli 2004

Close affinity

The mean interpopulation diet similarity value, according to the close affinity criterion (0.620 ± 0.230, n = 44) was much lesser than that calculated according to the general affinity criterion (see above).

Analysis of variance models (Table 3) showed that: 1) there was no single factor that produced a significant effect on the interpopulation diet variation; 2) with regard to the interaction terms between factors, the only significant effect on the interpopulation similarity values was determined by hunting strategy × venom, with ambushing, venomous species being less variable in their diet composition (Tukey HSD post-hoc test).

Discussion

This study allowed several generalizations, that should be discussed more in detail.

Why are there minor interpopulation dietary differences in snakes?

Lots of experimental studies have shown that snakes generally exhibit precise, genetically-determined, species-specific preferences for some prey types (for instance for fish, or for mammals, or for frogs, etc., Arnold 1981, Greene 2001). In addition, snakes are solitary predators (thus can-

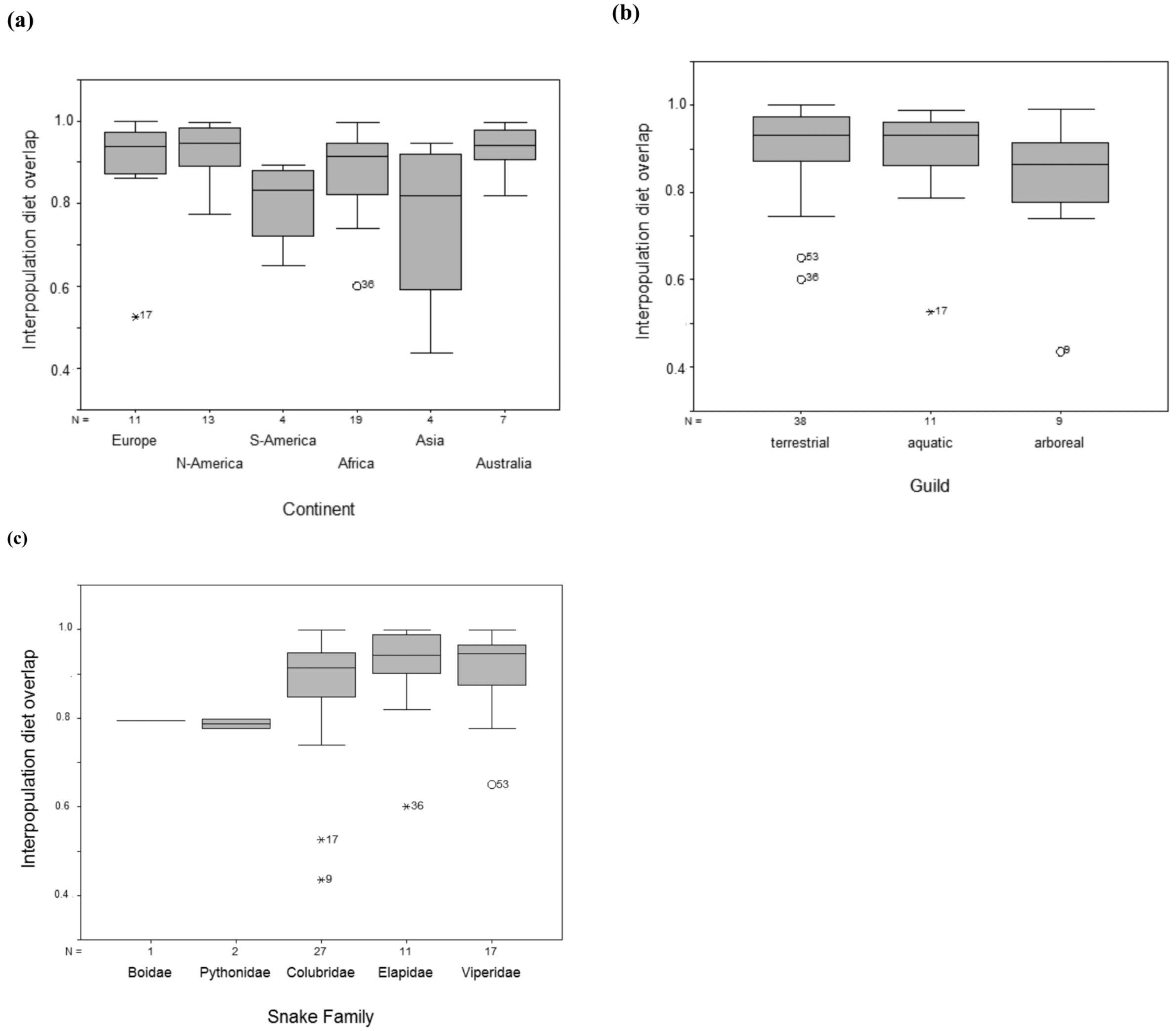

Fig. 2. Means (and dispersion measures) of the interpopulation diet overlap values (general affinity criterion) among continents (a), guilds (b), and snake families (c). Outliers in graphics: 9 = *Elaphe quadrivirgata,* 17 = *Natrix maura*, 36 = *Notechis scutatus*, 53 = *Sistrurus catenatus*. N = number of species.

not benefit of the advantages of group foraging; Clark and Mangel 1986), and are peculiar amongst carnivorous animals because they ingest their prey whole (Greene 2001). Because they cannot tear apart prey items (unlike most vertebrates) and because they eat relatively large prey items (Greene 2001), most snakes are gape-limited predators. Obviously