

FEEDING STRATEGIES OF THE VIPER *VIPERA URSINII URSINII* (REPTILIA: VIPERIDAE) IN THE APENNINES

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ABSTRACT

During a three-year period of research on the viper *Vipera ursinii ursinii*, observations on diet composition and feeding strategies were obtained. The major food items in terms of percentage were orthopterans, followed by rodents, lizards, birds, spiders and beetles. A considerable seasonal change in the diet composition was noted: invertebrates predominated in the diet only between July and September, as compared to the spring diet which was made up of vertebrates.

INTRODUCTION

Numerous works have reported data regarding various aspects of the ecology of *Vipera ursinii*, including Baron (1980, 1989), Naulleau (1973, 1984), Kotenko (1989), Saint Girons (1975, 1978, 1979, 1980) and Saint Girons and Naulleau (1981). The most recent studies on the feeding behaviour of these vipers have been carried out by Baron (1989) on Mont Ventoux (France) and by Kotenko (1989) in various areas of the Ukraine, such as the Orlova island. However, the feeding patterns of the Italian viper populations, restricted as they are to a few of the Apennine massifs, are not very well-known, and have been discussed only in general, layman's works whose observations seem to lack a systematic approach (cf. for example Bruno and Maugeri, 1977, 1984; Bruno 1983).

The aim of this paper is therefore to present a systematic study carried out over a number of years on the feeding activities of *V. ursinii* in the central Apennines, in the hope that these data may prove of interest in providing a better knowledge of certain aspects of the biology of this mountain viper.

MATERIALS AND METHODS

The vipers were observed during the whole of their active cycle, i.e. from mid April until the end of September each year from 1987 to 1989. All the data reported in this paper were obtained by analysing the gastrointestinal contents of *V. ursinii* specimens captured in two locations in the Abruzzi Apennines (Valle di Campo Imperatore, Gran Sasso d'Italia; monte Velino), at an altitude ranging from 1600 to 1850m.

The vipers were divided into two categories according to size: (1) vipers longer than 28 cm in total length and (2) vipers shorter than 28 cm in total length. 76 vipers were examined in the first category (of which 43 had identifiable food residuals in their gastrointestinal apparatus; \bar{x} = 56.6%) and 12 in the second category (of which 7 had food remains in the intestine \bar{x} = 58.3%). On the whole, the ingested matter was easily recognizable, mainly because only a few species of

potential prey are to be found in the habitats of these mountain vipers, including one species of Lacertidae (*Podarcis muralis*), two bird species (bearing in mind that *Anthus s. spinoletta* and *Phoenicurus ochruros* are the only species that nest at ground level in the valleys inhabited by *V. ursinii* and therefore may be prey to these snakes), and some invertebrates (particularly Orthoptera).

The small mammals of the studied areas are less known, and therefore we have not a complete list of the species inhabiting these environments; however, we have found in the viper stomachs only seven specimens of a Microtidae species. Since these remains had been particularly damaged by the digestive process, we have not identified the species in question, but, referring to Toschi's (1965) keys and to Graf's (1982) data, we believe that the rodent in question might be *Microtus nivalis*.

The vipers over 28 cm long were palpated in order to make them regurgitate their ingested prey, and were then immediately released. Since this operation may be dangerous for smaller specimens, these were analysed using Kjaergaard's method (1981).

Unfortunately, these methods do not always allow for the examination of all the gut contents. In order to overcome this problem it was necessary to analyse the faeces of 34 other vipers (all excluded from the total number of specimens quoted earlier, and all belonging to category 1).

Often it was possible to obtain more than one prey item from a single specimen, so the overall number of prey is considerably higher than the total number of animals caught (95 prey obtained from 43 specimens belonging to category 1 and 14 prey taken from seven specimens in category 2).

The ingested biomass was calculated by applying the same methods utilized by Brana *et al.* (1988), that is to say considering the "fresh" weight of the ingested prey if it was in very good condition. Obviously, when using the "fresh" weight there is the possibility that the weight may be underestimated. This risk was avoided by using this method only in a limited number of cases where the ingested prey had not been at all damaged by the digestive process (21.1% of the cases).

