

Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns

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Luiselli, L. 2006. Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. – *Oikos* 114: 193–211.

The role of interspecific competition as a key factor in the ecology of natural communities where species exploit limited resources is well established, and the study of competition dynamics in snake communities has received much attention in recent years. Twenty years ago, an acclaimed review (Toft 1985) suggested that snakes were atypical among vertebrates because sympatric species usually partition the food niche. Here, I review the articles published in the last two decades with the aim of finding any general geographical or guild patterns and assessing if Toft's main conclusion is still supported by new evidence. Where appropriate, I use Monte Carlo simulations to establish whether observed patterns of niche overlap are real, or if they have occurred by chance. My study shows clear congruence in the patterns of coexistence exhibited by snake communities in different regions of the world, i.e.: (1) cold regions of the northern hemisphere (high latitudes and altitudes) exhibit low species richness and a very low, or even absent, potential for interspecific competition; (2) aquatic snakes that form communities in temperate regions generally partition the food type available and exhibit a broad similarity in habitat use with subtle differences in microhabitat use; (3) terrestrial snake communities in temperate regions are very variable in terms of their coexistence dynamics and show no evidence of generalised patterns; (4) sympatric viperids in Europe, North America and, most interestingly, tropical Asia partition the available habitat but not the prey resource; (5) competition is much stronger in tropical snake communities, and the intensity of this process fluctuates throughout the year being most intense during periods of low food availability; (6) in general, tropical snakes partition the food resource (prey type and/or prey size), but when this resource is not partitioned competitive exclusion can occur.

Prey resource availability is a fundamental variable for all snake communities; this is clearly documented by studies on terrestrial snakes in Australia where, due to a relative scarcity of prey availability in the field, sympatry among species is much rarer than in other continents. I conclude that, although there are several notable exceptions, Toft's main conclusion is still supported by empirical evidence. However, I disagree with Toft's conclusion that most snakes are food specialists, and I contend that interspecific competition is important in structuring many (if not most) of the snake communities around the world.

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There are few really unifying general concepts in ecology, but the concept of interspecific competition has long been considered a major factor affecting the functioning

of natural communities where species exploit limited resources (Hanski 1987, Shorrocks 1990, Ray and Sunquist 2001, Krijger et al. 2001). Although there has

Accepted 29 August 2005
Subject Editor: Lennart Persson

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ISSN 0030-1299

been considerable controversy with regards to both the extent to which competition shapes the organization of sympatric communities and the problems associated with the 'ghost of competition past' (Connell 1980, Schoener 1982, Barabault 1991, Simberloff and Dayan 1991) it is, nevertheless, still considered by several authors as an important structuring force for natural communities comprising either closely related (Connell 1983, Brönmark et al. 1991) or distantly related and phenotypically dissimilar species (Hurlbert et al. 1986, Capizzi and Luiselli 1996a, Mokany and Shine 2003).

Snakes are highly successful predators that are widespread throughout much of the world, including extreme habitats such as desert and very cold areas north of the Arctic Circle, or at high altitude (>3000 m a.s.l.) (Greene 2001). They are, nevertheless, clearly more abundant in tropical and subtropical regions (Vitt 1987, Greene 2001). In some habitats, snakes are so abundant that they greatly affect the dynamics of their prey (Barabault 1971, 1987) (although the hypothetical relationship between cyclical fluctuations of prey abundance and specialised predation by snakes has never been demonstrated; Andersson and Erlinge 1977, Hanski et al. 1991). All snakes are carnivorous, and most of them forage only on living organisms (but see DeVault and Krochman 2002 for a review of snake predation upon corpses). In addition, they are peculiar amongst carnivorous animals because they ingest their prey whole (Greene 2001). They may also ingest prey with particular body dimensions that are much larger than their own (Greene 2001). Because of all these reasons, snakes often inhabit areas with a limited or ephemeral availability of resources and they are therefore suited for studies on the role of interspecific competition and resource partitioning. Indeed, according to an authoritative review published about 20 years ago, snakes are a notable exception among reptiles (and other carnivorous animals) in that they partition food resources (especially the prey type) and this helps to reduce the intensity of interspecific competition (Toft 1985, Vitt 1987).

Herpetologists have traditionally focused on lizards and frogs when studying the role and mechanisms of resource partitioning and interspecific competition (Toft 1985, Pianka 1986), whereas studies on the community ecology of snakes were largely neglected during the '70s and '80s (Reichenbach and Dalrymple 1980, Vitt 1987, but see Shine 1977, Brown and Parker 1982, Fitch 1982 for some classical examples of snake community studies). However, snakes have recently arisen to the 'status' of model organisms in studies of evolutionary ecology (Shine and Bonnet 2000, Shine 2002, Lourdaïs et al. 2003), and field studies on their community ecology have grown concomitantly in both advanced (Drobenkov 1995, Capizzi and Luiselli 1996a, Himes 2003a,b)

and developing countries (Orlov 1997, Luiselli et al. 1998). It therefore seems necessary to review recently published material and to respond to the following questions:

- 1) Is Toft's (1985) main conclusion (i.e. that snakes partition the food resource, and particularly the prey type) still valid?
- 2) Are there geographical patterns in the role that interspecific competition plays in organising snake communities? For instance, do snake communities follow the trend (Barabault 1987, 1991) to show higher levels of interspecific competition towards the tropics, and do the mechanisms of competition within snake communities also vary with latitude?
- 3) Can the patterns of resource use and interspecific competition in snakes be predicted on the basis of their guild? That is to say, at any given latitude, are the patterns of coexistence exhibited by sympatric aquatic snakes different from those of sympatric terrestrial or arboreal snakes?
- 4) Can we conclude that most communities of snakes around the world are governed by interspecific competition?

I will demonstrate that the impetuous advance of our understanding of snake community ecology 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 differences between species with respect to resource partitioning, which of course are not totally useful when studying the role and the intensity of the interspecific competition (Schoener 1974, Connell 1980).

Methods

I have reviewed mainly recent studies, i.e. post 1985, from peer-reviewed journals or, exceptionally, academic dissertations. I have referred to earlier studies only when they were particularly important for the analysis, or when my interpretation of the data therein was somewhat different from Toft's (1985) or that of the original authors. Every effort has been made to avoid unbalanced coverage of the literature from the different regions of the world, although where there is a difference in the amount of literature reviewed this reflects regional differences in the development of research on snake community ecology.

When necessary, I used niche overlap formulas (Pianka 1986) as an operative measure of the intensity of interspecific competition for each niche axis (spatial, food, temporal), assuming that higher formula values correspond to higher levels of actual competition

(Schoener 1974, 1982). Matrices of species counts by niche classification category were constructed, for each community of snakes, from datasets presented in the original papers. Niche overlap was quantified using Pianka's (1973) symmetric equation with values ranging from 0 (no overlap) to 1 (total overlap) (Gotelli and Graves 1996, Friggens and Brown 2005). To assess whether the observed overlap values of the various communities occurred by chance, the original species utilization matrices were randomised by shuffling the original values amongst the resource states (randomisation algorithm 3 of Lawlor 1980); for each pair 1000 random Monte Carlo permutations were generated using the software 'Ecosym 700'. Niche overlap values were calculated for each of these randomly generated matrices, and species-pair and community-summary statistics were computed (Friggens and Brown 2005). Actual overlap values were then compared to the distributions of the expected values. If competition within communities is low, then the overlap values for at least one of the three niche axes should be significantly lower than those observed in the other axes.

To examine the issues of geographical and guild patterns in snake competition, I subdivided the various published studies depending on (1) the geographic position of the study areas (at a continental level: Europe, North America, South and Central America, Africa, Asia, Australia), and (2) their guild (aquatic, terrestrial, arboreal; Luiselli et al. 1998).

Are there common geographical or guild patterns of resource partitioning in communities of snakes?

Europe

For Europe, I split the analysis into studies from (i) cold areas (i.e. at high latitudes or altitudes) and (ii) Mediterranean areas because species richness in snake communities is much lower in colder zones than in Mediterranean zones (Bruno and Maugeri 1990), and the number of interacting species influences the patterns and processes of competition (Connell 1983, Chapman and Reiss 1992). Indeed, in northern Europe and in the high altitudes of the Alps no more than 3 sympatric species can be found, whereas in Mediterranean Europe is quite common to observe 5-6 or even 8 sympatric species (Bruno and Maugeri 1990, Luiselli and Rugiero 1990, Capizzi and Luiselli 1996a). These latitudinal and altitudinal differences in terms of species richness are well expected because ambient temperature is the factor that correlates best with snake species richness at a global scale (Schall and Pianka 1978).

