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COMPLEMENTARY STUDY ON THE REPRODUCTIVE BIOLOGY IN FEMALE ADDER, *VIPERA BERUS* (L.), FROM EASTERN ITALIAN ALPS

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VIPERA BERUS
REPRODUCTION
SEX-RATIO PRIMAIRE
RESSOURCES NUTRITIVES
ALPES ORIENTALES
ITALIE

RÉSUMÉ – Ce travail explique quelques modalités de la reproduction des femelles de Vipère Peliade (*Vipera berus*), capturées dans une localité des Alpes orientales italiennes, pendant une période de deux ans. Les femelles se reproduisent tous les deux ans, en montrant un cycle reproductif biennal typique, qui représente la situation la plus commune chez les populations montagnardes des Vipères européennes. En comparaison avec d'autres populations de *Vipera berus* qui subissent une forte pénurie alimentaire (Andrén et Nilson, 1983), une remarquable homogénéité entre les paramètres reproducteurs a été observée pendant les deux ans d'études, probablement en raison d'une stabilité relative des sources potentielles de nourriture. En effet, la présente situation représente la norme dans les biotopes fréquentés par les Vipères européennes, où elles disposent toujours de plusieurs espèces-proies dont les fluctuations numériques éventuelles se compensent plus ou moins. Seule la sex-ratio primaire varie de façon significative et le nombre des femelles excède nettement celui des mâles. Pendant les deux années de recherche la mortalité des femelles reproductrices est très forte après la parturition. La perte relative du poids est plus forte chez les femelles mortes, que chez celles qui sont encore en vie. Enfin, la mortalité post-parturienne est nettement inférieure chez les femelles les plus grandes.

VIPERA BERUS
REPRODUCTION
PRIMARY SEX-RATIO
FOOD AVAILABILITY
EASTERN ALPS
ITALY

ABSTRACT – This paper describes some reproductive parameters of female adders (*Vipera berus*) studied in a mountain locality of the eastern Italian Alps during a two-year period of research. In this area, females reproduce in alternate years, showing a typical biennial reproductive cycle, which is the most common situation in mountain populations of European vipers. In comparison with adder populations living in areas with fluctuating food availability (see Andrén and Nilson, 1983), a remarkable homogeneity in the reproductive parameters was observed during the two study years, probably owing to a relative firmness of the potential food resources. In the study area, in fact, it was pointed out a high heterogeneity of potential preys, including amphibian, reptile and mammal species. Primary sex-ratio was the only parameter which significantly varied between years, the number of newborn females exceeding that of males. In both the study years, the mortality of reproductive females after their parturitions was extremely high, ranging from 30 to 40 %. Relative mass loss was significantly higher in dead females than in survived ones. Post-partum mortality was higher in smaller rather than in larger females.

INTRODUCTION

The adder (*Vipera berus* Linnaeus) is a viperid species whose wide range extends through most of Europe (Arnold and Burton, 1978), but it does not occur in the European regions characterized by a Mediterranean climate. In Italy it is present only in the southern slope of the Alpine Massif,

where it is more frequently observed than the other *Vipera* species (*V. ammodytes* and *V. aspis*). In the southern Alps, *Vipera berus* is widely distributed at altitudes ranging from 600 (Dolce and Lapini, 1990) to over 2 000 m a.s.l. (Ortner, 1975 and 1979; Marcuzzi, 1976), and it inhabits localities characterized by extremely different environmental parameters (e.g., climate, exposure, vegetation, etc.). Most of the ecological aspects

of the adder populations inhabiting sites characterized by different environmental conditions may vary considerably. Among these aspects, annual, seasonal and diel activity patterns, as well as feeding habits and reproductive frequency, may be affected by the different environmental conditions (see Capula and Luiselli, 1991; Luiselli and Anibaldi, 1991).

In this work we present information on the reproductive biology of female *Vipera berus* based on field studies carried out in a mid mountain site of the Carnic Alps (Friuli, NE Italy). Although several data regarding various aspects of the reproductive ecology of *Vipera berus* have been already reported (e.g., Vainio, 1931; Bernström, 1943; Saint Girons and Kramer, 1963; Andrén, 1981; Nilson, 1981; Andrén and Nilson 1983 and 1989; Saint-Girons, 1982 and 1985), no data on female reproduction of adders occurring in the southern slope of the Alpine Massif was yet published.

MATERIAL AND METHODS

This study was performed on a 25 ha area, located at about 1 100 m a.s.l. in the Carnic Alps (Sella Nevea, Tarvisio Forest, Friuli). The area is situated at 46° 26'N, 13°31'E of Greenwich, and it is characterized by stonepiles, delapidated walls and ruins at the borders of a Swiss mountain pine-wood. The ruins and the stonepiles are important hibernation sites in winter and night shelters from April to October.