The food niche breadth (B) was calculated using Simpson's (1949) diversity index:

$$B = 1 / \sum p_i^2$$

where p_i = the frequency with which each i th prey category was used. With this formula, all the Orthoptera remains were included in one category, while the other categories were made up of Microtidae, Motacillidae, Lacertidae, Coleoptera and Opilionidae.

In order to be able to study the feeding periods and the frequency of meals, 21 specimens (8 males and 13 females and all belonging to category 1) were marked and then released into a confined area (of approximately 1.5 hectare) with a superimposed grid system, situated in the Valle di Campo Imperatore (Gran Sasso) at approximately 1750m. The 21 vipers were marked by scale-clipping, and were excluded from the number ($N = 76$) of vipers over 28cm in length mentioned earlier.

RESULTS

COMPOSITION OF THE DIET

Vipers over 28cm long. The total of 95 ingested remains obtained and identified shows a considerably high degree of invertebrates present in the diet of these ophidians (83.2% of the identified prey), particularly Orthoptera (78.9%). Vertebrate remains were common, amounting to 16.8% of the total number of prey; these consisted of 6.3% Lacertidae (Reptilia, Sauria), 7.3% juvenile Microtidae (Mammalia, Rodentia), and 3.1% nestling Motacillidae (Aves, Passeriformes) (Table 1, Fig. 1).

Longer than 28 cm.	$N = 43$	
	n	% n
<i>Podarcis muralis</i>	6	6.3
Microtidae	7	7.3
<i>Anthus s. spinoletta</i>	3	3.1
Orthoptera Tettigonidae	6	6.3
Orthoptera Acrididae	46	48.4
Orthoptera undet.	23	24.2
Coleoptera undet.	1	1.2
Opilionidae undet.	3	3.2
	95	100

Shorter than 28 cm.	$N = 7$	
	n	% n
<i>Podarcis muralis</i>	1	7.2
Orthoptera undet.	10	71.4
Silphiidae (larva)	1	7.2
Opilionidae undet.	2	14.2
	14	100

TABLE 1. List of prey obtained from the gastrointestinal tract of *Vipera ursinii* captured in the Italian Apennines.

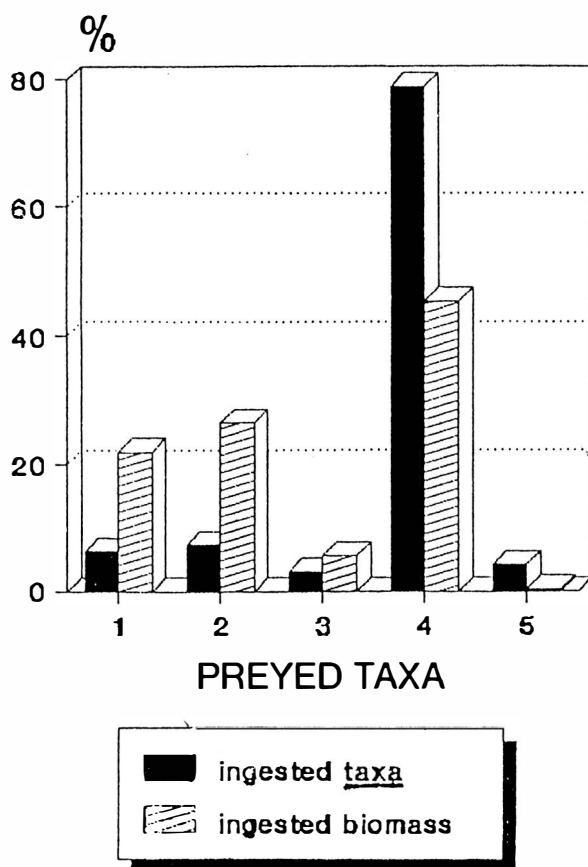


FIG. 1. Percent frequency of the preyed taxa (black columns) and their relative biomass percentages (striped columns) in *V. ursinii* in the studied environment: 1 = Lacertidae, Reptilia; 2 = Microtidae, Mammalia; 3 = Motacillidae, Aves; 4 = Orthoptera, Insecta; 5 = Other Prey (Coleoptera, Insecta; Opilionidae, Arachnida). These data are referred to specimens of more than 28 cm. in overall length.