Communities of snakes in the cold European regions

The three species that are found in cold European regions are *Vipera berus*, *Coronella austriaca* and *Natrix natrix* (Bruno and Maugeri 1990). These species exhibit clearly different food preferences: *V. berus* is mainly a rodent-eating species (Luiselli and Anibaldi 1991, Drobekov 1995), *N. natrix* an amphibian-eating species (Luiselli et al. 1997, Gregory and Isaac 2004) and *C. austriaca* a lizard-eating species (Fig. 1, Luiselli et al. 1996 and see Drobekov 1995 for another community of the same species, studied in Russia). Monte Carlo simulations compared to real data, on prey type and biomass, showed that species distribution across niche categories is significantly different from random (in both cases, $P < 0.001$), and hence the three species are really very different from each another in terms of niche characteristics. The interspecific overlaps were extremely low (*V. berus* vs *C. austriaca*, % prey items: 0.072, biomass: 0.082; *V. berus* vs *N. natrix*, 0.067 and 0.106; *N. natrix* vs *C. austriaca*, 0.002 and 0.005), hence confirming a very low potential for interspecific compe-

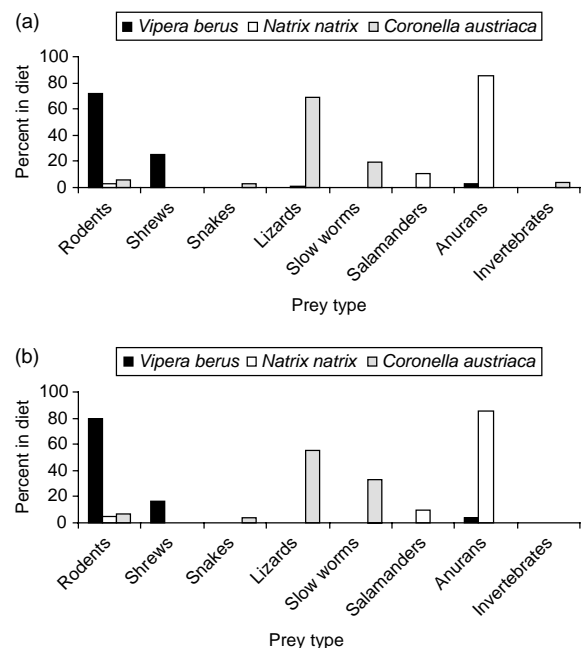


Fig. 1. Food partitioning (expressed as percent of the various prey types in the diets (a), and as percent of biomass (b) among three species of 'cold climate European' snakes at a high mountain locality in the Italian Alps. At the study area, the snow covering is continuous from November to April, and the species are sympatric. Data from Luiselli and Anibaldi (1991) and Luiselli et al. (1996, 1997) (all data from these sources being cumulated). Contingency table analysis revealed that the three species differed significantly ($P < 0.001$ at χ^2 test) in terms of frequency of occurrence of the various prey items and in terms of biomass contributions of the various prey items to the diets ($P < 0.01$ at χ^2 test). Sample sizes: *V. berus*, $n = 32$; *N. natrix*, $n = 190$; *C. austriaca*, $n = 118$.

tion for food under current circumstances. Although *V. berus*, *C. austriaca* and *N. natrix* apparently partition the food resource available, interspecific competition seems to have nothing to do with it. Indeed, these species' food preferences are typical of all of the other members of their genera: rodents are the preferred prey for all the other *Vipera* species (Saint Giron 1980, the unique exception being the small-sized *V. ursinii*), amphibians are the main prey for all the *Natrix* species (Santos and Llorente 1998) and lizards are the main prey for the only other member of the genus *Coronella*, i.e. *C. girondica* (Luiselli et al. 2001). Hence, the divergent dietary preferences of the three 'cold climate' species are genetically determined, and have nothing to do with limited resource availability. Direct interference competition may be present, because *C. austriaca* can occasionally eat the juveniles of the other species (Luiselli and Anibaldi 1991), but the frequency of occurrence of these cases of snake-eating by *Coronella* appear so rare (Fig. 1) that it is very unlikely that they can play more than a trivial role in the organization of these species' assemblages.

Apart from food, two other limited resources for cold climate ectotherms are the availability of suitable sites for egg-laying and basking. *Natrix natrix* females are known to travel extensively to find highly dispersed egg-laying sites (Madsen 1984, Luiselli et al. 1997), but the potentially high reproductive cost of this behaviour is not related to interspecific snake competition because *N. natrix* is oviparous while the other two species are live-bearing (Bruno and Maugeri 1990). On the other hand, the occurrence of interspecific competition for limited basking sites may be a potentially interesting area to study.

The Mediterranean communities

In Mediterranean Europe, there is a relatively high diversity of snake species in natural and well-managed areas (Luiselli and Rugiero 1990) and also in heavily altered and suburban sites (e.g. up to 6 sympatric species in an urban park in Roma, Rugiero 2004). The three hotspots for snake species richness are the Iberian peninsula, the Italian peninsula and the Balkans (Bruno and Maugeri 1990). Comparative studies to determine if there are general ecological patterns in snake community structure in these regions would thus be particularly valuable. Unfortunately, this type of study has received attention only in Italy; where up to 8 sympatric species can be found with a density of 3–23 snakes per ha in terrestrial habitats and 9–41 snakes per ha in aquatic habitats (Filippi 1995). All the species were very similar in terms of the timing of their above-ground activity periods (March to end of October) and daily activity patterns (strictly diurnal during April–June and late September–end of October; crepuscular and nocturnal in July–August) (Filippi 1995). However, there were

differences in terms of guilds with species of the genus *Natrix* being semi-aquatic and species of the genera *Vipera*, *Elaphe*, *Coronella* and *Coluber* being terrestrial (*Elaphe* may also be semi-arboreal at some sites) (Filippi et al. 1995).

With regard to the aquatic guild, freshwater environments on mainland Italy are generally inhabited by sympatric populations of two species, i.e. *N. natrix* (which is much more aquatic in Mediterranean regions than in northern latitudes or higher elevations) and *Natrix tessellata* (Bruno and Maugeri 1990, Luiselli and Rugiero 1991, Filippi 1995). The competitive interactions between these two species were studied by Filippi (1995) – spatial and habitat niches) and Luiselli and Rugiero (1991) (trophic niche). Filippi (1995) demonstrated that the two species were nearly identical in terms of spatial and habitat use but that *N. natrix* was observed significantly more often than *N. tessellata* on river banks, whereas the latter species was observed swimming more often. Based on this evidence, Filippi hypothesised that *N. tessellata* may spend more time in the water than its potential competitor, although the reasons for this difference remained unknown. Luiselli and Rugiero (1991) demonstrated that there was very clear food resource partitioning, with *N. tessellata* preying almost exclusively upon fish (accounting for more than 90% of its diet in terms both of prey items eaten and biomass) and *N. natrix* taking mainly anurans, to a lesser extent fish and very occasionally rodents and birds. Re-analysis of the original datasets of Luiselli and Rugiero (1991) and Filippi (1995) using Monte Carlo simulations confirmed that the distribution of these snakes across niche categories is significantly different from random ($P < 0.01$ in both cases). Hence, combining the data from Filippi (1995) and Luiselli and Rugiero (1991), I suggest that the two species probably use different microhabitats for foraging and that this lessens interspecific competition and allows coexistence in very many different localities – where both species can reach high densities and population sizes (Filippi 1995, Bologna et al. 2000).