Vipers were localized and captured during July-August 1988 and during July-August 1989 by exploring the study area along a standardized route; two surveys (the first in the morning, the latter in the afternoon) were performed each day, and altogether about 60 days were spent in the field. In order to determine the reproductive frequency of female adders, we captured 31 specimens (longer than 50 cm) during July-August 1988 in a site close to the study area; these vipers were marked by « scale-clipping » (see Saint Girons, 1952; Brown and Parker, 1976). In this site, a survey was carried out during July-August 1989-90, and some specimens formerly marked were recaptured ($N = 8$; 25.8 % of the vipers marked in 1988). The reproductive status of each recaptured specimen was compared with that of the same individual at the time of the first capture, and in this way the frequency of reproduction of each viper was determined.

The mass/total length ratio was used for determination of the female reproductive status (see Prestt, 1971; Nilson, 1981; Andrén, 1982; Andrén and Nilson, 1983). This method is particularly

useful in the field, although in laboratory conditions the X-ray analysis seems to be the better technique (see Naulleau and Bidaut, 1978 and 1981).

The pregnant females were brought to the laboratory, and the following parameters were checked: *i*) overall length of each female; *ii*) mass of each female before and after birth; *iii*) clutch mass of each female; *iv*) clutch size of each female; *v*) sex, overall length and mass of each young. Moreover, we determined « post-partum » mortality by counting the specimens which died in captivity between the birth and the release date. All specimens (either adult or young) were released at the capture point about 30 days after the birth. Juveniles which died in captivity were placed in 70 % alcohol, and they are now preserved in the herpetological collection of the Natural History Museum (Zoological Section) « La Specola », Florence.

All female adders used in this study were housed in indoor enclosures measuring 100 x 50 x 40 cm. Enclosures were lighted by « Gro-Lux » fluorescent lamps (40 W); humidity level was maintained at about 55-95 % (depending on the terrarium spots); diurnal temperature ranged between 24 and 32°C (varying from one spot to another), while nocturnal temperature ranged between 16 and 18°C. Since *Vipera berus* is a snake difficult to breed in captivity, one can hypothesize that our data on « post-partum » mortality were partially affected by this problem. However, in our opinion this problem has not influenced our findings: in fact, (1) we maintained the vipers under experimental conditions in which we were able to make them reproduce, and (2) our experiments lasted a too short time for causing unnatural mortality (on average, each viper was housed from 30 to 60 days in captivity).

Statistical analyses were performed by using both SPSS and STATGRAPHIC computer packages, all tests being two tailed. All tests were performed by using 95 % as confidence interval.

RESULTS

1. Reproductive patterns in 1988 and 1989

In 1988, 18 adult females (longer than 50 cm) were captured, of which 10 (55.5 %) were pregnant. In 1989, 10 out of 19 (52.6 %) captured females were pregnant. No statistically significant difference was tested between the two years with regard to the frequency of pregnant females ($p > 0.3$; X^2 - test, $df = 1$).

A biennial reproductive frequency was tested in the « scale-clipped » female adders ($N = 8$) recaptured during the research period.

The fact that the percentages of reproductive females exceeded 50 % (ideal value that would be expected in a biennial breeder) may be explained by considering that pregnant females usually spend in thermoregulation more time than non-pregnant ones (Saint Girons, 1978), thus resulting easier to be observed. This consideration may be true also for other biennial breeder snakes, in which the percentages of reproductive females may be annually significantly greater ($p < 0.05$) than 50 % (Volsoe, 1944; Tinkle, 1962; Fitch, 1965; Shine, 1977; Aldridge, 1979; Baron, 1990).

2. Female length and mass (before and after birth)

Female length in 1988 ($\bar{X} = 63.1 \pm 6.88$ cm, $r = 51 \times 71.6$ cm) did not differ significantly from that found in 1989 ($\bar{X} = 62.4 \pm 7.02$ cm, $r = 54.1/72.5$ cm) ($t = 0.202$, $p = 0.841$).

Female mass before giving birth was not significantly different in 1988 ($\bar{X} = 148.9 \pm 42.34$ g, $r = 81.8/217$ g) and in 1989 ($\bar{X} = 143.4 \pm 47.83$ g, $r = 67.6/211$ g) ($t = 0.273$, $p = 0.787$).

Female mass after giving birth did not differ in a statistically significant way between the two study years (1988: $\bar{X} = 79.5 \pm 20.65$ g, $r = 34.3/100$ g; 1989: $\bar{X} = 73.7 \pm 27.07$ g, $r = 28/111.9$, $t = 0.532$, $p = 0.601$).