	n	n'	n/n'
<i>Podarcis muralis</i>	6	6	1
Microtidae	7	4	1.7
<i>Anthus s. spinoletta</i>	3	1	3
Orthoptera	75	29	2.6
Coleoptera	1	1	1
Opilionidae	3	2	1.5

TABLE 2. Distribution of the total number of prey ($n = 95$) in relation to the total number of stomachs ($n' = 43$). (Vipers >28 cm. in total length.)

	n
<i>Podarcis muralis</i>	2
Rodents undet.	3
Orthoptera undet.	29
Chilopoda undet.	1
Coleoptera undet.	2
Undetermined Animal Residues	7

TABLE 3. List of prey residues obtained from 34 excreta of vipers >28 cm. in length. n is the total number of the excreta in which a single kind of prey has been discovered.

These 95 ingested remains were obtained from only 43 vipers ($\bar{x} = 2.2$ prey/stomach), and their distribution (in relation to the total number of stomachs) is carried to Table 2. Other prey residues were also obtained from some viper excreta ($n = 34$); this analysis revealed a fragment of a Chilopoda species, which was not observed in any other case during our research (see Table 3).

However, with regards to the biomass ingested, the overall percentage of vertebrates increases to a grand total of 54.2% of which 21.9% is made up of Lacertidae, 26.5% of Microtidae, and 5.6% of Motacillidae. In terms of biomass, the various species of Orthoptera constitute 45.4% of the total biomass ingested, while other invertebrate species (Coleoptera and Oplionidae) only make up 0.3% of the total (Fig. 1).

Vipers under 28cm long. Of the 14 ingested samples obtained (from only 7 specimens), no less than 13 consisted of Arthropoda (92.9% of the total), and only one of a very young Lacertidae (7.2%), less than a month old (Table 1).

ANNUAL FEEDING CYCLE AND SEASONAL DIETARY CHANGES

According to Baron (1989), the feeding period of the *V. ursinii* populations of Mont Ventoux is extremely limited, lasting from the end of June to the end of September, with an overall active period of approximately 6 months in adult males and approximately 5 months in adult females.

Our findings coincide widely with those of Baron, but the feeding period appears to start earlier among the Italian populations (at the beginning of June), while the end coincides completely with the observations made on the French populations.

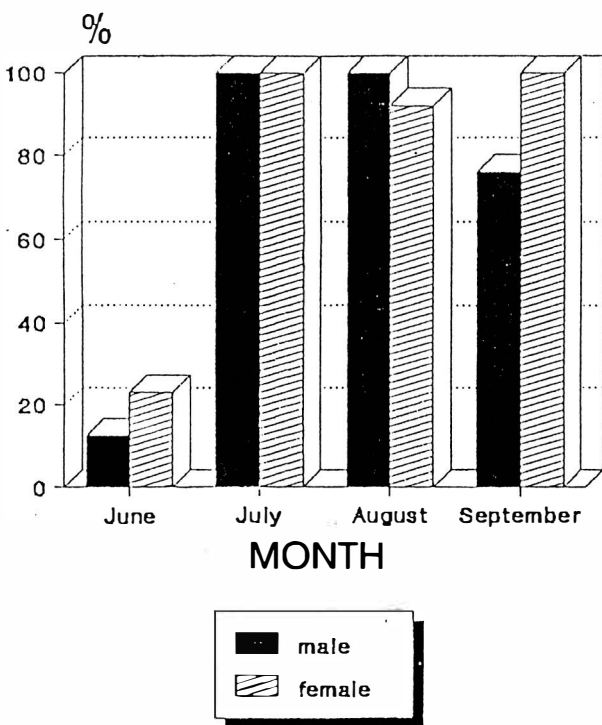


FIG 2. Percentages of males and adult females which feed in the different months of the annual feeding cycle, in the *Vipera ursinii* populations of the studied areas.