The island of Sardinia (Italy) contains two aquatic *Natrix* species; one is endemic i.e. *N. natrix cetti* and the other has been introduced i.e. *N. maura* (Stefani 1983, Bruno and Maugeri 1990). Field studies indicate that both species feed almost entirely upon amphibians (Fig. 2) and that their diets overlap widely ($O = 0.826$ on % of prey items, and $O = 0.994$ on the prey biomass); the distribution of the two species across niche categories is significantly different ($P < 0.05$) from random. We would then expect that, for an equivalent level of food resource availability at the various study areas, stronger competition for food should occur between the island pair of species than between the mainland pair of species. And, as an outcome of this, we would expect to find fewer sites where the two species are sympatric and perhaps even

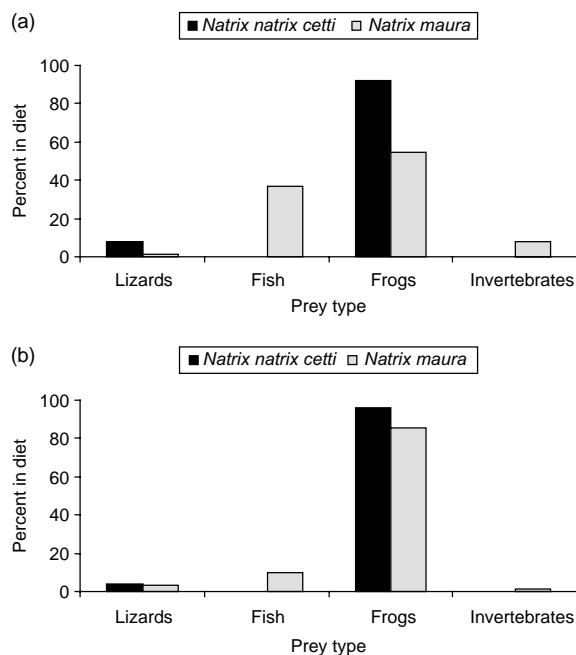


Fig. 2. Food habits of aquatic snakes in Sardinia. (a) shows the percent of the various prey types in the diets, and (b) the percent of biomass. Data came from Capula et al. (1994) (data relative to *Natrix natrix cetti*) and from Rugiero et al. (2000) (data relative to *Natrix maura*) (all data from these sources being cumulated). Sample sizes: *N.n. cetti*, $n = 13$, *N. maura*, $n = 79$. Note that the scarcity of data available for *N.n. cetti* depended on the extreme rarity of this species.

smaller population sizes of the weaker competitor on islands compared to regions of the mainland system. The observed patterns fully confirm these expectations i.e. throughout the whole of Sardinia the introduced species is widespread and abundant whereas the endemic species is extremely rare and confined to a handful of sites from which the other competitor is generally absent (Societas Herpetologica Italica, 2005). In the few sites where the two species are sympatric the introduced species is always much more abundant (Societas Herpetologica Italica, 2005), and the endemic *N. n. cetti* is significantly smaller than mainland conspecifics in terms of average body length and mass (Thorpe 1975, 1979, Stefani 1983, Bruno and Maugeri 1977, 1990). Indeed, mainland *N. natrix* (data in Filippi 1995) living in the absence of *N. maura* exhibit much higher growth curves and maximum lengths than Sardinian *N. natrix cetti* that live in sympatry with *N. maura* (data derived from Capula et al., unpublished report to the Nuoro Province Administration 2000); this is despite an almost identical size at birth (Fig. 3). Further to this, on the island of Corsica – where *N. maura* is rare – *N. natrix* has become widespread, locally abundant and even larger in size (Bruno and Maugeri 1990, Capula et al., unpubl.). These results are consistent with controlled experiments (e.g. using mosquitos and tadpoles – Griffiths et al.

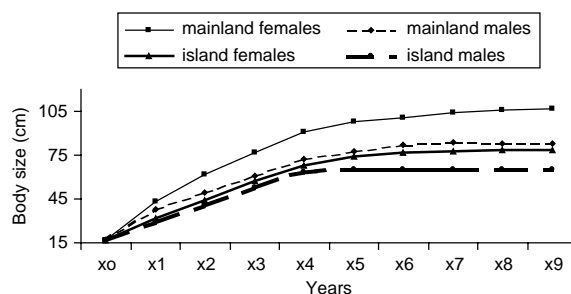


Fig. 3. Growth curves for mainland *Natrix natrix* living without a competitor-for-food, and island conspecifics (sub-species *cetti*) living in sympatry with a competitor-for-food (i.e. *Natrix maura*). The growth curves diverged significantly (although male growth was slower and male maximum size smaller than females for both populations), and the island population attained much smaller body size than the mainland population.

1993, Mokany and Shine 2003) and imply that the growth of *N. natrix* is suppressed by the presence of its competitor.

Filippi (1995) suggests that these competitive effects may vary temporally, for example with seasonal reductions in water depth that can result in much higher localised densities of water snakes (both *N. natrix* and *N. tessellata*) and, as such, possibly lead to higher competition for food at this time.

With regard to the terrestrial guilds, the occurrence of interspecific competition for egg-laying and basking sites seems to be unlikely. Indeed, it is usually easy for Mediterranean snakes to find both suitable egg-laying (Filippi 1995) and basking sites (Filippi 2001), and so these resources are clearly not limited in pristine or semi-pristine habitats. Generally, these sympatric species show a similar usage of habitat and substratum types (Filippi 1995, 2001) even at a regional level (Hofer 2001), and this pattern can remain relatively constant across time (10+ years; Rugiero et al. 2002, Filippi and Luiselli 2006). However, in altered landscapes human activities may have removed all the woodland cover and most of the suitable egg-laying sites, and hence there may be competition for the remaining sites. This issue has never been studied in any detail, but it is well known that tens of females from different species may deposit their eggs into a single communal nesting site that may involve a fair deal of travel to reach (Lapini 1983, L. Luiselli, unpubl.). Indeed, northern European populations of *N. natrix* are often forced to travel extensively to find a few good egg-laying sites (Madsen 1984). Competition for egg-laying sites in altered habitats may be a fertile area for future research.

The availability of food resources for snakes is often temporally and spatially variable (e.g. in an agro-forest, inhabited by five species of snakes, small mammal abundance is higher in autumn than in any other period and varies considerably between habitats; Capizzi and

Luiselli 1996b) and snakes should often therefore be opportunists. Indeed, Capizzi et al. (1995) demonstrated that all four sympatric terrestrial species (*Elaphe longissima*, *Elaphe quatuorlineata*, *Coluber viridiflavus* and *Vipera aspis*), inhabiting an agro-forest habitat in the surroundings of Rome, fed on particular prey types (small mammals or lizards) solely in relation to their relative abundance in the field and not following species-specific preferences for less common prey. Rugiero and Luiselli (1995) describe a similar relationship between prey type availability and prey consumption by snakes in an Italian woodland. Furthermore, Capizzi and Luiselli (1996a) compared trapping data for small mammals with diet data from four sympatric snake species (*E. longissima*, *E. quatuorlineata*, *C. viridiflavus* and *V. aspis*) and from four sympatric owl species (*Athene noctua*, *Strix aluco*, *Asio otus* and *Tyto alba*) inhabiting the same landscape, and demonstrated that the snakes preyed on forest-associated small mammals whereas the owls preyed on rodents from semi-cultivated open grassy areas. They concluded that (i) competition for food was higher between phylogenetically related than between phylogenetically unrelated taxa (due to a separation of habitats preferred for foraging) and that (ii) interspecific competition for food was likely to be quite strong amongst the sympatric snakes. Although the snakes consumed similar prey types (mean overlap values (sensu Pianka 1986) = 0.823) they diverged considerably in terms of prey size taken; all species differed but *E. quatuorlineata* was notable because it ate much larger prey than any other species. Re-analysis of the original datasets (Capizzi and Luiselli 1996a) confirm that the distribution of snakes and owls across niche categories are significantly different from random ($P < 0.001$ for % of prey items and $P < 0.0001$ for prey biomass), hence confirming that this community of predators is structured in accordance with predictions from competition theory. Preliminary data collected from another Mediterranean site (Filippi 1995) also indicate this pattern of prey-size partitioning between species, but the dataset is too small to provide strong evidence (data comprises 58 prey items from six snakes species cf. 337 prey items from four species in Capizzi and Luiselli 1996a).

A distinct pattern of coexistence is exhibited by sympatric viperids (genus *Vipera*). Young snakes are sit-and-wait predators of lizards and adult snakes predate small mammals (Saint Girons 1980, Bea et al. 1992). They appear to prey on the most abundant lizard and small mammal species at each site (Capizzi et al. 1995, Capizzi and Luiselli 1996a, Monney 1996). In the relatively few sites where two or more species coexist, the vipers retain almost identical food preferences but partition the available habitat. This pattern is observed within sympatric populations inhabiting ecologically diverse landscapes e.g.: agro-forest in western France

(*V. aspis* and *V. berus*, Saint Girons 1975a, Duguy and Saint Girons 1978); mountain slopes in Switzerland (*V. aspis* and *V. berus*, Monney 1996) and calcareous valleys in northeastern Italy (populations of: *V. ammodytes* and *V. aspis*; *V. aspis* and *V. berus*; *V. ammodytes*, *V. aspis* and *V. berus*; Lapini 1983). As a general rule in sympatric areas, *V. berus* is linked to forested and cooler zones, *V. aspis* to the drier and sunny zones (Saint Girons 1975a, Monney 1996) and *V. ammodytes* is always linked to rocky areas (Lapini 1983). Saint Girons (1975b, 1978) has also demonstrated that this habitat partitioning is mediated via the different thermal needs and thermoregulation abilities of the various species.