Female length and mass were positively correlated either in 1988 or 1989, before (1988: *Pearson corr. coeff.* = 0.94, $r^2 = 90.14$ %, *Y-intercept* = -219.42 ± 43.29 , *slope* = 0.58 ± 0.06 ; ANOVA: *F-ratio* = 73.16, *d.f.* = 1, $p = 0.00003$; 1989: *Pearson corr. coeff.* = 0.97, $r^2 = 95.25$ %, *Y-intercept* = -270.81 ± 32.89 , *slope* = 0.66 ± 0.05 ; ANOVA: *F-ratio* = 160.40, *d.f.* = 1, $p = 0$ as well as after birth (1988: *Pearson corr. coeff.* = 0.83, $r^2 = 69.63$ %, *Y-intercept* = -78.47 ± 37.07 , *slope* = 0.25 ± 0.05 ; ANOVA: *F-ratio* = 18.34, *d.f.* = 1, $p = 0.0026$; 1989: *Pearson corr. coeff.* = 0.94, $r^2 = 88.42$ %, *Y-intercept* = -152.14 ± 29.06 , *slope* = 0.36 ± 0.04 ; ANOVA: *F-ratio* = 61.11, *d.f.* = 1, $p = 0.00005$) (see Figures 1 and 2).

3. Female mass loss and mortality

Female mass loss when giving birth was not significantly different in the two years (1988: $\bar{X} = 69.2 \pm 27.40$ g, $r = 47.5 / 117$; 1989: $\bar{X} = 69.7 \pm 21.61$ g, $r = 39.6 / 99.1$ g; $t = -0.045$, $p = 0.964$). In the studied population, as well as in some Swedish adder populations (Andrén and Nil-

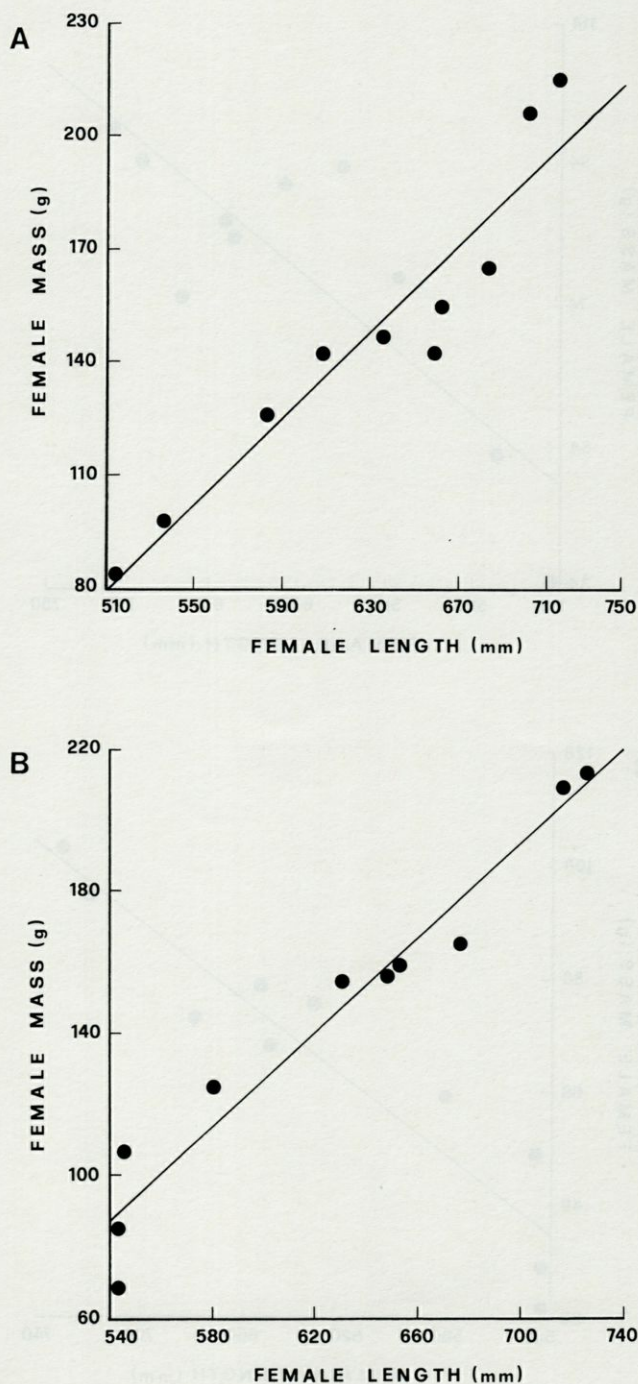


Fig. 1. - Correlation between female length and mass before giving birth in 1988 (graphic A) and 1989 (graphic B).

son, 1983), the clutch mass represented only a part of the total mass loss. The mean value of mass loss/clutch mass ratio was 1.75 ± 0.12 (range = 1.612 / 1.98) in 1988 and 1.64 ± 0.24 (range = 1.32/2.14) in 1989. On the whole, this parameter averaged 1.70 ± 0.19 (range = 1.32 / 2.14). This does mean that, in the sample studied, clutch mass represented about 55-60 % of the total mass loss.