The feeding patterns of individual specimens vary considerably from period to period (Fig. 2). On the whole, it is possible to conclude that a low percentage of specimens feeds in June (12.5% of males and 23% of females respectively), while from July to September these percentages reach very high values: in males the maximum percentages were obtained in July and August (100% of the specimens), and in females in July and September (after their births) (again 100%). Pregnant females also usually feed during their gestation period, and for example, we observed a female eating a young hamster (weighing 8g) only 7 days before giving birth (in captivity).

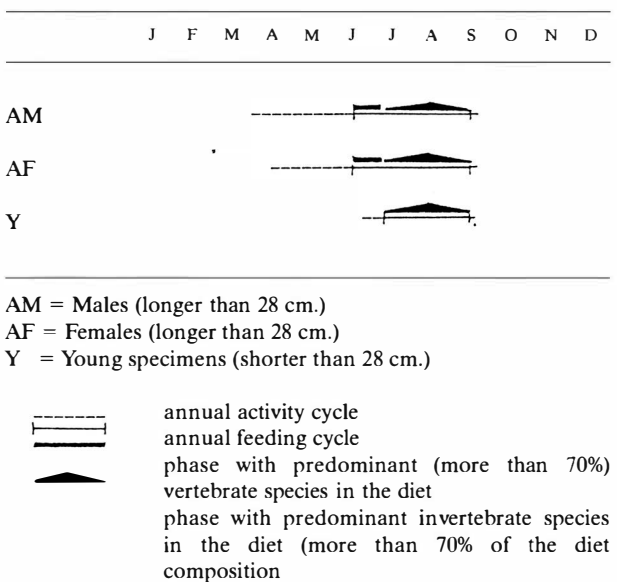


FIG. 3. Pattern of the annual activity cycle in the studied populations of *Vipera ursinii*.

A considerable seasonal change was observed in the composition of the vipers diet ($P < 0.001$), presumably in accordance with the availability of prey (Fig. 3). Thus, in June, when Orthoptera are not easily found in the areas under study, the few vipers that feed (approximately 19% of the specimens) prey exclusively on small vertebrates (81.8% of all the ingested vertebrate remains obtained during this research study). Females appear to feed more frequently at this time than males (differences significant at $P < 0.01$), who never feed before the end of the mating season (75% of the marked vipers left in the confined area (as described in "Materials and Methods") who fed in June were females, and 66.6% of the prey obtained in June came from female specimens). 100% of the rodents obtained in this study, 100% of the bird remains and 16.6% of the lizard remains were obtained from the gastrointestinal apparatus of females in June, while only 50% of the total remains of Lacertidae were obtained from males during this month.

From July to September, as a result of the "population explosion" of the various species of Orthoptera found in the high pastures in the Abruzzo mountains, vertebrates practically disappear from the vipers' diet altogether (only two specimens of *Podarcis muralis* were removed from the vipers' stomachs during this period) and are replaced by Orthoptera, which then became the main nutritional resource for the vipers in the area (92.6% of

the total prey obtained). Both sexes prey on the various species of Orthoptera indiscriminately. These are chosen without any particular criteria except size. Only grasshoppers over 15mm long are preyed upon by vipers in category 1, while those in category 2 (and in particular those under 22cm long) prey upon Orthoptera smaller than those mentioned earlier. It should be borne in mind that only 5.3% of the Orthoptera found in the stomachs of the vipers in category 1 were smaller than those mentioned above and, furthermore, these were not very much smaller (with length ranging between 11 and 13.5mm). Here too, the data recorded in this study are largely in accordance with Baron's (1989) findings.