Summarized patterns for European snake communities

In conclusion, my review of the European snake literature suggests that:

- i) Interspecific competition is unlikely to occur amongst (a) northern European snakes and (b) snakes living at high altitudes in the alpine chain. (However, one interesting area to investigate is the thermal relationship between species and the role of competition for suitable basking sites).
- ii) Among semi-aquatic snakes from Mediterranean Europe, food type partitioning lessens competition between sympatric species. If resource partitioning does not occur, yet interspecific competition for food is strong, then one of the competitors may become locally or regionally threatened; e.g. *N. n. cetti* is critically endangered in Sardinia (Corbett 1989) due to competition with the introduced *N. maura*.
- iii) Sympatric terrestrial snakes in Mediterranean areas partition the available food resource by selecting prey of different sizes, rather than by taking prey of different types – although they usually take the most abundant prey species in the environment. An exception occurs with sympatric viperids, which always partition the available habitat.

North America

As in Europe, North America shows a clear decrease in snake species richness with both latitudinal and altitudinal gradients (Schall and Pianka 1978, Vitt 1987). To compare these geographical effects on snake distribution between N. Europe and N. America, I (somewhat arbitrarily) considered for my analysis all the species found at approx. 40° N or above. I examined the distribution maps of all the 121 North American snake species (Rossi and Rossi 2003, Campbell and Lamar 2004) and determined that just 17 species (14%) are distributed in the cold regions of the northern United States and Canada. In addition, upon dividing the

territory roughly into three zones (west, central and east), I determined that the number of species that are potentially sympatric is quite low (Table 1).

The difference in the number of species in the cold regions of Europe compared to North America is likely to be due to historical reasons, i.e. to the glacial periods in which European species became 'squeezed' between glaciers from the north and south (Borkin 1986, Stugren 1986), a situation that was different in North America.

For every potentially sympatric species in the North American zones, I examined diet preferences, body sizes and habitat use all in relation to phylogeny (Rossi and Rossi 2003, Campbell and Lamar 2004, for a synthesis of the natural history of these species) and determined that there is such high species-specificity in terms of predicted niche that the potential for interspecific competition is certainly low; this parallels the case of the cold-climate snakes of Europe, shown above. The only exception is when *Thamnophis* species occur in sympatry, under these circumstances competition may occur due to species' similarities in body size, diet and general habits (Rossi and Rossi 2003). However, an excellent comparative study at eight sites on Vancouver island by Gregory (1978, 1984) concluded that three sympatric species of *Thamnophis* (*T. sirtalis*, *T. ordinoides* and *T. elegans*) were generally similar in terms of their main niche dimensions (all were quite generalist) and that there was little support for the hypothesis that competitive interactions may have had a central role in shaping the community. It seems, therefore, that the potential for interspecific competition between sympatric snakes is low in the colder regions of both North America and Europe – where species richness is low (see Pough 1966 for an analysis of the altitudinal distribution of snakes in the mountains of Arizona). The same may not be true in the central and southern latitudes of North America, where there is in general a higher snake species richness

than in comparable regions in Europe, both in aquatic and terrestrial habitats.

With regard to the aquatic guilds, a series of papers have examined the dynamics of coexistence of five species of *Nerodia* and *Regina* in Louisiana (Mushinsky and Hebrard 1977a,b, Hebrard and Mushinsky 1978, Mushinsky et al. 1980, 1982). The results of these investigations indicate that the various species: (i) exhibit wide-ranging similarity in habitat use, with some important differences in microhabitat utilization; (ii) exhibit an evident pattern of food resource partitioning based on prey type (although this was complicated by ontogenetic changes in diet composition and prey size); and (iii) show considerable differences in daily activity (which is, however, not a reliable niche dimension, Jacksic 1982). Patterns of food type partitioning were also noticed in a community of seven species in Louisiana (Kofron 1978) and three species in Arkansas (Byrd et al. 1988), whereas in a water snake community in Kentucky species were shown to use similar habitats, with some subtle interspecific differences in microhabitat use (Laurent and Kingsbury 2003). In this latter study, the authors also used randomisation procedures to confirm that the distribution of their data did not occur by chance, and hence this study is particularly valuable. A recent laboratory study carried out in Mississippi demonstrated that interspecific competition between two water snakes (*Nerodia sipedon* and *Nerodia rhombifer*) may occur at high snake densities, and that *N. sipedon* may be a superior exploitative food competitor to *N. rhombifer* because it has a faster rate of gastric breakdown (Himes 2003a). Himes (2003a) suggests that this difference in competitive abilities may be important in summer when river water levels are very low, and this may result in a higher abundance of the better competitor observed at this time. Himes (2003b) also analysed the feeding ecology and potential for interspecific competition between two species of water snakes which are neither similar in size and body architecture nor phylogenetically closely related (i.e. the colubrid *N. sipedon* and the viperid *Agkistrodon piscivorus*) and found great differences in terms of both prey type selection and olfactory perception, thereby concluding that competition between them should be low.

In general, studies on water snake communities from North America confirm the broad patterns observed in water snakes communities in Europe, i.e. food type partitioning occurs between species which utilise broadly similar habitats (but subtly dissimilar microhabitats). It would be interesting to explore the physiological and morphological correlates of patterns of resource partitioning. In Europe, for instance, the piscivorous *N. tessellata* has a head shaped differently from that of the batrachophagous *N. natrix* (see photos in Bruno and Maugeri 1977, 1990) but broadly similar to that of the North American *Nerodia*, (whereas the head shape of *N.*

Table 1. List of the snake species found in North America, approximately at 40° N or above, in relation to three different regions (i.e. western, central and eastern regions).

Western regions	Central regions	Eastern regions
<i>Charina bottae</i>	<i>Heterodon nasicus</i>	<i>Lampropeltis triangulum</i>
<i>Coluber constrictor</i>	<i>Thamnophis radix</i>	<i>Nerodia sipedon</i>
<i>Pituophis catenifer</i>	<i>Thamnophis sirtalis</i>	<i>Opheodrys aestivus</i>
<i>Thamnophis elegans</i>	<i>Sistrurus catenatus</i>	<i>Storeria dekayi</i>
<i>Thamnophis ordinoides</i>		<i>Storeria occipitomaculata</i>
<i>Thamnophis sirtalis</i>		<i>Thamnophis sauritis</i>
<i>Crotalus viridis</i>		<i>Thamnophis sirtalis</i>
		<i>Crotalus horridus</i>

matrix is similar to that of North American *Thamnophis*). It is more than likely that differences in prey type selection between sympatric species may also, to some extent, be linked with skull morphology (Dwyer and Kaiser 1997) or chemosensory perception (in turn a product of neuro-physiological and morphological differences) (Mushinsky and Lotz 1980). Differences in microhabitat utilization may also be linked with species-specific differences in evaporative water loss (Winne et al. 2001).

With regard to the terrestrial guilds, resource partitioning and competitive interactions between sympatric species have been studied in a variety of different areas in North America, but mainly in dry desert areas. The various studies are not consistent in terms of their conclusions, and it is difficult to find general patterns within the datasets. Perhaps this lack of any clear general patterns may also depend on the fact that most of the study areas were not ideal for testing resource partitioning and interspecific competition mechanisms. Indeed, at some study areas resources (food and habitat) were not limited, and hence sympatric snakes exhibited much overlap in their usage of them. For example, Reynolds and Scott (1982) show that where rodent prey were very abundant all the snake species (three viperids and two colubrids) fed in a complementary way, and the same happened at another prey-unlimited site with a community of one colubrid and one viperid (Diller and Wallace 1996). In addition, competition for space was not evident in either area as snakes shared basking sites, hibernacula etc. without any observable behavioural interactions (Reynolds and Scott 1982, Diller and Wallace 1996). In other study systems, the sympatric snakes were from very different lineages, and their different resource use patterns appeared to be shaped more by phylogenetically determined life-history and morphological differences (mediated locally by emergent factors e.g. rainfall in the cold Great Basin cold desert) than by competitive mechanisms (Parker and Brown 1980, Brown and Parker 1982). However, American scientists have documented some very interesting cases of resource partitioning amongst sympatric terrestrial snakes. Rodriguez-Robles et al. (1999) analysed a large sample of museum specimens and observed that three colubrid species (*Arizona elegans*, *Rhinocheilus lecontei*, *Pituophis catenifer*) are sympatric throughout most of their range and share broadly similar prey (feeding on both small mammals and lizards); the frequencies of consumption of each prey type were, however, distinctly different – thus demonstrating a pattern of food resource partitioning over a large geographical range. Also, Fitch (1982, 1999) studied snake community ecology for about 50 years and clearly demonstrated the occurrence of food resource partitioning between 12 species of sympatric snakes in Kansas. The reason for this spectacular case of food resource partitioning is

almost certainly a mixture of (i) divergent life-histories between phylogenetically dissimilar species (e.g. evolved sit-and-wait vs active foraging strategies etc. such as the differences observed between some terrestrial species e.g. *Crotalus horridus* and *Pituophis melanoleucus* or between surface litter species e.g. *Storeria dekayi* and *Lampropeltis triangulum*), and (ii) competitive mechanisms (e.g. between the closely related *Lampropeltis calligaster* and *L. triangulum* or between *Coluber constrictor* and *Elaphe obsoleta*). Food type partitioning was also found in sympatric populations of *T. sirtalis sirtalis* (which ate mainly birds) and *C. constrictor foxii* (which ate mainly rodents) (Olson and Warner 2001), but once more these two species belong to quite different Colubrid lineages.