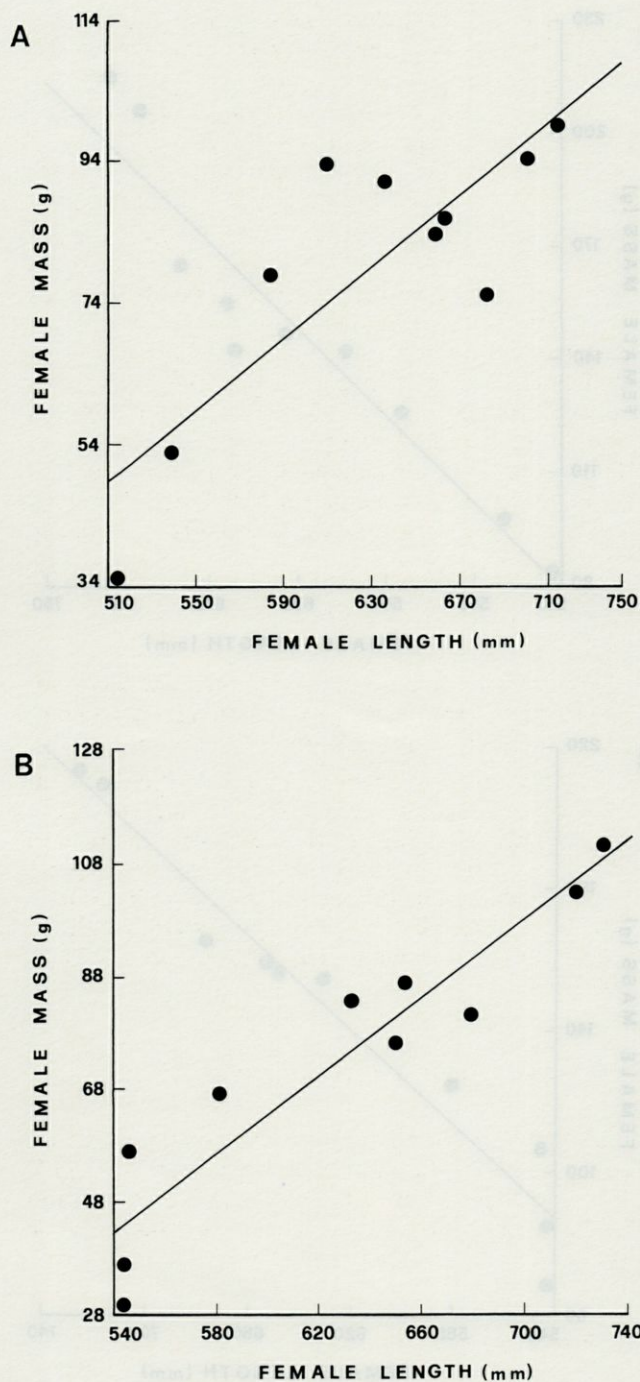


Fig. 2. - Correlation between female length and mass after giving birth in 1988 (graphic A) and 1989 (graphic B).

Relative mass loss was $45.95 \pm 8.26\%$ in 1988 and $49.37 \pm 4.97\%$ in 1989. Therefore, it did not vary significantly between the two years ($t = -1.119$, $p = 0.277$). Our results were relatively similar to those obtained by Fleury and Naulleau (1990), who reported an averaging relative mass loss of about 40%. However, the variations in the relative mass loss after parturition appeared to be extremely wide: Pomianowska-Pilipiuk (1974),

for example, observed in Polish adders a mean relative mass loss of $73.72 \pm 31.82\%$ ($N = 9$), with values ranging from 33.64 to 131.15%.

Mean body mass of « post partum » females was 79.47 ± 20.66 g in 1988 and 73.75 ± 27.07 g in 1989. These means did not differ significantly (two tailed $t = 0.168$, $d.f. = 18$, $p > 0.5$). The values we obtained are very similar to that reported by Saint Girons and Naulleau (1981) for French adders ($\bar{X} = 76.14 \pm 24.13$, $N = 14$).

