FEMALE LIFE HISTORY TRAITS OF THE ASPIC VIPER (*VIPERA ASPIS*) AND SAND VIPER (*V. AMMODYTES*) FROM THE MEDITERRANEAN REGION

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ABSTRACT: Females of 205 Aspic Vipers (*Vipera aspis*) and 37 Sand Vipers (*V. ammodytes*) were examined to describe and compare reproductive features. In free-ranging *V. aspis*, the mean maternal snout-vent length (SVL) was 55.1 ± 4.8 cm (range 41.6–66.0 cm, N = 71), and the mean litter size was 6.9 ± 2.4 (range 1–13, N = 72). Parturition occurred between 13 August and 13 September, but nearly 80% of births occurred between 20 August and 5 September. The proportion of reproductive females of *V. aspis* from the study area suggests that on average they show an annual reproductive cycle. There was a positive correlation between maternal SVL and litter size. Litter size was significantly lower in *V. a. hugyi* than in *V. a. francisciredi*, after SVL was taken into account. In *V. ammodytes*, maternal SVL was 60.5 ± 4.4 cm (range 52.0–67.0 cm, N = 17), and mean litter size was 5.6 ± 1.1 (range 4–8, N = 17). Parturition occurred between 26 August and 19 September, but nearly 60% of births occurred between 7 and 10 September. The proportion of breeding females suggests a biennial reproductive cycle in *V. ammodytes*. There was a significant positive correlation between maternal SVL and litter size. Four of 17 reproductive females died 11–24 days after parturition, thus demonstrating a significant cost of reproduction in terms of post-partum survival.

INTRODUCTION

Reproductive strategies and related cycles of snakes, particularly of female viperids, have been the subject of interest among evolutionary ecologists in the past 20 years (Naulleau and Saint Girons, 1981; Andrén and Nilson, 1983; Seigel and Fitch, 1984; Duvall et al., 1992, 1993; Madsen and Shine, 1992; Schuett, 1992; Saint Girons, 1994, 1996; Bonnet et al., 1994, this volume; Luiselli, 1995; Almeida-Santos and Salomão, this volume; Beaupre, this volume; Höggren and Tegelström, this volume). Viviparous snakes are considered capital breeders and have the ability to store large fat reserves for reproduction (Bonnet et al., 1998, this volume). Feeding activity during and after gestation increases fitness and reproductive output, but where there is reduced or absent food intake during pregnancy females may: (1) not reproduce, (2) produce a relatively small litter, or (3) perish during the post-partum period (Naulleau and Saint Girons, 1981; Andrén and Nilson, 1983; Luiselli, 1992; Madsen and Shine, 1992; Bonnet and Naulleau, 1994; Bonnet et al., 1994; Zuffi et al., 1999a).

The Aspic Viper (*Vipera aspis*) and Sand Viper (*Vipera ammodytes*) of the western Palearctic region are medium-sized viperids. *Vipera aspis* ranges from northwestern France south to Italy and Sicily (Saint Girons, 1997), covering about 1,600 km from NW to SE and about 12° of latitude (49° to 37°N), and reaching 2,500 m in elevation in the Pyrenees and 3,000 m in the Alps (Arnold and Burton, 1980). *Vipera ammodytes* ranges from northeastern Italy and southern Austria throughout the Balkan Peninsula to Greece (Crnobrnja-Isailovic and Haxhiu, 1997). Its range covers about 1,200 km from NW to SE and about 11° of latitude (47° to 36°N), and *V. ammodytes* reaches 2,500 m in elevation in the southern portion of its range (Arnold and Burton, 1980).

Female *V. aspis* from northernmost localities do not reproduce in consecutive years, and are reported as biennial, triennial, or even quadrennial breeders, as suggested by Saint Girons (1957a, b), and subsequently demonstrated by Bonnet and Naulleau (1996) and Saint Girons (1996). The poor body condition of post partum females, combined with the short feeding period following parturition, explains the low frequency of breeding (Naulleau and Bonnet, 1996). Although there are limited data on the reproductive characteristics of *V. ammodytes* (Biella, 1983; Bruno and Maugeri, 1990), we hypothesize that females of this species show irregular reproduction as a result of ecological and latitudinal differences. This trend is prevalent in most species of Palearctic viperids (Saint Girons, 1957a, b; Madsen and Shine, 1992; Capula and Luiselli, 1994; Luiselli, 1995; Naulleau and Bonnet, 1996; Zuffi et al., 1999a; Bonnet et al., this volume).