Studies on sympatric North American viperids confirmed the patterns of habitat resource partitioning observed in different ecological contexts in Europe. For instance, habitat resource partitioning was observed between *Crotalus atrox* and *Crotalus molossus* in south-eastern Arizona (Pough 1966) and between three rattlesnake species (*Crotalus tigris*, *C. atrox* and *C. molossus*) in the Sonoran Desert, where they differed in habitat usage within and between seasons but were remarkably similar in terms of home range sizes, activity patterns, thermal ecology and yearly intake of food (Beck 1995).

It would be interesting to know if, in northern latitudes, niche width (in terms of habitat selection and food habits) is narrower in the American species than in the European species – thus reflecting the difference in species richness. However, data from equivalent studies in the two continents are insufficient at present to analyse this.

Africa

Although it has one of the most diverse and spectacular snake faunas, studies on snake community ecology in Africa have been largely neglected (Toft 1985). However, recent African studies have highlighted some very noteworthy patterns of resource partitioning and interspecific competition, particularly in forest habitats.

General theory (Pianka 1966, Rhode 1992) suggests that there should be higher competition in tropical areas than in temperate areas. This prediction is fully supported by snake studies in tropical Africa and Madagascar; at least if we follow some widely accepted criteria for evidence of interspecific competition in snakes (Reichenbach and Dalrymple 1980). For instance, in a wet savannah in Ivory Coast, Barbault (1987) observed that species richness was much higher than in a comparable temperate habitat and that the biomass of snakes was constantly around 1/10 of the total biomass of their amphibian prey. He thus confirmed that preda-

tion by snakes partially controlled the population dynamics of the various amphibians. In general, studies from Europe and North America show that the number of sympatric species at a site ranges from 2–8 (with a few notable exceptions e.g. 18 species for a snake community in Kansas-Fitch 1999, but in this study area some species were so rare that they were captured just once in 50 years). With regard to Africa, Andreone and Luiselli (2000) examined the snake communities at 44 forest sites in Nigeria and Madagascar, and found that the number of sympatric species sometimes exceeded 13–16 species, with a peak of 24 species in one Nigerian rainforest. The number of sympatric species was linked to the habitat type (Andreone and Luiselli 2000); rainforest communities always contained high numbers of species (maximum 43-Politano 1998), whereas deciduous forests in Madagascar housed far fewer (mean = 4, range 0–7, $n = 5$ sites). Forest-derived savannas in central Nigeria and mangroves in southern Nigeria also show a high species richness (both contain 18 sympatric species-Akani et al. 1999, Luiselli and Akani 2002). Many other descriptive studies confirm that Afrotropical habitats may easily house more than 20 sympatric species of snakes at one site (Schmitt 1996, Politano 1998).

This high species richness at African sites implies that several species may utilise the same resource. For instance, up to eight species were found to prey upon the same species of amphibians and seven upon the same species of rodents in a Nigerian forest (Luiselli et al. 1998), and up to eight species preyed upon lizards in Madagascar (Andreone and Luiselli 2000). So, competition may well occur when these resources are limited. Resource limitation may be seasonal, for example in one Southern Nigerian forest the abundance of rodents and amphibians is high in the wet season (Akani et al. 2004, Angelici and Luiselli 2005) but in the dry season the biomass of these prey is much reduced (Angelici and Luiselli 2005, Luiselli 2006). Hence, food competition at this time is expected to be strong amongst the sympatric snakes (Luiselli 2006) especially given that all snakes, even large ones, appear to be abundant in the area (Luiselli et al. 2005a) (which is contrary to the general rule predicting that top/large predators should be relatively rare-Cohen et al. 1993, Spencer 2000, Ahlring and Carrell 2001).

Patterns of resource partitioning in a snake community in a southern Nigerian rainforest were studied by Luiselli et al. (1998 – food resource) and Luiselli and Akani (1999 – habitat resource). This community comprised 24 sympatric species belonging to diverse phylogenetic lineages and to different 'ecological guilds' (terrestrial, arboreal, aquatic, subterranean). Most species were present at low population sizes but a few (no more than 2–3 species in each guild) were abundant. The majority of species show a complementary use of habitat, concentrating mainly in moister areas (i.e.

swampy forest patches) (Luiselli and Akani 1999) where the density of their prey (anurans and rodents) is higher (Politano 1998). Food niche overlap (both prey type and biomass) between species did not correlate significantly with the rank of phylogenetic similarity, and the mean overlap values for species within a guild did not differ among guilds (Luiselli et al. 1998). Competition intensity was highest within guilds – as was expected, and prey size rather than prey type appeared to be the resource that was partitioned (Luiselli et al. 1998). Multivariate analyses revealed pairs of species that should compete most intensely i.e.: (i) the cobras (*Naja melanoleuca* and *Naja nigricollis*), (ii) the large-sized vipers (*Bitis gabonica* and *Bitis nasicornis*), (iii) the marsh snakes (*Natriciteres fuliginoides* and *Natriciteres variegata*), (iv) the water snakes (*Afonatrix anoscopus* and *Grayia smythii*), and (v) the large arboreal snakes (*Dendroaspis jamesoni* and *Toxicodryas blandingii*). Each of these species pairs (apart from pair (v)) have subsequently been the subject of careful studies that have allowed us to understand some intriguing patterns of coexistence in the variable rainforest environment.

The two cobras are active-searching predators with large home ranges and a very generalist diet (feeding on rodents, lizards, frogs, toads, birds and even fish; Luiselli et al. 2002). Although basically similar in terms of their ecological traits, they have diverged considerably in terms of habitat use; *N. melanoleuca* is linked to mature and stable forest and *N. nigricollis* to variable environments like grassy forest edges, plantations and derived savannas (Luiselli and Angelici 2000). Although still sub-optimally adapted to life in the rainforest, *N. nigricollis* appears to have extended its range in the last thirty years in response to deforestation (Butler and Reid 1990, Luiselli 2001, 2002), thereby challenging other species with a similar niche. As a result of this apparently increased competition, *N. melanoleuca* has been extirpated from many forested areas where it was common just a few decades ago, whereas the invading *N. nigricollis* is nowadays abundant and widespread in both deforested areas and mature secondary forests (Luiselli 2003). This provides firm evidence that, under particular ecological conditions, the outcome of interspecific competition between terrestrial snakes may be dramatic; resulting in the extirpation of species adapted to stable pristine environments by 'ecologically superior' invaders adapted to life in more variable environments.

Competition between the huge *Bitis* vipers is entirely different. Both species (*B. gabonica* and *B. nasicornis*) are terrestrial, sit-and-wait predators, superbly adapted to life in the forest litter (Greene 2001). In southern Nigeria they exhibit nearly identical habitat use (Butler and Reid 1990, Politano 1998) and, because home ranges are very small, it is easy to find high densities of both species within a very small area (Politano 1998, Luiselli et al., unpubl.). Dietary analysis of a large sample of

sympatric snakes (524 *B. gabonica* and 392 *B. nasicornis*) shows that both vipers feed primarily on two abundant rodent species (*Lemniscomys striatus* and *Cricetomys gambianus*) (Luiselli and Akani 2003). Prey size taken was also similar (Akani and Luiselli, unpubl.), and their coexistence therefore seems to be facilitated by a higher rate of consumption of alternative prey (i.e. amphibians) by *B. nasicornis* (19.4% of total prey items; 15.7% of total prey biomass) than by *B. gabonica* (0.5% of prey items; 0.1% of biomass) (Luiselli and Akani 2003). This pattern did not occur by chance ($P < 0.05$), and so we can see that even highly sedentary sit-and-wait predators again rely on food partitioning to enable coexistence.

