WINTER ACTIVITY IN A COASTAL POPULATION OF *VIPERA ASPIS* (REPTILIA, VIPERIDAE)

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RÉSUMÉ

L'activité hivernale d'une petite population de *Vipera aspis* (4 mâles adultes et 3 femelles adultes) a été étudiée au cours de trois hivers à l'aide du radio-pistage. Presque tous les individus sont restés actifs, se cachant simplement sous les feuilles, se déplaçant d'un refuge à l'autre en effectuant des distances d'environ 150 m. Approximativement 50 % des serpents étaient actifs au soleil (29 % du total des journées d'observation). Les domaines vitaux et les zones de principale fréquentation sont statistiquement identiques entre les sexes, bien que légèrement supérieurs chez les mâles. Les tailles observées pour les domaines vitaux sont remarquablement grandes pour des périodes hivernales durant lesquelles l'activité est censée être très réduite. Des déplacements, courts et longs, sont relativement plus fréquents chez les mâles que chez les femelles. Des températures ambiantes favorables liées à la position géographique, et donc à la zone climatique de la zone d'étude, semblent être le stimulus principal pouvant expliquer la forte activité hivernale de la population étudiée.

SUMMARY

Winter activity patterns in a little coastal population of *Vipera aspis* (4 adult males, 3 adult females) have been studied during three winters using radiotracking. Most of studied specimens are mainly active, hiding just under leaves, moving from a refuge to another, covering up to 150 m. About 50 % of snakes were active in the sun (29 % of total days). Home ranges and core areas were similar between sexes, even if males attained at larger home ranges. Recorded home ranges were relatively large with respect to those presumed for the winter season, during which the reported activity is usually absent or reduced. Short and long displacements and movements were relatively higher and more frequent in males than in females. Favourable temperatures due to the geographic position and climatic situation of the area seemed the major stimulus for this asp viper population to be active.

INTRODUCTION

Most of the snake species of temperate zones inhabiting mainland areas and/or living at high latitudes and altitudes usually do not display any activity

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during the winter (Saint Girons, 1952; Viitanen, 1967; Brown *et al.*, 1974; Gregory, 1982; Martin, 1993). However, North American Colubrids and Viperids in natural hibernacula have been found to have locomotor microactivity in winter. That movement of over-wintering snakes is regulated by inversion of the thermal gradient is subject to debate (Jacob & Painter, 1980; Sexton & Hunt, 1980; Brown, 1982; Macartney *et al.*, 1989; Weatherhead, 1989). In Nearctic pitvipers, a negative relationship has also been confirmed between latitude and the frequency of some activity patterns (Sexton *et al.*, 1992). Furthermore, in most species of Australian Elapids, mild winters are presumed to stimulate activity in the open (Shine, 1979).

The Asp Viper (*Vipera aspis*) is one of the ten species of the genus *Vipera* in Europe (Gasc *et al.*, 1997). Its distribution extends throughout northwestern France to Sicily, and from about 3 000 m in the Alps to sea level (Arnold & Burton, 1980). Although the biology, ecology, and behavioural ecology of this species have been studied for many years in most regions (Saint Girons, 1952, 1994; Naulleau, 1966; Bonnet & Naulleau, 1993; Naulleau *et al.*, 1996), there is little information on its activity patterns during the winter (Duguy, 1963).

The population of Asp Vipers distributed along the Ligurian Sea coasts of northern Tuscany (central Italy), lives in meteorological conditions which are probably favourable for activity in late autumn and early and/or late winter. A very short period of winter dormancy has already been recorded (M.A.L.Z., M.M., pers. obs.) for vipers that hibernate singly, probably related to the particularly mild climate of this stretch of coast. As this part of the coast is ecologically quite similar to most of the western (Ligurian and Thyrrenian Seas), eastern (Adriatic Sea) coasts of central Italy, and coasts of southern France, we consider our study area as a particularly good ecological model typical of such a Mediterranean habitat of Italy.