30% (1988) and 40% (1989) of the studied females were observed to die after giving birth. In both years the vipers died 3-21 days after parturitions. All the specimens which died weighted less than 77 g after the birth, and their mass loss ranged between 39.6 and 88 g. In the two study years the relative mass loss of the died specimens varied between 45 and 58.6% ($\bar{X} = 51.88 \pm 6.24\%$), while the same parameter ranged between 34 and 54% ($\bar{X} = 45.39 \pm 6.26\%$) in the survived vipers. Concerning the relative mass loss, the two categories (died and survived specimens) differed in a statistically significant way ($t = 2.213$, $p = 0.04$). Based on this evidence, it seems that the death of some females may depend on their considerable mass loss and possibly on « stress » or other factors. However, the sample studied was too small to give firm conclusions (see Luiselli, 1992).

4. Female length and clutch size

Mean clutch size did not differ significantly in the two study years (1988: $\bar{X} = 8.2$; 1989: $\bar{X} = 8.9$; t test, n.s.).

Mean clutch size of alpine females (considering together the two study years) did not differ significantly (using two tailed t -test) from mean clutch size of French females, which was $\bar{X} = 7.06 \pm 2.78$ ($N = 18$) according to Saint Girons and Naulleau (1981).

Female length and clutch size were highly positively correlated both in 1988 and in 1989 (1988: *Pearson corr. coeff.* = 0.88, $r^2 = 77.97\%$, *Y-intercept* = -17.041 ± 4.76 , *slope* = 0.039 ± 0.007 ; ANOVA: *F-ratio* = 28.32, $d.f. = 1$, $p = 0.00071$; 1989: *Pearson corr. coeff.* = 0.97, $r^2 = 95.35\%$, *Y-intercept* = -20.11 ± 2.27 , *slope* = 0.046 ± 0.003 , ANOVA: *F-ratio* = 164.27, $d.f. = 1$, $p = 0$) (see Figure 3). A significant correlation between these parameters was already observed in other adder populations (e.g., Andrén and Nilson, 1981, 1983).

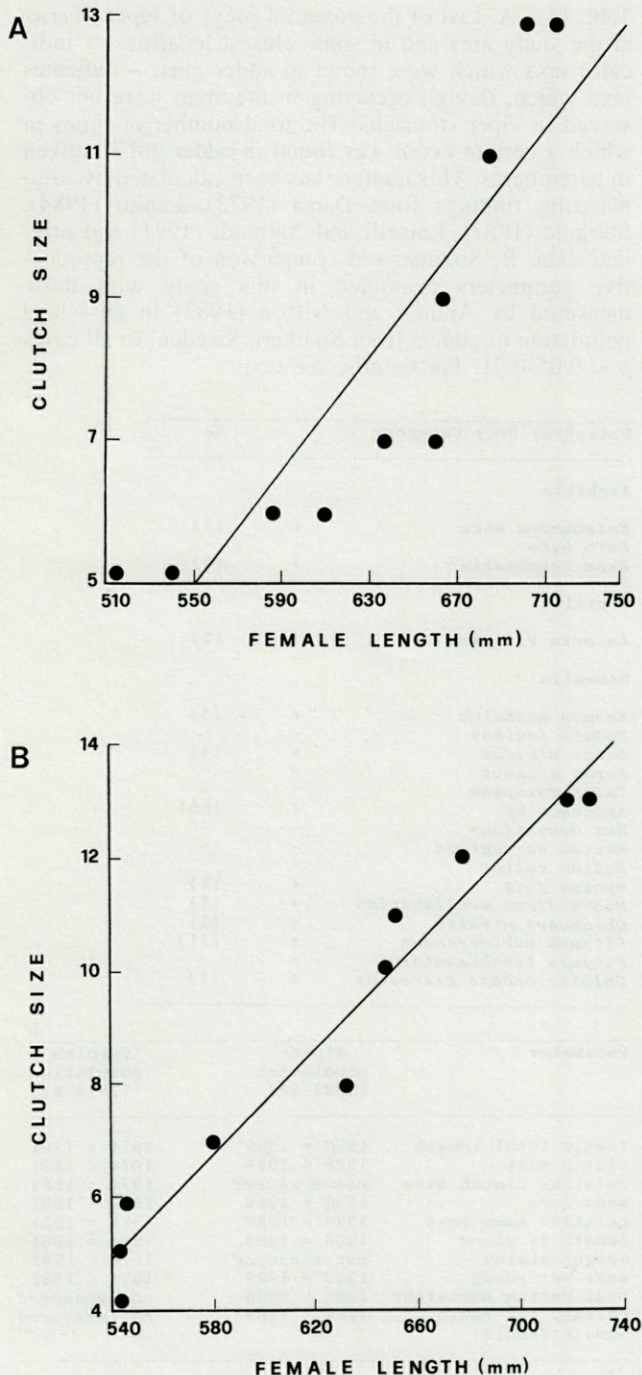


Fig. 3. — Correlation between female length and clutch size in 1988 (graphic A) and 1989 (graphic B).