FREQUENCY OF FEEDS

The frequency with which vipers feed seems to differ in the various phases of the annual feeding cycles. In June and in the first ten days of July the vipers eat irregularly (on average only once during the whole period), while they feed much more often in the second half of July to September (in fact, during this period, vipers caught 1-7 large Orthoptera (over 3.5cm long) every 2-3 days ($\bar{x} = 4.2$; $n = 79$), which they keep in their mouths until the victim has become completely immobilised and can be swallowed. Furthermore, taking into account that adult *V. ursinii* usually catch prey that weigh less than 8g (or swallow a total quantity of prey lower than this in terms of weight), stomach contents are small. Baron (1989) also noted this in the Mont Ventoux vipers, unlike Bruno and Maugeri, who wrote in 1977 (p. 172) "Un esemplare adulto sembra che possa ingollare fino a 100 cavallette al giorno".

DISCUSSION

The diet of the *V. ursinii* populations studied includes species belonging to eight families (of which three are vertebrates) and eight genera. Relative to the size of the food niche breadth, the value ($B = 1.57$) is considerably lower than any which have been obtained in various populations of *V. aspis* (Saint Girons, 1980; Luiselli and Agrimi, 1990), *V. berus* (Brana *et al.*, 1988). The food niche breadth was remarkably wider in June than in the following months (Fig. 4). The essential differences between *V. ursinii* and the other European species of *Vipera* are not only in the value of the food niche breadth, but also in the taxonomic composition of their diet, since in the abovementioned species (*V. aspis*, *V. berus*, *V. seoanei*) the adult diet is predominantly composed of small mammals (Soricidae, Muridae and Microtidae). They constitute over 60% of the prey in *V. aspis* in western France (Saint Girons, 1980) and in central Italy (Luiselli and Agrimi, 1990), of *V. berus* in England (Prestt, 1971), Poland (Pomianowska, 1974) and Italy (Luiselli, 1990), of *V. seoanei* in the Cantabricos mounts (Braña *et al.*, 1988), of *V. latastei* in Spain (Bea and Braña, 1988), while they are largely substituted by orthopterans in the case of *V. ursinii*.

Extremely important differences also emerge from a comparison of the diet of the young vipers (in the first three years of life). Lizards make up a large part of the diet of the other palaeartic species (from 31.5% in the case of *V. berus* specimens in England (Prestt, 1971) to 80% of those studied by Pielowsky (1962) in Poland; from 80.77% of *V. aspis* specimens in central Italy