snake skulls are characterized by enormous distensibility (presumably adapted to increase gape, Shine 1991), nonetheless the maximum size of prey ingestible is limited by the size of the snake's head or body (as these two variables are highly correlated) (Savitsky 1983). Given that the majority of the snake species studied to date exhibit low to moderate intraspecific dimorphism in mean body size (but there are some exceptions, see Luiselli 2006a), it can be suggested that most of the species should exhibit low interpopulation variability in prey ingestion ability. Therefore for most species, given a) the expected minor interpopulation differences in prey size, and b) the genetically-determined prey type preferences, there should be minor interpopulation variations in dietary habits, i.e. exactly the conclusion given by this study. The species which showed the highest interpopulation diet divergence (i.e. the outliers with less overlap value in my analysis) should as a consequence be searched especially among those species with a stronger interpopulation variation in body size. This is verified by data: indeed, the outliers of my analysis showed very remarkable differences in average body size, which are in fact accomplished with dietary composition shifts (Hasegawa and Moriguchi 1989 for *Elaphe quadrivirgata* and Shine 1987b for *Notechis scutatus*). This pattern depends on the fact that snakes are gape-limited predators, thus their intraspecific variation in mean body

Table 3. Comparative results of the effects of the various variables on the interpopulation diet overlap. 1-way ANOVAs were used for measuring the effects of single factors, and GLM – general factorial design for measuring the effects of the interaction terms between independent factors. Effects with significant values are in boldface.