This study illustrates the following points: (1) *Vipera aspis* is active (as defined by change in location between observations) during the winter in Mediterranean environments of Italy, (2) activity range of studied individuals is very variable between them, and (3) winter activity in *V. aspis* seemed to be linked to environmental factors.

MATERIALS AND METHODS

STUDY AREA AND THE SPECIES

The study area is 3 km E of the Ligurian Sea coast and about 10 km SW of Pisa, within the "Migliarino, San Rossore, Massaciuccoli" natural park (43° 39' 45" N, 10° 17' 30" E). It is characterized by ecotonal environments of mediterranean wood and grassy areas and by mild temperate winters. Two separate sites were used. We used seven adult *Vipera aspis* (four males: no. 4, 22, 36, 51; and three females: no. 10, 33, 52) (female *V. aspis* mature at SVL = 41.5 cm, Bonnet & Naulleau, 1996). The average total length and mass (± 1 SE) of males was 67.8 ± 4.1 cm and 115.8 ± 14.1 g respectively; total length and mass of females was 63 ± 7.9 cm and 147.3 ± 11.1 g.

METHODS

The research was carried out from December to February in three winters (late 1992-early 1996). Observations began each year in early December, when the

feeding activity of all the snake species of this area (e.g. *Natrix natrix, Hierophis viridiflavus* and *Vipera aspis*) ceased and ended when the snakes started their feeding activities and mating period (31 Jan.-16 Feb.).

The snakes were ventrally marked with scale clipping, and equipped with two-component epoxy-coated radiotransmitters (Biotrack, SS2, $16 \times 8 \times 9$ mm, 2.2 g weight after coating; three months battery life; 10 cm long antenna). The transmitter signal had a 50-200 m range and worked at 150.000-150.999 Mhz. The receiver was a 12 channel AVM model. Transmitters were mounted externally with Ciofi & Chelazzi's (1991) method, partly modified: the radiotransmitters were attached dorsally anterior to the tail; the nylon cord remained just beneath the skin and was not inserted in a microtube. This procedure was followed because of the high degree of flexibility of the viper's skin compared to that of other species (Ciofi & Chelazzi, 1991). No evident damage or pain for the snakes was recorded.

ACTIVITY

Snake activity was evaluated on the basis of daily occurrence of long (> 10 m) or short (< 10 m) movements, or lack thereof in relation to sun or shade and to location within or outside a refuge. The presence of a refuge was evaluated by the constant pattern of inactivity at a given one m^2 site or by a continuous shuttling behaviour from different directions to the same place.

INDEPENDENCE OF DATA RECORDING

For each snake we recorded an average of three fixes a day, two or three times a week. The independence of consecutive fixes, to avoid autocorrelation of data, was calculated following the methods of Schoener (1981) and Swihart & Slade (1985) (Table I).

Specimens were selected from a part of the activity period of a large population of several vipers, during a co-worker's thesis (M.M.) in 1992-1994,

TABLE I

Test for fix independence. Viper = number and sex (f = female; m = male); n = number of observations; m = number of pairs of consecutive records; e = eccentricity of home range, that is major axis/minor axis; t^2/r^2 = value of Schoener ratio; t^2/r^2 critic = critic values of Schoener ratio; P = probability value; H_0 = results of the null hypothesis. In bold significant values.