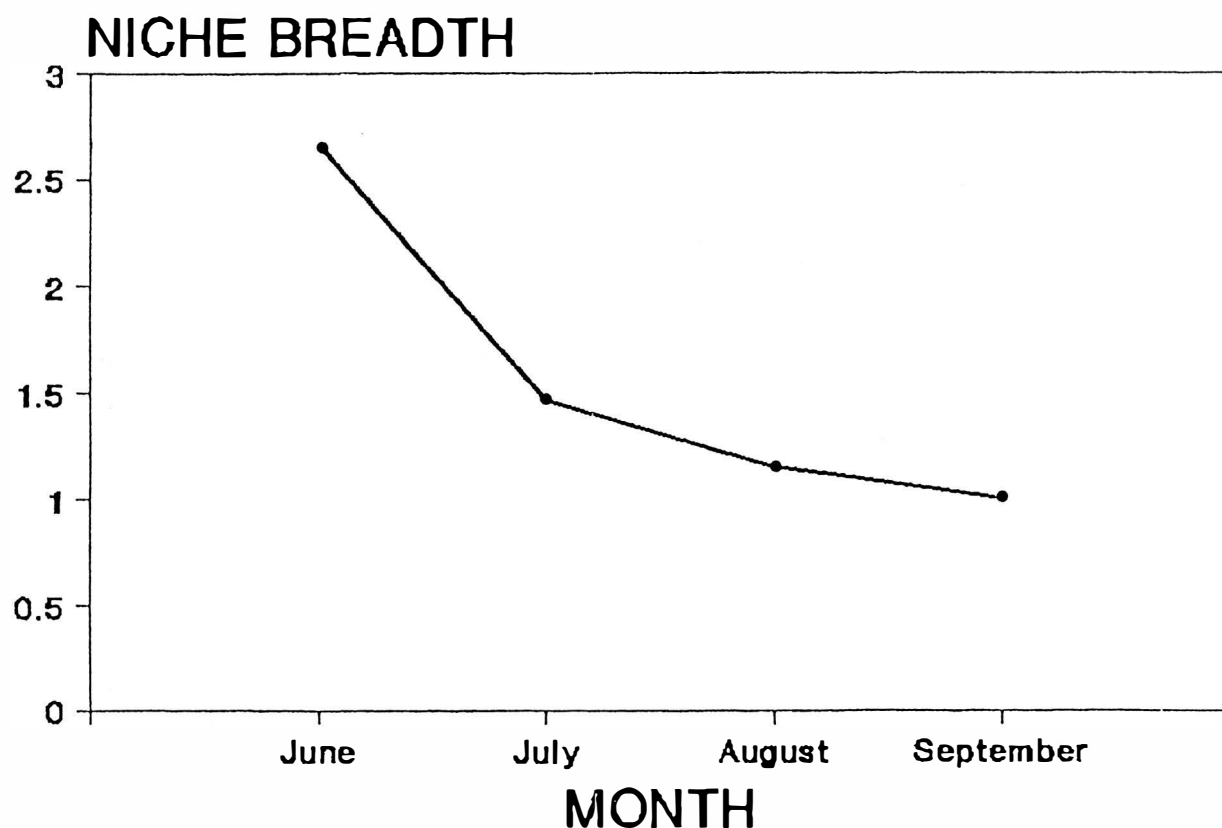


FIG 4. Monthly variation of the food niche breadth (calculated using a Simpson's diversity index, 1949) applied to the taxonomical composition of the diet.

(Luiselli and Agrimi, 1990), to 100% of those in western France (Saint Girons, 1980); in the case of young Orsini's vipers, however, their diets consists, almost exclusively, of arthropods. Moreover, with the exception of *V. ursinii*, the other species of *Vipera* catch invertebrates only in exceptional cases, as recorded by Smith (1951) and Pomianowska (1974) in the case of *V. berus*, Bea and Braña (1988) in the case of *V. latastei* and by Beschov (1977) in the case of *V. ammodytes*.

In the *V. ursinii* populations studied in this paper lizards, generally weighing under 8g, form the main prey in the first part of the annual feeding cycle (66.6%), particularly for male vipers (75% of the cases recorded in June, and 50% in August). Microtidae were caught only by females, and only in late June (in this period they represented 63.6% of the prey caught by females, and 66.6% of the feeds, taking into account that all three *Anthus* fledglings were found in one stomach, and that a *Podarcis* was extracted from another stomach). The three *Anthus s. spinoletta* fledglings were found in a 415mm long female caught in late June in Valle di Campo Imperatore. With regard to this, it is possible to state that preying on fledglings is a fairly rare occurrence that takes place only with species that nest in *Juniperus communis nana* bushes, where vipers often shelter.

Invertebrates, abundant in the diet of *V. ursinii* in Ukraine (Kotenko, 1989) and France (Baron, 1980, 1989), strongly predominate in the diet (97.5%) only between July and September, as compared to the spring diet, which is made up only of vertebrates. It is thus possible to conclude that there is a considerable seasonal influence on the diet. A seasonal change was noted by Kotenko (1989) in the populations of *renardi* subspecies on the island of Orlova (Ukraine), where the vipers prey on ducks and sand-pipers in May-June, and on *Microtus arvalis* and *Lacerta agilis* during the other months.

Furthermore, with regards to the duration of the trophic period, there are important differences between the two-size categories of vipers, given that those in the second group usually begin their annual activity in the first ten days of July (feeding begins shortly after the middle of the month), at the beginning of "Orthoptera phase" of the annual trophic cycle. In this case also our data largely agree with those of Baron (1989), since this period of activity lasts about three months (or a little longer) in both Italy and France.