In Italy, most vipers in the western and central Alps, from the northern to southern Appennines, and some minor islands and Sicily, are allocated to *V. aspis* (but see Zuffi, 2002), although there are also some populations of *V. ammodytes*, *V. berus*, and *V. ursinii*. Unfortunately, few populations have been studied with respect to their ecology. Studies, however, have been conducted on Alpine populations of *V. berus* (Luiselli and Anibaldi, 1991; Capula et al., 1992; Luiselli, 1995), central Italian populations of *V. aspis* (Luiselli and Agrimi, 1991; Saviozzi and Zuffi, 1997; Zuffi, 1999; Zuffi et al., 1999a, b), eastern Alpine Italian *V. ammodytes* (Luiselli, 1996), and the

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Table 1. Reproductive condition and ecological factors obtained from preserved *Vipera aspis* in museum collections. N = number of specimens.

	N	$\bar{x}$ ± SD	Range
Elevation (m)	95	501.23 ± 488.42	0–2,000
Latitude (in degrees)	126	43.74 ± 2.15	37.5–46.19
Food (0 = absent, 1 = present)	138	0.33 ± 0.47	0–1
Fat-bodies	147	1.99 ± 0.81	1–3
Month	147	7.25 ± 2.06	3–12
Fertilized eggs	30	7.13 ± 2.52	1–14
Embryos	22	8 ± 3.06	1–15

central Italian populations of *V. ursinii* (Agrimi and Luiselli, 1992).

Because the Italian peninsula shows a wide range of elevational and latitudinal gradients (e.g., up to 3,000 m in elevation, over 1,200 km in length), as well as small to large islands (e.g., Montecristo, Elba, and Sicily), we studied *V. aspis* and *V. ammodytes* to test phenotypic plasticity of reproduction in these relatively wide-ranging species.

MATERIALS AND METHODS

Study Area

The study area for *V. aspis* is in Arnino, 10 km SW of Pisa, and inside the "Parco Regionale di Migliarino, S. Rossore, Massaciuccoli." The site is ca. 6 ha and consists largely of cultivated land with sandy soil. Drainage canals bordered by reeds (*Phragmites* sp.) divide the fields, and mixed woods (*Pinus pinea*, *Quercus ilex*) border the southern portion of the site. Winters are warm, and the minimum and maximum temperatures of the two coldest months average 0°C and 15°C (Rivano, 1988). In general, the study area represents habitat typical of the Tyrrhenian Sea coastline. The site was chosen because it lies within a protected area, and because in structure (i.e., sandy area, proximity to the sea, bushes bordering pinewoods) this area is comparable to many areas of the Mediterranean region.

The main study area consists of two sites, one at 170–200 m in elevation (site A, Canale Monterano; Luiselli and Rugiero, 1990) and the other at 300–700 m in elevation (site B, Tolfa Mountains; Luiselli and Agrimi, 1991). At site A there are ancient ruins, and the area contains different types of woodland and active solfataras (fumaroles); the ground is volcanic, tufaceous, and highly mineralized. Water is abundant, and willows (*Salix* sp.) and alders (*Alnus* sp.) predominate, although in the southern part, woodlands of *Quercus cerris* and *Castanea sativa* are more typical (Luiselli and Rugiero, 1990). Site B constitutes six locations in the Tolfa Mountains with similar climatic conditions, exposure, and vegetation. Bushes are mainly *Spartium*, *Paliurus*, and *Cytisus,* and the woody *Pyrus pyraster* is found on the edges of *Fagus* and *Quercus* woodlands. Field data for *V. aspis* from Tuscany were collected from 1990 to 1996 (Saviozzi and Zuffi, 1997; Zuffi, 1999; Zuffi et al., 1999a, b), from the Tolfa Mountains (Latium) from 1986 to 1989 (Luiselli and Rugiero, 1990; Luiselli and Agrimi, 1991), and from Castel Fusano (Latium) and the Alimini lakes (Apulia) from 1992 to 1994 (L. Luiselli, unpublished).