The third study system consists of two (up to 40 cm long) marsh snakes (*Natriciteres* spp.) that are nearly identical in shape, size and general habits (activity patterns, habitat use, food preferences). Dunger (1972) predicted that this high overlap in all niche dimensions would result in the two species exhibiting a supplementary distribution in Nigeria; with *N. variegata* being more common in the southwest and *N. fuliginoides* being more common in the southeast (i.e. they should competitively exclude each other). Previous studies have not detected a difference between these species in terms of habitat use (Politano 1998), therefore Luiselli (2003) studied their foraging ecology in six separate areas – three of which contained only *N. fuliginoides* and three where the two species were sympatric. The results of this comparative study demonstrated that the feeding ecology of *N. fuliginoides* shifts greatly in the presence of its potential competitor in terms of both prey type consumed and predator size–prey size relationships (again, the patterns differ significantly from chance after Monte Carlo simulations of the original dataset; $P < 0.005$). In particular there is: (i) a shift towards eating many invertebrates and away from a diet based on many small vertebrates; (ii) a shift towards eating many terrestrial organisms from a diet based on many aquatic organisms; (iii) a shift in mean prey size (for females) towards eating relatively larger prey from a diet based on smaller prey. In this case, the intensification of competition results in a partitioning of prey type, prey size and microhabitat for foraging, compared to a more generalised diet in the absence of the competitor (Luiselli 2003).

The study system of the aquatic snakes *Grayia smythii* and *Afronatrix anoscopus* provides an indication of another pattern of resource partitioning in the presence of a limited resource. These snakes are sympatric in a wide variety of freshwater ecosystems in southern Nigeria and show a nearly identical habitat usage year-round (Luiselli et al. 2005b). Thus, they apparently do not partition the spatial resource. Their prey (mainly anurans) exhibits strong seasonal fluctuations i.e. highly abundant in the wet months and scarce/absent in the dry months (Fig. 4a, Luiselli 2005, 2006).

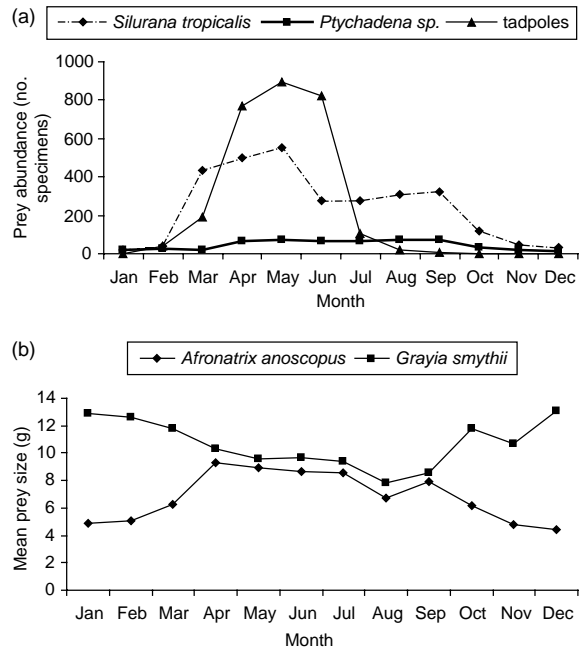


Fig. 4. Variation of the mean prey size (g) of two sympatric water snakes in southern Nigeria, in relation to the month-by-month availability of their main prey resources. Note that the mean prey size of the two species tended to diverge during the periods of low food availability (dry season months). Sample sizes: $n = 676$ for *Afronatrix anoscopus*, and $n = 390$ for *Grayia smythii*.

Both snake species forage according to the availability of their preferred prey but obviously partition the food resource in the dry season by foraging on prey organisms of similar type but of very different size. *Afronatrix* actually feeds on slightly smaller prey than *Grayia* throughout the year, but during the dry months this difference is greatly exaggerated (Fig. 2b) (and this is not a chance effect; $P < 0.001$). The diel activity patterns of the two species may have some role in this type of food resource partitioning, because *Afronatrix* becomes much more nocturnal than *Grayia* during the dry season (both species are typically diurnal in the wet season) (Luiselli 2006). Perhaps *Afronatrix* pursues very small prey at night during the dry season because small anurans may be inactive during the day in the dry season. *Grayia smythii*, conversely, may actively search out the very large (aestivating?) adult anurans during the day.

The general patterns emerging from studies in tropical Africa is that snake communities may be very rich and interspecific relationships very complex. Competition seemingly plays a major role in structuring these relationships and results in either competitive exclusion or, more usually, different patterns of resource partitioning of prey type, prey size, or both. In every case, resources are limited in the dry season and competition thus fluctuates seasonally. Studies on snakes in African

forests therefore enable us to test the response of the various species to a fluctuating intensity of competition. It will be absolutely necessary in future to study the ecological relationships among sympatric snakes in other African ecotypes e.g. deserts, semi-deserts and montane areas.

Central and South America

As expected, because of its latitude, the snake fauna of Central and South America can be extremely species rich, especially in lowland rainforests. However, the number of sympatric species may vary considerably e.g. 19 species in a semi-arid Caatinga habitat in Brazil (Vitt and Vangilder 1983), 53 species in a lowland rainforest in Ecuador (Duellmann 1978), 66 species in a forest reserve in Manaus, Brazil (Martins and Oliveira 1998), and 89 species in the rainforest of Iquitos, Peru (Dixon and Soini 1975). Rainforest systems like those described by Duellmann (1978) and Dixon and Soini (1975) are so complicated that it is nearly impossible to establish any clear patterns of coexistence amongst species. In my opinion, it is likely that the structure of these systems will be affected by a complex set of causes rather than any one clear factor (i.e. high prey resource availability, resource partitioning (produced by inter- and intra-specific competition) of food, habitat and micro-habitat, phylogenetically divergent life-history traits, predation pressure etc.) Martins and Oliveira (1998) have also shown that historical factors (phylogeny and biogeography) have probably played very important roles in determining the current structure of Brazilian snake communities (see also Cadle and Greene 1993 for similar conclusions).

Studies of simpler systems with far fewer species may highlight important patterns of resource partitioning. Stafford (2003) studied the ecology of three species of forest racers (*Dendrophidion*: Colubridae) and found that they differed very slightly in terms of prey selection (80% of their diets were composed of small frogs) but they differed more clearly in terms of prey size. A similar pattern was observed by Sieb (1984) in racers of the genus *Drymobius* where one species (*D. margaritiferus*) preys on organisms of a much larger size than its potential competitor (*D. chloroticus*) even though both species select a similar type of prey. Prey type, however, was the main resource partitioned by five sympatric species of amphibian-eating snakes (Vitt 1983), and three species of coral snakes (*Micrurus*: Elapidae) (although the latter study had only a small sample size) (Henderson et al. 1979).

An interesting study is that of the huge Neotropical treeboas particularly because the community ecology of the Boidae and Pythonidae has rarely been studied (Henderson 2002). The number of sympatric boine

species ranges from 2 to 6 in Central and South America; north of about 17° N only one species is present (*Boa constrictor*), but six sympatric species are found in a narrow region in north-eastern Brazil and French Guyana (Henderson 2002). Examination of prey selection by the various boids (compiled in Henderson 2002) shows evident partitioning with the *Eumeces* species, especially the anaconda (*E. murinus*), being much more generalist than the other species (Table 2). Thus Henderson's (2002) data suggest that food resource partitioning is certainly important for reducing inter-specific competition between sympatric boids.

Asia

Relatively few studies on resource partitioning and competition in snakes are available from Asia (both temperate and tropical), and most studies are from Japan (e.g. a long-term study in Kyoto, Fukada 1992). The coexistence dynamics of two sympatric colubrids, *Elaphe quadrivirgata* and *Rhabdophis tigrinus*, has been studied in different areas and environmental contexts, and we get some very noteworthy results by comparing these studies. Both in Kyoto (Fukada 1992) and in Yamagata Prefecture in northern Japan (Kadowaki 1992, 1996) the two species feed almost exclusively upon anurans, which are abundant and perhaps unlimited, and there is no apparent food partitioning at these sites (Fukada 1992, Kadowaki 1992, 1996). However, where the amphibian resource is limited (i.e. in Yakushima Island, southwestern Japan) the two species completely partition food type: *E. quadrivirgata* eats only reptiles (lizards and geckos) and *R. tigrinus* eats only anurans (Tanaka and Ota 2002). In addition, the two species also differ in terms of their thermal ecology, as *E. quadrivirgata* selects higher substratum temperatures, maintains higher body temperatures and is active at higher ambient temperatures than *R. tigrinus* (Tanaka and Ota 2002). Differences in the thermal ecology of these species is also found in Kyoto (Fukada 1992). So, analogous to African snake communities, Japanese snakes may partition food type in the presence of strong interspecific competition and may indeed show considerable shifts in prey selection (Luiselli 2003), thus showing a high potential flexibility in their dietary habits.