In addition, the annual feeding cycle seems to be less tied to the reproductive state than it is in other species of temperate zone vipers such as *V. seoanei* (Braña *et al.*, 1988), for example. In fact, the males and the females begin feeding after the mating period, which is usually around the middle of May, and feeding continues until the end of September. This constitutes an exception to the general model, which envisages an interruption of the trophic period in pregnant females during the second phase of the gestation period (Prestit, 1971; Saint Girons, 1979).

Finally, in comparison with other temperate zone vipers, *V. ursinii* employs some remarkably different predatory techniques. Unlike the other vipers, they hold the prey in their mouth until it is swallowed and, under our observation in captivity, tend to use this technique both with Orthoptera and with rodents and lizards.

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REFERENCES

- Baron J.P. (1980). Données sur l'écologie de *Vipera ursinii ursinii* au Mont Ventoux. *Bull.Soc.Herp.Fr.* 14, 26-27.
- Baron J.P. (1989). Feeding of *Vipera ursinii ursinii* (BONAPARTE, 1835) in the Mont Ventoux (France): diet and feeding cycle. *Abstracts of the First World Congress of Herpetology*, Canterbury.
- Bea A. & Braña F. (1988). Nota sobre la alimentación de *Vipera latastei* BOSCA' 1878 (Reptilia, Viperidae). *Munibe* 40, 121-124.
- Beschov, W. (1977). Über die Biologie und Ökologie der Schlangen im Maleshevskigebirge (Sudwestbulgarien). 3. Nahrung und Fortpflanzung der Sandotter (*Vipera ammodytes meridionalis* BOULENGER). *Ekologiya* (Sofiya) 3, 3-12.
- Braña, F., Bea, A., Saint Girons, H. (1988). Composición de la dieta y ciclos de alimentación en *Vipera seoanei* LATASTE 1879. Variaciones en relación con la edad y el ciclo reproductor. *Munibe* 40, 19-27.
- Bruno, S. (1983). *Le vipere d'Italia e d'Europa*. Bologna, Edagricole.
- Bruno, S. and Maugeri, S. (1977). *Retili d'Italia*. Milano, Martello.
- Bruno, S. & Maugeri, S. (1984). *Serpenti d'Italia*. Milano, Martello.
- Graf, J. D. (1982). Génétique biochimique, zoogéographie et taxonomie des Aricolidae (*Mammalia*, *Rodentia*). *Rev. Suisse Zool.* 89, 749-787.
- Kjaergaard, J. (1981). A method for examination of stomach content in live snakes and some information on feeding habits in common viper (*Vipera berus*) in Denmark. *Natura Jutlandica* 19, 45-48.
- Kotenko, T. I. (1989). *Vipera ursinii renardi* (Reptilia, Serpentes) in Ukraine. *Abstracts of the First World Congress Herpetology*, Canterbury.
- Luiselli, L. M. (1990). Life history of a *Vipera berus* population in the Southern Alps. *I Congresso Luso-Espanhol Herpetologica*, Lisboa. (Abstract).
- Luiselli, L. M. and Agrimi, U. (1990). Alimentacao da *Vipera aspis francisciredi* nos Montes da Tolfa. *I Congresso Luso-Espanhol Herpetologica*, Lisboa. (Abstract).
- Naulleau, G. (1973). Les Serpentes de France (Colubridés, Viperidés *Rev. Fr. Aquar. Herpet.* No. special, hors série, 9-24.
- Naulleau, G. (1984). Les Serpentes de France. *Rev. Fr. Aquar. Herpet.* fasc. 3-4, 2nd edition.
- Pielowski, Z. (1962). Untersuchungen über die Ökologie der Kreuzotter (*Vipera berus* L.) *Zool. Jb. Syst.* 89, 479-500.
- Pomianowska, I. (1974). Energy balance and food requirements of adult vipers (*Vipera berus* L.) *Ekol. Pol.* 22, 195-211.
- Prestit, I. (1971). An ecological study of the viper *Vipera berus* in southern Britain. *J. Zool. Lond.* 164, 327-418.