The study area for *V. ammodytes* is in Pontebba, in the Carnic Alps province of Udine in northeastern Italy, at an elevation of 700 m. Detrital-alluvial cones

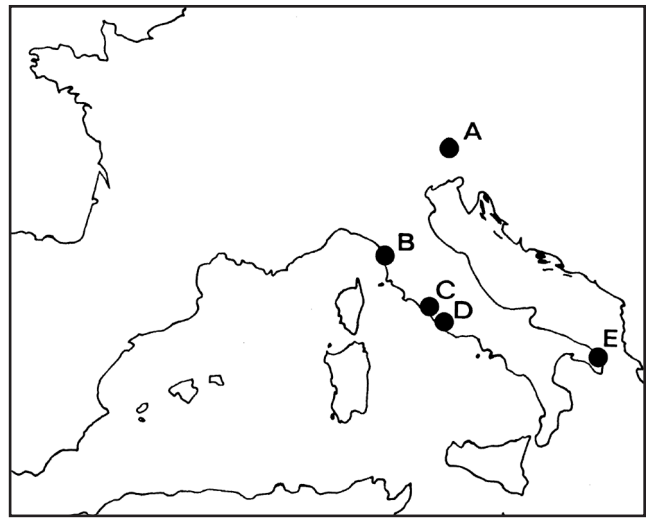

Fig. 1. Study areas. *Vipera ammodytes*, A = Pontebba (Carnic Alps, northwestern Italy); *Vipera aspis francisciredi*, B = Arnino (central Italy); C = Tolfa Mountains (central Italy); D = Castel Fusano (central Italy); *Vipera aspis hugyi*, E = Alimini lakes (southern Italy).

characterize this rocky region, which is at the limits of *Abieti-Fagetum* woodland. In this area *V. ammodytes* is locally abundant (average density = 15–22 adults/ha). Field data were collected between 1987 and 1994 (Capula and Luiselli, 1994; Luiselli, 1996).

DATA COLLECTION

Vipers were captured by hand, sexed by inspecting coloration features and tail morphology, and palpated to determine reproductive status. Pregnant females were brought to the laboratory and maintained until parturition, which occurred from several days to four weeks. The following were recorded (see Capula et al., 1992): (1) total length of each female, (2) mass of each female before and after birth; (3) litter mass of each female; (4) litter size for each female; (5) sex, total length, and mass of each neonate. Moreover, we determined post partum mortality by counting specimens that died in captivity within 30 days after birth. Fifty-three pregnant *V. aspis* were studied from the following localities (north to south): Arnino (N = 3); Tolfa Mountains (N = 34); Castelfusano (N = 9); Alimini Lakes (N = 7), and 17 pregnant *V. ammodytes* (of 37 adult females) were studied from Pontebba (Fig. 1). Data on reproduction were also obtained from dissection of 162 preserved specimens from major herpetological collections in Italy (see Zuffi and Bonnet, 1999). Status of embryonic development was considered as complete (i.e., females carrying well-developed offspring; M. Zuffi, unpublished) for 19 of 162 individuals, and these were considered in the analysis of females from the field sites. From preserved specimens we also obtained additional data on reproduction, such as an estimation of fat body reserves as a visual percentage of fat bodies on the ventral surface. These were coded as 1 (0–33.3% ventral surface), 2 (33.4–66.6% of ventral surface), or 3 (66.7–99.9% of ventral surface). The number of fertilized eggs, number of embryos, litter size, and food presence (0 = absent; 1 = present) were also recorded.

DATA ANALYSIS

Statistical analyses were carried out on log-transformed variables (SVL, TL, litter size), and tested for normality. Linear regression and one-way ANOVA (Multiple Range Tests: LSD) were used to: (1) find relationships between pairs of variables (e.g., SVL vs litter size) and (2) test for differences between variables (e.g., litter size between subspecies). Category variables (fat body levels, food presence) were analyzed with non-parametric statistics (Mann-Whitney U test, χ^2).

RESULTS

Vipera aspis

In central Italy, ovulation occurs in mid- to late May (Zuffi et al., 1999a), relatively earlier than in west-central France (Saint Girons, 1952; Naulleau, and Bonnet, 1996). Fat body reserves were significantly higher during the first gestation period (i.e., "egg-carrying" females, May to July; Fig. 2a) than in the second gestation period (i.e., females with embryos, August to October; Fig. 2b) (Mann-Whitney, $U = -3.697$, $P = 0.0002$). Females from coastal areas fed longer (late January to early December); Zuffi et al. (1999b) showed relatively high fat body presence in *V. aspis*, until the end of pregnancy (Zuffi et al., 1999a).

Average maternal SVL was 55.1 ± 4.9 cm (range 41.6–66.0 cm, N = 71), and mean litter size was 6.9 ± 2.4 offspring per female (range 1–13, N = 72). Parturition occurred between 13 August and 13 September, but nearly 80% of total events occurred from 20 August to 5 September. The proportion of breeding females suggests, on average, an annual reproductive cycle (75% of females at the Tolfa Mountains, to 100% at Arnino and Castelfusano, respectively, 100% in the Alimini Lakes population) in specimens from central and southern Italy that occur below 700 m in elevation. No females collected after parturition died (N = 53).