Another interesting study is that of the snake communities on the Izu Islands, southeastern Japan (Hasegawa and Moriguchi 1989). These islands are inhabited by four closely related species, i.e. *Elaphe climacophora*, *Elaphe conspicillata*, *E. quadrivirgata*, and *Dinodon orientalis*. On the islands where they are sympatric, snakes partition food type but not habitat: *E. climacophora* feeds mainly on rodents (birds as secondary prey), *E. conspicillata* feeds only on rodents, *E. quadrivirgata*

Table 2. Summary of the diet data available for 11 species of boas from Central and South America (raw data available in Henderson 2002). Numbers indicate the number of families within each group which were eaten (for instance: 4/4 in birds, means that a given snake fed on four different families of birds out of four sampled). Abbreviations: C.a. = *Corallus annulatus*; C.b. = *C. blombergi*; C.c. = *C. caninus*; C.cr. = *C. cropanii*; C.h. = *C. hortulanus*; C.r. = *C. ruschenbergerii*; E.c. = *Epicrates cenchria*; E.d. = *Eunectes deschauenseei*; E.m. = *Eunectes murinus*; E.n. = *Eunectes notaeus*.

Prey type	Boa	C.a.	C.c.	C.cr.	C.h.	C.r.	E.c.	E.d.	E.m.	E.n.
Fishes	1/5	0	0	0	0	0	0	0	1/5	5/5
Amphibians	0	0	0	0	1/3	0	1/3	0	1/3	0
Reptiles										
Turtles	0	0	0	0	0	0	0	0	2/2	1/2
Lizards	2/5	0	1/5	0	1/5	1/5	1/5	0	2/5	1/5
Snakes	0	0	0	0	0	0	0	0	1/1	0
Crocodiles	0	0	0	0	0	0	0	0	2/2	1/2
Birds	9/21	0	0	0	5/21	1/21	1/21	0	5/21	8/21
Mammals										
Marsupials	1/2	0	1/2	1/2	0	1/2	0	0	0	1/2
Edentates	2/2	0	0	0	0	0	0	0	1/2	0
Bats	1/3	0	0	0	2/3	1/3	1/3	0	0	0
Primates	2/3	0	0	0	0	0	0	0	1/3	0
Carnivores	4/4	0	0	0	0	1/4	0	0	0	2/4
Perissodactyls	0	0	0	0	0	0	0	0	1/1	0
Artiodactyls	2/3	0	0	0	0	0	0	0	2/3	0
Rodents	8/9	1/9	1/9	0	2/9	1/9	3/9	0	4/9	3/9
Lagomorphs	1/1	0	0	0	0	0	0	0	0	0

eats scincid lizards and *D. orientalis* eats only small lizards. On islands where *E. quadrivirgata* is sympatric only with *E. climacophora* its diet is more diverse than on islands inhabited by all four species – where it only eats the scincid *Eumeces okadae* (although this is not the most common prey species). On the islands where it is the only snake species present it feeds much more like a generalist predator and attains a gigantic size (over 200 cm in length, versus an average length of about 80 cm on the other islands); this large size is probably a result of foraging on abundant sea birds' eggs and chicks (Hasegawa and Moriguchi 1989). The dietary spectrum of *E. quadrivirgata* thus varies remarkably depending on the number of potential competitors; it is much more generalist in areas without potential competitors (where its growth rate is also much higher). This pattern of a dietary shift to and from generalism parallels African *Natriciteres*, and the reduced growth in areas of high competition is similar to that of Italian mainland and island populations of *N. natrix*.

In tropical Asia, as with Africa and Central and South America, species richness at a site may be very high (>20 sympatric species; Orlov 1995, Ziegler 2002), and hence the complexity of interspecific relationships is also high. Unfortunately, there have been no studies with large datasets on the community ecology of Asiotropical snakes; although detailed data on the ecological attributes of single species are available (Shine et al. 1999). Studies on sympatric viperids from the eastern Himalayas, albeit with relatively small sample sizes, do show spatial (macro- and micro-habitat) and altitudinal differences between phylogenetically closely related and ecologically similar species, but neither prey nor temporal resources are clearly partitioned (Orlov 1997).

Australia

Studies on Australian snake ecology are often extremely advanced (Shine 1991) but generally only describe the evolutionary ecology of single species and not communities (Shine and Lambeck 1985, Shine 1986a,b, Shine and Madsen 1997, Fitzgerald et al. 2002).

As a general rule, terrestrial snakes in Australia, especially mammal eating species, tend to feed on relatively small prey (Shine 1987) because of the scarcity of large prey in the environment (Morton and Baynes 1985); they are thus expected to be relatively unselective with respect to prey type and prey size (sensu: optimal foraging theory – Shine 1987). Indeed, three species of copperheads (*Austrelaps*: Elapidae) confirm this prediction by feeding on a broad range of prey with a high overlap in terms of prey type and prey size (Shine 1987). The same opportunistic feeding strategies were also detected in six sympatric elapid snakes from New South Wales, which show high overlap in prey type but less overlap in prey sizes (Shine 1977); they also share similar foraging strategies, spatial ecology and thermal requirements (Shine 1979). Shine (1977) has also shown that sympatry is much more uncommon in Australian elapids than in North American species, and he attributed this fact to a scarcity of potential prey; he also concluded that the prey-size differences between sympatric elapids are consistent with the interpretation of interspecific competitive exclusion.

Finally, food type partitioning has been observed amongst three species of sympatric water snakes (Homalopsiine: Colubridae) (Nobbs and Blamires 2004), and this again confirms the pattern observed in European and North-American water snakes that all belong to a distinct clade of colubrids (i.e. Natricinae).

Marine and subterranean snakes

Species living in the sea or underground are not analysed in this review for two reasons: (i) community ecology studies of marine species have not developed sufficiently since the last review by Vitt (1987); (ii) studies on subterranean species have examined the ecological traits of only single species (Webb and Shine 1993) and there has been no published attempt at analysing the functioning of their communities.

Overall comparisons

Comparisons between different studies in different regions of the world are obviously complicated by a series of extraneous confounding variables including, for example, different methodologies, different modes of data presentation and analysis, different environmental influences, different types of interactions between species etc. It is thus very difficult to find homogenous patterns because, if they exist at all, they may be masked by the above-mentioned variables. I think, however, that this review has revealed some important general patterns and evident congruence in the dynamics of coexistence of snake communities from different regions of the world:

- i) Snake communities from the cold regions of the northern hemisphere (high latitudes and altitudes) exhibit a low specific richness at each site, and a very low or even absent potential for interspecific competition.
- ii) Water snake communities in temperate regions of the northern hemisphere generally partition the available food type and exhibit a broad similarity in habitat use with subtle differences in microhabitat use. My opinion is that the intensity of interspecific competition in temperate aquatic snake communities may depend on a wide variety of interacting factors such as: species-specific morphology; chemosensory perception; physiological tolerance to evaporative water loss; and proximate external factors (sensu Barbault 1991) like prey resource availability and seasonal fluctuations in water depth. I predict that competition will be higher in conditions of drought than in rainy periods, and in species-rich rather than species-poor communities.
- iii) Terrestrial snake communities in temperate regions (Europe and North America) show highly variable coexistence dynamics and no general and predictable unifying patterns are evident – except within the Viperids, which in Europe, North America and, most interestingly, tropical Asia always partition the available habitat.
- iv) Tropical regions are inhabited by very species-rich communities and competition is therefore thought

to be higher than in temperate regions. African snake communities follow this prediction and show that the intensity of the competition fluctuates throughout the year, being more intense during the dry months when food availability is lower. Although patterns differ depending on the type of species' interactions, all the studies in Africa and South America demonstrate that food (prey type, prey size, or both) is the resource partitioned by sympatric species, and that when this resource is not partitioned competitive exclusion can occur (e.g. as with the cobras).

- v) Prey resource availability is a fundamental variable that affects the structure and functioning of all snake communities; this is clearly documented by studies on terrestrial snakes in Australia – where sympatry among species is much rarer than in other continents due to a relative scarcity of prey availability in the field.

Is the main Toft's (1985) conclusion (i.e. that snakes partition the food resource, and particularly the prey type) still valid?

Since Toft's (1985) review the number of field studies on snake community ecology has grown tremendously and this has produced new evidence from a diverse range of systems.

A series of 37 independent study systems, distributed throughout the world, which gave very clear resource utilization patterns by coexisting snakes, are summarized in Table 3. In most cases, the communities partitioned the food resource (56.8%), and in a lower proportion of cases the spatial (= habitat) resource (27%), whereas the temporal resource (2.7%) and the thermal resource (5.4%) were just occasionally partitioned. Cases of high overlap along all the niche dimensions were rare (8.1%), and often were characterized by the extirpation of one of the competitors from the area. The frequency of occurrence of all these cases differed significantly from the null hypothesis of a random distribution (observed versus expected $\chi^2 = 38.0$, $df = 4$, $P < 0.0001$), and the frequency of cases of food niche partitioning significantly exceeded that of all the other four types of niche axis partitioning ($\chi^2 = 24.99$, $P < 0.0001$).