Viper	n	m	e	t^2/r^2	t^2/r^2 critic	P	H_0
f 10	12	9	0	0	1.75-1.74	< 0.25	rejected
m 22	92	69	3.9	16 400	1.85	> 0.25	**Supported**
f 33	60	45	5.6	132.75	1.81	> 0.25	**Supported**
m 34	21	16	4.8	0	1.71-1.69	< 0.25	rejected
m 36	64	48	1.5	965.07	1.85	> 0.25	**Supported**
f 37	32	27	15.9	0.573	1.96	< 0.25	rejected

whilst the 1994-1996 data were part of a thesis of another member of the workgroup (F.G.). This experiment was carried out to test the power of the method and validity of most of the data from our radio monitored vipers. We selected four daily fixes at two hour intervals (e.g.: 0900, 1100, 1300, 1500), in order to obtain the same number of fixes in the same day interval for all the individuals. The sample was composed of females no. 10, 33, 37 and of males no. 22, 34, 36, monitored from 13 December 1992 to 13 April 1994 (Macchia, 1995). Testing the 1992-1994 sample of radiotracked vipers, according to Swihart & Slade (1985), we obtained a significant independence of consecutive radio fixes at a two hour interval for male no. 22 and for females 33 and 36, whilst for the other three test vipers the chosen interval time was not significant (Table I). On average, vipers do not distribute randomly throughout the area, but tend to use all available ecotonal habitats (Macchia, 1995). This behaviour explained that the home range of female no. 37 (Swihart & Slade's 2nd case) was quite regularly linear according to the presence of an artificial canal. Observations relative to female 10 and male 34 were autocorrelated. These snakes were always immobile between 0900 and 1300, and they moved only in the following interval times. For this reason, even if not statistically significant, we considered as biologically relevant all data coming from these last three specimens.

Each fix was transferred onto a map within each one m^2 cell of grid reference, designed using natural and artificial topographic marks in the field. This allowed us to limit any source of error to a maximum of one snake length (on average ± 50 cm). This approach enabled us to verify if and how space usage patterns varied in time and with which frequency for each specimen. At each fix, ambient temperatures (i.e.: air at 10 cm height and ground surface temperature, both shaded), atmospheric conditions, individual behaviour (e.g.: basking, movement) and position on the ground were recorded.

STATISTICAL ANALYSES

The home range and core area estimations were calculated with the 95 % and 50 % Harmonic Mean contours respectively (Dixon & Chapman, 1980; Tiebout & Cary, 1987), with the software McPaal, version 2.1. Statistical analyses were performed with a STATGRAPHICS for Dos (version 2.1, 1986) personal computer software. All tests performed were non-parametric. Variability in the types of movement (i.e. absence, short, long) per month and according to sex was analyzed with the Kruskal-Wallis test for k independent samples. Differences between two sample averages (i.e. absence of movements *vs* short movements) were analysed with the Mann-Whitney test, and home range estimations according to the Kolmogorov-Smirnov test (Ciofi & Chelazzi, 1991).

RESULTS

ACTIVITY

We considered 364 fixes relative to the displacements and general ecology. Males no. 22 and 51 and female no. 33 entered a refuge, underground or under

leaves, not much more than 63 % of the overall time (male 22: 10 % in 20 days; male 51: 50 % in eight days; female 33: 63.16 % in 19 days); they spent most of the time on the ground surface under leaves and in tufts of grass (male 22: 90 % in 20 days; male 51: 50 % in eight days; female 33: 36.84 % in 19 days). Male no. 4 and female no. 10 were mainly inactive and hidden inside a single refuge (male 4: 77.78 % in 18 days; female 10: 83.33 % in 18 days), and displaced only occasionally (12 and 38 m respectively; Table II). The last two vipers (male no. 36, female no. 52) spent a variable time out of their refuges (male 36: 64.71 % in 17 days; female 52: 12.50 % in 16 days), basking in sight (male 36: 41.18 % in 17 days; female 52: 12.50 % in 16 days) (Table II); they also made some occasional short movements in the shade (Table III). For the 52 snake days on which activity was recorded, air temperature ranged from 5.3 to 20 °C (avg. = 13.1 ± 0.3; $n = 64$) and ground temperatures from 5.8 to 19 °C (avg. = 12.9 ± 0.4; $n = 64$). In the 64 days when snakes were inactive, air temperatures ranged from -1.4 to 17.8 °C (avg. = 9.6 ± 0.3; $n = 183$) and ground temperatures from -0.6 to 21.3 °C (avg. = 9.9 ± 0.3; $n = 183$). No feeding behaviour was observed in this period; the last and first feeding snakes were collected in early December and early February. Even if our sample size is relatively small, males seemed on average more mobile (Table II), more active in the open and more visible than females (Table III). We observed that average mean daily distance of three out of four males and of one out of three females (Table II), was greater with respect to other western France *Vipera aspis* (Naulleau *et al.*, 1996), clearly suggesting a clearcut positive influence of latitude and climate on activity patterns (Sexton *et al.*, 1992; Bonnet & Naulleau, 1996; Zuffi, 1999).