There was a positive correlation between maternal SVL and litter size ($r = 0.5309$, adjusted $r^2 = 0.2714$, ANOVA, $F_{1, 69} = 27.083$, $P = 0.0001$; equation: litter size = $-8.0293 + 0.2707_{SVL}$; Fig. 3a). Litter size was significantly lower in *Vipera a. hugyi* from southern Italy (5.1 ± 1.1, N = 8) than in *V. a. atra* from northwestern Italy (7.8 ± 1.9, N = 5) and *V. a. francisciredi* from northeastern to central Italy (7.1 ± 2.5, N = 59; one-way ANOVA, $F_{2, 69} = 2.697$, $P = 0.0745$, NS); LSD multiple range test of *hugyi* vs *francisciredi* was significantly different ($P < 0.05$), even when they had similar SVL (*atra*: 53 ± 3.8 cm, N = 5; *francisciredi*: 55.5 ± 4.9 cm, N = 58; *hugyi*: 53.8 ± 4.5 cm, N = 8; one-way ANOVA, $F_{2, 68} = 0.9706$, $P = 0.384$, NS).

Analysis of feeding activity of the Italian taxa *V. aspis atra*, *V. a. francisciredi*, and *V. a. hugyi* revealed a statistical similarity from north to south (e.g., from *atra* to *hugyi*) with respect to percentage of fed vs non-fed reproductive females of 66.7% (N = 20), 44.3% (N = 88), and 38.5% (N = 18), respectively ($\chi^2 = 2.0707$, $df = 2$, $P = 0.3551$). Feeding activity of reproductive *V. aspis* was more frequent in egg-carrying

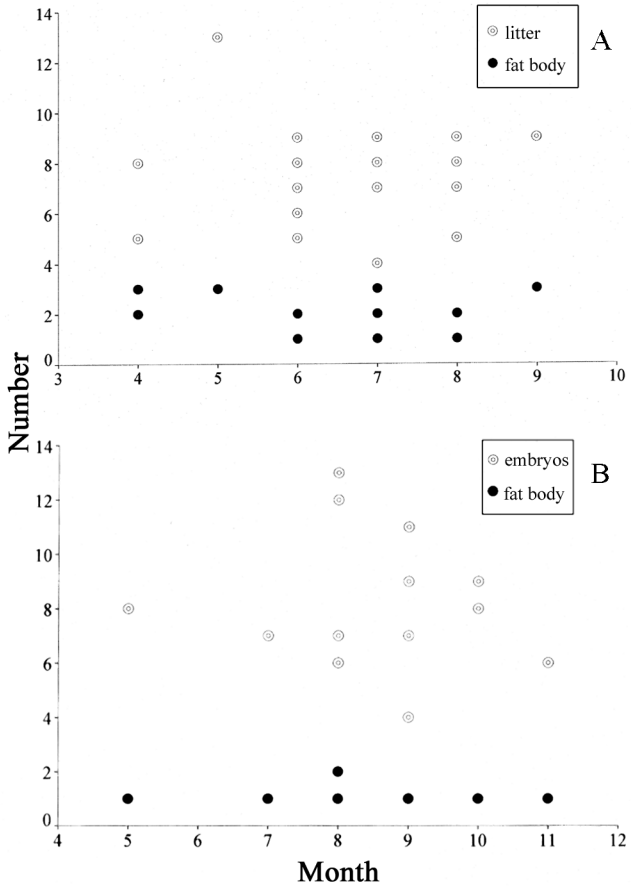

Fig. 2. Fat body reserves of female *Vipera aspis*. (A) Egg-carrying individuals. (B) Embryo-carrying (pregnant) individuals.