Hence, I think that Toft's conclusion remains broadly supported, although there are several important refinements that need to be made to it. First, although my review confirms that food is the resource most often partitioned by sympatric snakes, this pattern is more evident in aquatic than in terrestrial snake assemblages and interspecific competition is of little importance at higher latitudes or altitudes. Additionally, some communities partition prey type whilst others partition prey size.

Table 3. Studies on resource utilization patterns by coexisting snakes throughout the world. Study cases are divided by continent. The niche axis eventually partitioned, the outcome of the coexistence process (e.g. sympatry, extirpation, etc), and the selected references for each study case are presented. The snake species of each study case are listed when their number was lower than four.

Species	Country	niche axis partitioned	outcome of the coexistence process	selected references
Europe				
<i>Vipera berus</i> , <i>Natrix natrix</i> , <i>Coronella austriaca</i>	Italy	food	all species occurring at a same area	this study
<i>Vipera berus</i> , <i>Natrix natrix</i> , <i>Coronella austriaca</i>	Russia	food	all species occurring at a same area	Drobenkov 1995
<i>Natrix natrix</i> , <i>Natrix tessellata</i>	Italy	food	all species occurring at a same area	Luiselli and Rugiero 1991
<i>Natrix natrix</i> , <i>Natrix tessellata</i>	Italy	food	all species occurring at a same area	filippi 1995
<i>Natrix maura</i> , <i>Natrix natrix cetti</i>	Sardinia	high overlap in all axes	extirpation of one of the competitors	this study
Four species	Italy	habitat	all species occurring at a same area	Capizzi et al. 1995
<i>Vipera aspis</i> , <i>Vipera berus</i>	Switzerland	habitat	all species occurring at a same area	Monney 1996
<i>Vipera aspis</i> , <i>Vipera berus</i>	France	habitat	all species occurring at a same area	Saint Girons 1975a
<i>Vipera aspis</i> , <i>Vipera berus</i> , <i>Vipera ammodytes</i>	Italy	habitat	all species occurring at a same area	Lapini 1983, 1988
North America				
<i>Thamnophis ordinoides</i> , <i>Thamnophis sirtalis</i> , <i>Thamnophis elegans</i>	Canada	high overlap in all axes	all species occurring at a same area (scarce competition)	Gregory 1978, 1984
Five species (<i>Nerodia</i> and <i>Regina</i>)	USA	micro-habitat; food; temporal niche	all species occurring at a same area	Mushinsky et al. 1980, 1982
Seven species	USA	food	all species occurring at a same area	Kofron 1978
Three species	USA	food	all species occurring at a same area	Byrd et al. 1988
<i>Nerodia sipedon</i> , <i>Nerodia rhombifer</i>	USA	food	all species occurring at a same area	Himes 2003a
<i>Arizona elegans</i> , <i>Rhinocheilus lecontei</i> , <i>Pituophis catenifer</i>	USA	food	all species occurring at a same area	Rodriguez-Robles et al. 1999
12 species	USA	food	all species occurring at a same area	Fitch 1982, 1999
<i>Thamnophis sirtalis</i> , <i>Coluber constrictor</i>	USA	food	all species occurring at a same area	Olson and Warner 2001
<i>Crotalus atrox</i> , <i>Crotalus molossus</i>	USA	habitat	all species occurring at a same area	Pough 1966
<i>Crotalus atrox</i> , <i>Crotalus molossus</i> , <i>Crotalus tigris</i>	USA	habitat	all species occurring at a same area	Beck 1995
Africa				
24 species	Nigeria	food, habitat	all species occurring at a same area	Luiselli et al. 1998, Luiselli and Akani 1999
<i>Naja melanoleuca</i> , <i>Naja nigricollis</i>	Nigeria	habitat	all species occurring at a same area	Luiselli and Angelici 2000

Table 3 (Continued)

Species	Country	niche axis partitioned	outcome of the coexistence process	selected references
<i>Bitis gabonica</i> , <i>Bitis nasicornis</i>	Nigeria	food	all species occurring at a same area	Luiselli and Akani 2003
<i>Natriciteres variegata</i> , <i>Natriciteres fuliginoides</i>	Nigeria	food	all species occurring at a same area	Luiselli 2003
<i>Natriciteres fuliginoides</i> , <i>Natriciteres variegata</i>	Nigeria	high overlap in all axes	extirpation of one of the competitors	Luiselli 2003
<i>Grayia smythii</i> , <i>Afronatrix anoscopus</i>	Nigeria	food	all species occurring at a same area	this study
Central and South America				
<i>Dendrophidion</i> (three species)	several countries	food		Stafford 2003
Five species	Brazil	food	all species occurring at a same area	Vitt 1983
Six species of boas	several countries	food, habitat		Henderson 2002
Asia				
<i>Elaphe quadrivirgata</i> , <i>Rhabdophis tigrinum</i>	Japan	food, thermal niche	all species occurring at a same area	Tanaka and Ota 2002
<i>Elaphe quadrivirgata</i> , <i>Rhabdophis tigrinum</i>	Japan	thermal niche	all species occurring at a same area	Fukada 1992
Four species	Japan	food	all species occurring at a same area	Hasegawa and Moriguchi 1989
Australia				
Six species	Australia	food (prey size)	all species occurring at a same area	Shine 1977
Three species of Homalopsine snakes	Australia	food	all species occurring at a same area	Nobbs and Blamires 2004

Sometimes, this type of resource partitioning does not occur year round, but only during periods of high competition (low resource availability e.g. as with Nigerian water snakes). I have also shown the importance of habitat resource partitioning in viper communities both in temperate and tropical regions. Contrary to Toft's study, I have shown that many snakes are not prey specialists but are generalists (e.g. many European terrestrial snakes, African cobras, Australian elapids etc.) and they will take the most abundant prey species in their environment. This dietary generalism and flexibility of many snake species must be taken into account when analysing coexistence models in these communities.

Are there geographic patterns that relate to the occurrence of interspecific competition within in snake communities?

I think that my review provides evidence of some geographical patterns of importance, i.e.: (i) interspecific

competition is not important at high latitudes or altitudes; (ii) competitive interactions are stronger in tropical regions; and (iii) competitive interactions are especially evident among species living in fluctuating environments with seasonal variations in prey abundance.

Can patterns of resource use and interspecific competition in snakes be predicted on the basis of their guild?

For generalisable answers to this question we would ideally need an analysis of replicate study systems containing the same groups of interacting species in several environmental contexts. Unfortunately, these types of comparisons are still uncommon. In the best studied cases (i.e. European terrestrial vipers, Japanese terrestrial colubrids, and water snakes in Europe and North America) the results obtained are very encouraging, as very similar interspecific coexistence patterns occur within each guild under very different climatic and

environmental contexts (Saint Girons 1975, Duguy and Saint Girons 1978, Lapini 1983, Monney 1996). I therefore suspect that similar congruences may be found in other study systems, and I strongly encourage researchers to collect field data on this. When we have sufficient case studies for comparison it should be possible to predict patterns of resource use by sympatric snakes based on their guild and habitat type.

Can we conclude that most communities of snakes around the world are governed by interspecific competition?

There are real problems in demonstrating the occurrence and intensity of competition from resource utilization data (Connell 1980). It is therefore very hard to definitively answer the question above without experimental tests of competition (e.g. removal studies). However, the large datasets collected in recent years lend at least some tentative considerations: (i) interspecific competition is predicted to be weak in northern latitudes and at higher altitudes where the few coexisting species clearly differ in terms of resource requirements; (ii) interspecific competition is certainly important in temperate regions under certain environmental contexts, for instance on islands with limited food resources (e.g. Izu Islands, Japan and *Natrix* species in Sardinia); (iii) interspecific competition is certainly important in the best studied tropical communities, as exemplified by studies on the competitive exclusion of cobras following deforestation, and by the facultative dietary generalism in Nigerian *Natriciteres fuliginoides* in the presence of a potential competitor. So, considering that most snake species occur in the tropics (where communities are species-rich and where the potential for interspecific competition has been shown to be high), we can be almost certain that interspecific competition is an important force in the structuring of many communities living in a great variety of environmental conditions. I therefore strongly urge researchers to continue collecting data on the resource use patterns of snakes in a great variety of climates and environmental contexts.

Acknowledgements – I thank Dr Jerry Lea (York) for very helpful comments on the manuscript and for the linguistic revision.

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