Source	DF	Mean Square	F	p
General affinity criterion				
Continent	5	2.603E-02	2.063	0.085
Climatic region	1	1.313E-02	0.951	0.334
Guild	2	2.495E-02	1.864	0.165
Family	4	1.281E-02	0.924	0.457
Venom	1	3.297E-02	2.451	0.123
Hunting strategy	1	2.044E-03	0.146	0.704
Continent × climatic region	**1**	**7.563E-02**	**6.960**	**0.011**
Continent × guild	5	1.219E-02	0.947	0.460
Continent × family	4	2.534E-02	2.268	0.077
Continent × venom	4	2.178E-02	1.924	0.122
Continent × hunting strategy	**4**	**2.812E-02**	**4.634**	**0.037**
Climatic region × guild	**2**	**5.037E-02**	**4.136**	**0.022**
Climatic region × family	2	9.119E-03	0.642	0.530
Climatic region × venom	1	2.657E-04	0.020	0.889
Climatic region × hunting strategy	1	2.328E-03	0.164	0.687
Guild × family	4	1.249E-02	0.887	0.479
Guild × venom	2	2.996E-02	2.373	0.103
Guild × hunting strategy	2	1.324E-02	0.972	0.385
Family × venom	1	1.521E-02	1.080	0.304
Family × hunting strategy	2	3.058E-02	2.278	0.113
Venom × hunting strategy	1	5.545E-08	0.000	0.998
Continent × hunting strategy × guild	2	1.577E-02	1.396	0.261
Close affinity criterion				
Continent	5	7.685E-02	1.510	0.218
Climatic region	1	2.030E-02	0.375	0.543
Guild	2	4.586E-02	0.854	0.433
Family	4	8.269E-02	1.644	0.183
Venom	1	0.147	2.875	0.097
Hunting strategy	1	9.056E-02	1.727	0.196
Continent × climatic region	–	–	–	–
Continent × guild	4	2.737E-02	0.506	0.732
Continent × family	3	2.926E-02	0.579	0.633
Continent × venom	3	7.241E-03	0.138	0.936
Continent × hunting strategy	3	5.499E-02	1.068	0.375
Climatic region × guild	2	7.769E-02	1.494	0.237
Climatic region × family	2	2.256E-02	0.514	0.603
Climatic region × venom	1	2.720E-04	0.005	0.943
Climatic region × hunting strategy	1	2.705E-06	0.000	0.994
Guild × family	3	2.602E-02	0.152	0.927
Guild × venom	2	2.079E-02	0.383	0.684
Guild × hunting strategy	2	2.606E-02	0.487	0.618
Family × venom	1	5.810E-02	1.138	0.293
Family × hunting strategy	2	9.351E-02	1.941	0.158
Venom × hunting strategy	**1**	**0.359**	**8.528**	**0.006**
Continent × hunting strategy × guild	1	1.169E-02	0.202	0.657

size (and hence in head size) may strongly condition the maximum size of their prey, and in turn their diet composition.

The effect of continent × climatic region

Dietary diversity of a predator is certainly influenced by the diversity of the prey sources (Iwasa et al. 1981, Green 1984, 1990, Stephens and Krebs 1986). Biodiversity (and hence prey diversity) is not equally distributed through the world, but there are particular "hotspots" in tropical regions and in some continents, and in overall there is much more difference in the composition of animal communities between two adjacent areas in the tropics than elsewhere (MacArthur 1972, Rosenzweig 1995, Gaston 2000). Thus, it is predictable that there should be higher interpopulation variations in a predator's diet composition in those continents associated with tropical biodiversity hotspots, i.e. South-America, Asia, and Africa, than in the other continents. The climatic region effect was also significant when associated to guild effect, in that arboreal snakes from the highly species-diverse continents tended to show higher interpopulation diet variation. This may once more depend on the very different patterns in the prey type diversity between tropical and temperate regions also at the level of the arboreal guild. The continental-climatic region effects were not significant under the close affinity criterion, but it may depend on that, for several species, it was impossible to calculate the close affinity values from the original sources (Table 2).