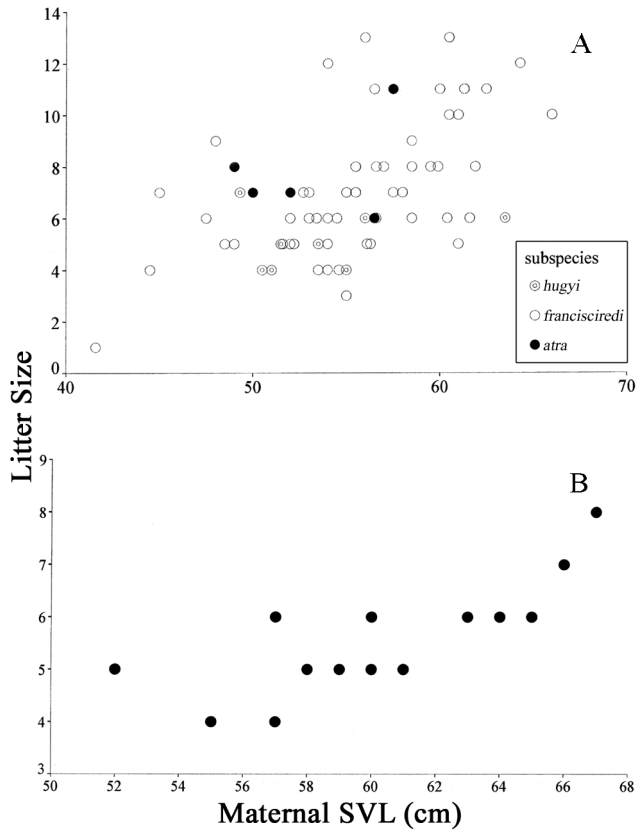

Fig. 3. Maternal snout-vent length (SVL) vs litter size in (A) *Vipera aspis* and (B) *Vipera ammodytes*.

females (7/16), than in embryo-carrying (pregnant) females (1/12).

Timing of parturition was dependent on latitude and suitable local climate, and typically from early to mid August in warmer areas (Zuffi et al., 1999a; L. Luiselli, unpublished) to the end of October in colder areas with higher elevation (e.g., 800–1,500 m; M. Zuffi, unpublished).

Vipera ammodytes

Seventeen of 37 adult *V. ammodytes* studied were pregnant. Maternal SVL was 60.5 ± 4.4 cm (range 52.0–67.0 cm, N = 17), and the mean litter size was 5.6 ± 1.1 (range 4–8, N = 17). Parturition occurred from 26 August to 19 September, but nearly 60% of births occurred between 7 and 10 September. The proportion of breeding females (17 of 37 adult females, 46%) suggests a biennial reproductive cycle. There was a significant positive correlation between maternal SVL and litter size ($r = 0.82$, adjusted $r^2 = 0.652$, ANOVA, $F_{1, 15} = 31.068$, $P = 0.0001$; equation: litter size = $– 6.977 + 0.20779_{SVL}$; Fig. 3b). Females fed on small prey until ca.10 days before giving birth. Four of 17 reproductive females (23.5%) died within 11 to 24 days after parturition, thus demonstrating a significant cost of reproduction in terms of post-partum survival.

DISCUSSION

The analysis of reproductive relationships of Aspic Vipers (*V. aspis*) and Sand Vipers (*V. ammodytes*) of the Mediterranean region revealed a direct relation between maternal SVL and litter size. *Vipera ammodytes* and the Southern Aspic Viper (*V. aspis hugyi*; but see Zuffi, 2002) show a strong similarity with respect to reproduction (e.g., small litter size with respect to female body size), but differed from other *V. aspis* subspecies (present work) and *V. berus* (Capula et al., 1992; Madsen and Shine, 1992). The two species (*V. aspis* and *V. ammodytes*) live in very different habitats (i.e., mountains vs coastal habitats), and show different reproductive characteristics (biennial vs annual; high maternal mortality rate vs no

maternal mortality rate). *Vipera ammodytes* also showed marked differences in reproductive characteristics when compared to *V. berus*, a well-studied species that occupies similar ecological conditions (Capula et al., 1992; Luiselli, 1992; Capula and Luiselli, 1994; Luiselli, 1995).

Comparative analysis of morphological characters of the *V. aspis* group in southern Europe revealed pronounced differences in the number of ventral scales, a character that has been used indirectly to count the number of vertebrae in snakes (Saint Girons, 1978). Among members of the *V. aspis* group that were studied, the number of ventral scales was significantly lower in *V. a. hugyi* (Zuffi and Bonnet, 1999; Zuffi, 2002). Even with a greater body length than *V. aspis*, the number of ventral scales in females of *V. ammodytes* ($\bar{x}$ = 149.53 ± 3.52, N = 15) is comparable to that of *V. a. aspis* ($\bar{x}$ = 150.00 ± 3.22, N = 17) and *V. a. francisciredi* ($\bar{x}$ = 149.32 ± 4.07, N = 74), is lower than that of *V. a. atra* ($\bar{x}$ = 154.83 ± 3.31, N = 23), and is relatively higher than that of *V. aspis hugyi* ($\bar{x}$ = 144.42 ± 2.84, N = 19) (Zuffi and Bonnet, 1999). Other viperid snakes of comparable length show marked differences in the number of vertebrae (e.g., *V. latasti*: Saint Girons, 1953; *V. monticola*: Broadmann, 1987).

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