- Saint Girons, H. (1975). Observations préliminaires sur la thermorégulation des Vipères d'Europe. *Vie et Milieu* 25, Fasc. I, Série C, 137-168.
- Saint Girons, H. (1978). Thermorégulation comparée des Vipères d'Europe. Etude biotéléométrique. *Terre et Vie* 32, 417-440.
- Saint Girons, H. (1979). Les cycles alimentaires des Vipères européennes dans des conditions semi(naturelles). *Ann. Biol. Anim. Bioc. Biophys.* 19, 125-134.
- Saint Girons, H. and Naulleau, G. (1981). Poids des nouveau-nés et stratégies reproductives des Vipères européennes. *Rev. Ecol (Terre et Vie)* 35, 597-616.
- Simpson, E. H. (1949). Measurement of diversity. *Nature* 163, 688.
- Smith, M. (1951). *British Amphibians and Reptiles*. London, Collins.
- Stjernberg, M. (1978). Huggorm som holkfagelplundrare (A Viper *Vipera berus* plundering nest-box with nestlings of *Parus major*). *Memoranda Soc. Fauna Flora Fenn.* 54, 1-58.
- Toschi, A. (1965). Fauna d'Italia, III. *Mammalia (Lagomorpha, Rodentia, Carnivora, Artiodactyla, Cetacea)*. Bologna, Calderini.

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PHOSPHATE AND CALCIUM LEVEL VARIATIONS IN THE PLASMA OF THE SNAKE *VIPERA ASPIS* DURING THE ANNUAL CYCLE AND THE REPRODUCTIVE PERIOD

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ABSTRACT

The measurement of phosphate and calcium levels in the plasma of *Vipera aspis* during two consecutive year cycles shows significant seasonal variations. For males and non-breeding females, phosphate levels are higher during the active period of the year than during hibernation. Conversely, calcium levels appear generally more elevated for the hibernating period than for the active period. Breeding females present an important increase of phosphate and calcium levels with a peak near ovulation. Clearly, this phenomenon is related to vitellogenesis. The relationship between plasma phosphate and calcium levels and bone tissue mineralization is discussed, the latter being the only reservoir of these mineral salts available to the snake.

INTRODUCTION

Literature on annual variations of plasma calcium and phosphate levels in non-mammalian vertebrates is scarce (see Dacke, 1979; Clark, 1983). Variations of calcium level have been studied more than those of phosphate. It appears that fish (Booke, 1964; Meunier, 1978) and amphibians (Robertson, 1978; 1985) present significant annual variations of calcium level. For reptiles, we are not aware of any publications dealing with calcium and phosphate variations during the entire annual cycle. During the breeding period, however, female fish (Lopez and Martelly-Bagot, 1971; Martelly, Milet, Legrand, Girard and Fontaine, 1979), amphibians (Dacke, 1979), reptiles (Dessauer and Fox, 1959; Dacke, 1979) and birds (Dacke, 1979) are all known to exhibit an increase of plasma calcium and phosphate levels. These data suggest that the regulation of plasma calcium and phosphate levels in these groups is quite different from that of mammals, because they show such high and significant natural annual variations. Nevertheless, for reptiles and especially for snakes, the available data are so scarce that they prevent any

general conclusions concerning phosphocalcic regulations.

This work, part of a more general study dealing with the phosphocalcic metabolism of *Vipera aspis* (Alcobendas and Castanet, 1985; Alcobendas and Baud, 1988; Alcobendas, 1988; Alcobendas, Baud and Castanet, 1991), presents data concerning plasma calcium and phosphate level variations in this species during the annual cycle and breeding period.

MATERIALS AND METHODS

MATERIAL

Some of the vipers used in this study originated from a wild population living in the center of France (Loir et Cher), (capture permission delivered by the french Ministry of Environment). Before the beginning of the experiment these vipers remained at least six months in captivity. A second sample was born at the laboratory, from parents which also originated from the same locality. Finally some females caught in nature in June were immediately punctured.