The effects of hunting strategy × venom, and of hunting strategy × continent

Although the hunting strategy taken alone did not have significant effect on snake interpopulation diet variation, it had significant effect when interacted with continent (general affinity criterion) and with venom (close affinity criterion). Taking into consideration both these significant models, it can be generalized that snake species with sit-and-wait foraging strategy had significantly less interpopulation variability of diet composition, especially if venomous and if living in Africa, Asia and South America. It is difficult to reconduct this pattern to a clearly predictable hypothesis. I tentatively explain this pattern by two alternative, mutually not-exclusive hypotheses: 1) it may be suggested that sit-and-wait populations of snakes are in general more selective in their habitat/micro-habitat choice, because they depend mainly on camouflage for ambushing with success. Thus, they may encounter more easily the same type of prey in the various localities where they live because the interpopulation variability in habitat type is lesser than in active foragers. 2) Alternatively, it is possible that snakes developed an ambush foraging strategy to hunt efficiently on a precise type of prey, and consequently their diet composition evolved in a more "fixed" way than in active foragers. Hypothesis (1) is verified by some sit-and-wait African species that, although with a wide distribution, are found everywhere in the same types of microhabitat (for instance, *Bitis nasicornis,* see Luiselli 2006c), but is contradicted by other species which show a tremendous variability in habitat and microhabitat selection (e.g. *Vipera aspis*, Bruno 1985). Hypothesis (2), on the other hand, seems to be more consistent with data coming from other types of predators (Stephens and Krebs 1986), and thus more reliable in order to explain the observed pattern.

Concerning the fact of being venomous, this factor likely determines less interpopulation variability in diet composition because snake venoms have evolved to kill a precise prey type (Daltry et al. 1998, Creer 2000, Creer et al. 2002), and hence it is not convenient for a species that has evolved a costly type of prey-specific killing apparatus to shift considerably from one prey type to another depending on its habitat and locality (Heatwole and Poran 1995). However, there are exceptions to this rule (Daltry et al. 1998), and some highly venomous species (e.g. the African cobras *Naja melanoleuca* and *Naja nigricollis*) show very high variability in their prey type preferences in relation to the habitat type (Luiselli et al. 2002), this pattern being in agreement with the fact that they are active foragers (Luiselli et al. 2002).

The non-effect of family

The taxonomic distribution of snakes along the factors influencing interpopulation diet variation (i.e. continent, climatic region, venom, and hunting strategy) is not equal, but nonetheless shows considerable lability. For instance, 1) venom is associated almost exclusively with species of two families (Elapidae and Viperidae), 2) sit-and-wait strategy is associated essentially with species of the family Viperidae and is very rare in the Colubridae, 3) presence in tropical regions is associated essentially with Boidae, Pythonidae and several Elapidae, and 4) the most species-rich families (Colubridae, Elapidae, and Viperidae) are broadly distributed across continents. The interaction of these factors with family is therefore never straightforward, and this explains why family did not affect interpopulation diet variation in snakes. Indeed, there are cases of species with very low dietary interpopulation variability in all the three species-rich families (for instance: *Hemorrhois hippocrepis* for the Colubridae, *Dendroaspis jamesoni* for the Elapidae, and *Bitis gabonica* for the Viperidae), and species with high interpopulation diet variability as well (for instance: *Elaphe quadrivirgata* for the Colubridae, *Notechis scutatus* for the Elapidae, and *Crotalus lepidus* for the Viperidae). In any case, it is noteworthy that family is the only factor considered in this paper that did not have effect on interpopulation diet variation either alone or in conjunction with other factors. This reinforces even more the evidence that snake family is completely uninfluent for determining whether a species will change its diet composition depending on the various populations.

Future studies

Although greatly expanding during the recent years, the international literature on snakes is still far from being sufficiently complete to let us understanding all the causes, consequences and correlates of interpopulation dietary variations. Thus, for the future, I would suggest the scientists to study more and more populations of the various snake species from the diet ecology point of view, especially with regard to those species which may exhibit complex patterns of interpopulation dietary variations (for instance, those species which are intraspecifically strongly variable in mean body size or in foraging strategy) or that have been poorly studied up to now. I would also encourage to continue studying the feeding ecology of the well-known species, by adding new populations living in particularly critical environmental contexts (for instance, populations living at the geographic borders of the species' range, or in extreme environmental conditions compared to the usual characteristics of the species' range, etc). It will also be important to study from a interpopulation comparative perspective the relationships between predator size and prey size, which is still a relatively neglected subject in contemporary research of snake feeding ecology.

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