5. Female mass and clutch size

Female mass was correlated with clutch size before parturition in both study years (1988: *Pearson corr. coeff.* = 0.93, $r^2 = 87.55\%$; ANOVA: *F-ratio* = 56.27, *d.f.* = 1, $p = 0.0007$; 1989: *Pearson corr. coeff.* = 0.96, $r^2 = 92.66\%$; ANOVA: *F-ratio* = 101.01, *d.f.* = 1, $p = 0.00001$).

Both ordinate intercepts and slopes of the two regression lines did not differ significantly (ANCOVA, $p > 0.05$).

Female mass after parturition was highly correlated with clutch size in 1989 (*Pearson corr. coeff.* = 0.93, $r^2 = 87.12\%$; ANOVA: *F-ratio* = 54.089, *d.f.* = 1, $p = 0.00008$). However, this correlation was significantly lower in 1988 (*Pearson corr. coeff.* = 0.59, $r^2 = 35.38\%$; ANOVA: *F-ratio* = 4.38, *d.f.* = 1, $p = 0.069$). Significant differences ($p < 0.01$) can be found analysing by ANCOVA the ordinate intercepts and slopes of these regression lines. The presence of a positive correlation between female mass (after parturition) and clutch size in the studied sample is not surprising, as Saint Girons and Naulleau (1981) observed that it seems to be a general trait in West European viperids (*Pearson corr. coeff.* = 0.902, $p < 0.01$).

6. Female length and young size

Female length and young size (considering both length and mass) were not positively correlated either in 1988 or in 1989 (in both cases $p > 0.05$).

In both study years total length (which was on average 18.5 cm, $r = 13.9 / 21.6$ cm) and mass (on average 4.7-5.2 g) of the newborn vipers were extremely close to those observed in other parts of the wide range of the species, e.g. in France (see Saint Girons and Naulleau, 1981; Naulleau, 1984) and in Sweden (see Andrén and Nilson, 1983).

7. Female length and relative mass loss

Female length and relative mass loss were not correlated in 1988 (*Pearson corr. coeff.* = 0.114, $r^2 = 1.31\%$), while there was a relative correlation in 1989 (*Pearson corr. coeff.* = -0.409, $r^2 = 16.75\%$).

8. Primary sex-ratio

Sex-ratio of young adders differed significantly from 1:1 in 1988 (63.4% [$N = 52$] of females versus 36.6% [$N = 30$] of males; $p < 0.05$; X^2 test with 1 *d.f.*), while it was very close to this value in 1989 (51.7% [$N = 46$] of females versus 48.3% [$N = 43$] of males; $p > 0.05$; X^2 test with 1 *d.f.*).

9. Dates of parturitions

Young snakes were born between 28th August and 8th September in 1988; between 26th August and 10th September. The parturition periods were

similar in both years (80 % of parturitions occurred at the end of August in 1988, and 90 % in the same period during 1989). In the studied population the dates of parturition were practically identical to those observed in some *Vipera berus* populations from northern France (Saint Girons, 1982 and 1985; Saint Girons, Duguy and Naulleau, 1989) and southern Finland (Viitanen, 1967). However, it must be stressed that in Sweden parturitions usually occur 15-20 days earlier (see Nilson, 1981; Madsen, 1989 a).

10. Potential food resources

On the basis of the faunistic data gathered by several authors, 20 different species of potential preys were observed in the study site and in neighbouring localities (Table I).

Among these, 10 species were effectively found in the adder guts (see Darsa, 1972; Luiselli and Anibaldi, 1991): i.e., the frog *Rana temporaria*, the lizard *Lacerta vivipara*, and eight small mammals belonging to the families Soricidae, Muridae, Gliridae and Arvicolidae. Since some of the mammal species included in the list (i.e. *Rattus*, *Talpa*, *Myoxus*) are relatively large sized, they could be preyed by large adders only during their first years of life. Therefore, the role of these mammals in the viper diet should be extremely small. The list reported in Table I, does not include some bird species which could be occasionally preyed by the adders. Nestlings of Passeriformes, in fact, were occasionally observed in the adder guts, either in the southern Alps (Bricchetti, 1976; Luiselli and Anibaldi, 1991) or in northern areas of the wide range of this viper (Stjernberg, 1978).

DISCUSSION

The female adders of the Alpine study site are characterized by a biennial reproductive cycle, with reproduction occurring in alternate years.

The biennial cycle was observed also in some Swiss and Swedish *Vipera berus* populations (see Saint Girons and Kramer, 1963; Nilson, 1981), and it seems to be a common reproductive pattern in ovoviviparous snakes from temperature zones, especially in viperids (see Fitch, 1949; Glissmeyer, 1951; Tinkle, 1962; Saint Girons, 1974 and 1982).

In the snake species characterized by a biennial cycle, maximum fat body size is reached during the spring time of the reproductive year, while minimum fat body size is reached near parturition; gradual fat body increasing during autumn and during the subsequent year is also characteristic

Tabl. I. - A, List of the potential preys of *Vipera berus* at the study area and in some closest localities. + indicates taxa which were found in adder guts; - indicates taxa which, though occurring in the area, were not observed in viper stomachs. The total number of times in which a certain taxon was found in adder guts is given in parentheses. This number has been calculated by summarizing findings from Darsa (1972), Lapini (1984), Stergulc (1987), Luiselli and Anibaldi (1991) and original data. B, Summarized comparison of the reproductive parameters examined in this study with those measured by Andrén and Nilson (1983) in an island population of adders from Southern Sweden. In all cases $p < 0.05-0.01$. For details, see text.

Potential Prey Category	No	A
Amphibia		
<i>Salamandra atra</i>	+	(1)
<i>Bufo bufo</i>	-	-
<i>Rana temporaria</i>	+	(1)
Reptilia		
<i>Lacerta vivipara</i>	+	(2)
Mammalia		
<i>Neomys anomalus</i>	+	(3)
<i>Neomys fodiens</i>	-	-
<i>Sorex alpinus</i>	+	(4)
<i>Sorex araneus</i>	-	-
<i>Talpa europaea</i>	-	-
<i>Apodemus sp.</i>	+	(20)
<i>Mus domesticus</i>	-	-
<i>Rattus norvegicus</i>	-	-
<i>Rattus rattus</i>	-	-
<i>Myoxus glis</i>	+	(1)
<i>Muscardinus avellanarius</i>	+	(1)
<i>Chionomys nivalis</i>	+	(1)
<i>Pitymys subterraneus</i>	+	(11)
<i>Pitymys liechtensteini</i>	-	-
<i>Chlethrionomys glareolus</i>	+	(1)

Parameter	B	
	Alpine population (1988-89)	Swedish population (1974-81)
female total length	1988 = 1989	1974 = 1981
clutch size	1988 = 1989	1974 < 1981
relative clutch mass	not measured	1974 = 1981
mass loss	1988 = 1989	1974 < 1981
relative mass loss	1988 = 1989	1974 = 1981
length of young	1988 = 1989	1974 = 1981
weight status	not measured	1974 < 1981
mass per young	1988 = 1989	1974 < 1981
post-partum mortality	1988 < 1989	not measured
primary sex-ratio (male:female)	1988 < 1989	not measured

of temperate zone snakes showing this reproductive pattern (see Nilson, 1981; Seigel and Ford, 1987). Although the biennial cycle appears to be the general reproductive pattern of the female adders living in mid-mountain alpine localities (e.g., between 900 and 1 400 m a.s.l.), this is not the only reproductive cycle observed amongst alpine *Vipera berus*. In alpine adder populations inhabiting areas located above the wooded zone (2 200-2 500 m a.s.l.), the biennial cycle is usually replaced by a three-year one, probably due to the unfavourable thermal conditions of these extreme environments (see Capula and Luiselli, 1991). A similar situation has been observed even in some

northern populations of *Vipera aspis*, in which females reproduce every three or four years (Saint Girons, 1957), though they normally reproduce every year in the southern part of the species range, i.e. in areas characterized by Mediterranean climate (Luiselli and Agrimi, 1991).

The percentages of reproductive females observed in each year at the study site were not significantly different from those observed by Prestt (1971) in southern Britain (59 %; $N = 49$) and by Vainio (1931) in Finland (53 %; $N = 87$), while they were significantly lower than that observed by Volsoe (1944) in Sweden (68 %; $N = 118$). Recently, different authors have suggested that reproductive frequencies are controlled both by food availability and population structure (Aldridge, 1979; Blem, 1982; Diller and Wallace, 1984), and that remarkable year-to-year variations in the breeding proportion occur in viperids (Andrén and Nilson, 1983). According to Saint Girons (1957), Tinkle (1962), Saint Girons and Kramer (1963), Gibbons (1972), and Aldridge (1979), the major factor implicated in the control of the female reproductive frequency is energy, and a biennial cycle may be due to spring foraging success (Wharton, 1966). The other reproductive parameters appear to be particularly influenced by food availability also, and therefore they may vary significantly between years (Andrén and Nilson, 1983).

On the other hand, a significant homogeneity was observed in some parameters of the alpine adder population (comparisons with Andrén and Nilson's data are shown in Table IB), at least during the two-year research period. For instance, the breeding proportion did not vary significantly from 50 %, while in the Swedish population studied by Andrén and Nilson (1983) it ranged from 30 % (in a situation of low food availability) to 75 % (when food resources were very abundant). The reasons of the high stability are not clear, but we think that this homogeneity could be correlated with a probable firmness of the food resources. In fact, in our study area (1) the heterogeneity of potential preys was significantly higher than that found by Andrén and Nilson (1983) in their study site (in which the only potential prey of adders was *Microtus agrestis*), and (2) the estimated food niche breadth ($B = 3.5$, according to Simpson's diversity index) was wide (see Luiselli and Anibaldi, 1991). It can be therefore stated that alpine adders may dispose of an abundant availability of food resources. Although we have no data about the numerical fluctuations of the potential preys, it seems to be highly improbable that all food resources could simultaneously decline, thus affecting the reproductive efforts of the adder population. The great taxonomical diversity of the potential prey types (including am-

phibians, reptiles and mammals of various families differently adapted to the alpine environmental conditions) could avoid itself the possibility of a simultaneous decline of the various food resources in the area. In fact, it must be stressed that the factors affecting densities of small mammal species are largely different from those affecting amphibian or reptile ones.

Unexpectedly, sex-ratio was the most variable parameter in the *Vipera berus* population studied. Primary sex-ratio was not significantly different from 1 : 1 in 1989; on the other hand, during 1988 the number of females exceeded that of males at a $p < 0.05$ level (considering together the two study years, females amounted to 57.3 % of the total). This is surprising, as Prestt (1971) found 40 newborn males and 39 newborn females in a total of 10 female adders captured in southern Britain during a three year period of research. In agreement with the general theory, predicting that parents should contribute the same effort to and sons as daughters over the population as a whole (Fisher, 1930), primary sex-ratios of snakes are frequently statistically close to 1 : 1 (Parker and Plummer, 1987), while only four known exceptions are male-biased (see Fitch, 1960; Fukada, 1960; Shine and Bull, 1977; Gutzke *et al.*, 1985), and one is female-biased (Fukada, 1956). This yearly variation is really difficult to be interpreted. If we consider that the mortality of reproductive females was particularly high in the two study years ($r = 30 / 40$ %), a discussion topic can be introduced: is it the high mortality of reproductive females correlated with the deviation from an equal sex-ratio, in favour of a major production of females? This working hypothesis needs further investigations. However, (1) since at our research site the sex-ratio of specimens longer than 34 cm is about 1.9 : 1 in favour of males (Luiselli and Anibaldi, 1991) and (2) since primary sex-ratio is in favour of females, we may conclude that the mortality of these latter is largely higher than that of the males. In this case, our data are widely in agreement with those of Madsen (1989 b), who observed a statistically significant higher mortality in reproductive rather than in non-reproductive female and in male adders from southern Sweden. Unfortunately, there is no general agreement between the various field studies on adders with regard to this argument: e.g., Volsoe (1944) has found 177 males and 174 females in the area he investigated, so that it seems that the higher mortality ratio of reproductive females might depend on local factors. One of these factors is probably the environmental temperature Saint Girons (1981) found significant increases of mortality during years having particularly hot summer. When mortality of gravid females is particularly high, melanism may represent a phenotypic condition favouring « post-par-

tum » survival (Luiselli, 1992). It is well known that melanistic snakes are superior in thermoregulation (Gibson and Falls, 1979) and that they may accumulate heat radiation more rapidly than normal coloured ones, resulting in longer activity (and consequently in an increased time for autumnal foraging) and in larger body sizes (Andrén and Nilson, 1981; Luiselli, 1992; Luiselli and Capula, 1992). The prolonged autumnal feeding period is probably of crucial importance for accumulating energy reserves, and it might be one of the principal causes favouring survival of melanistic gravid adders (Luiselli, 1992). The ecological advantages of being black appear to be significantly higher in female rather than in male adders (see Luiselli, 1992). However according to Andrén and Nilson (1981), the increased body size of black adders might be an important selective advantage also in males, as it would increase the number of their victories during sexual combats.

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