In the months of the study males were immobile with a similar frequency (Kruskall-Wallis test = 5.42, $P > 0.06$); we found individual significant difference in the frequency of short movements throughout this period (Table III) (Kruskall-Wallis test = 4.34, $P < 0.05$). Females spent much more time in their refuges than the males, with no significant difference between the monthly distribution of movements (absence, Kruskal-Wallis test = 4.23, $P > 0.1$; short, Kruskal-Wallis test = 2.33, $P > 0.3$). On average, the female pattern during winter was characterized by a significantly higher immobility with respect to movement, that is short movement (Mann-Whitney test = -2.78, $P < 0.05$). Female no. 33 and males no. 22, 36, 51 displaced frequently within a few days to different sites, as far as 50-150 m from their main refuge, throughout all the considered periods (Table IV). Short and long movements in sight were slightly more frequent, though not significantly, in males than in females in January, and similar in December and February (Table IV).

HOME RANGES

No significant relationship between movement or home range *vs* sex was found, but a tendency towards a higher mobility and activity in males seems also possible (Table II, IV). The average ($\pm$ SE) male home range estimation was not significantly greater (23.23 ± 16.09 m^2) than that of the females' (2.46 ± 1.52 m^2) (Table II) (Kolmogorov-Smirnov test = 0.5, $P > 0.7$). Male core area estimation (2.33 ± 0.78 m^2) was also greater with respect to that of the females (1.467 ± 1.0 m^2) (Table II), but not significantly different (Kolmogorov-Smirnov test = 0.33, $P > 0.9$). In addition, males no. 22 and 36 had quite wide home ranges

TABLE II

Activity patterns, home range and core area estimations. "ID" means identification number of viper activity = days with vipers in sight, moving undercover or underground; inactivity = days with immobile vipers; hidden periods = days during which activity was recorded only with radiotransmitters (see text for explanations).

Sex	ID	Month	Fixes (N)	Days (N)	Activity (days, N)	Inactivity (days, N)	Hidden period	Total distance (m)	Mean daily distance (x ± sd)	Distance range (m)	Home range (95 %, m²)	Core area (50 %, m²)
m	4	12-2	60	18	4	14	18	12.0	1.2 ± 0.1	0-2	1	1
m	22	12-2	66	20	18	2	2	197.3	11.6 ± 6.4	1-43	61	1
m	36	12-2	58	17	11	6	10	157.1	13.1 ± 2.1	2-20	27.5	4
m	51	12-1	25	8	4	4	4	136.0	11.3 ± 5.2	1-43	3.4	3.3
f	10	12-2	37	18	3	15	18	38.0	9.5 ± 2.2	1-2	0	0
f	33	12-2	63	19	7	12	12	58.0	3.9 ± 1.0	1-14	4	1
f	52	12-2	55	16	5	11	14	36.0	3.6 ± 0.9	1-10	3.5	3.4
Total			364	116	52	64	78					

TABLE III

Displacement patterns of winter vipers (absolute frequency). "N" = absence of movements; "S" = short movements; "L" = long movements; "sun" = in sight; "shade" = not in sight or underground (see text for explanations).

	Males				Females		
	4	22	36	51	10	33	52
December							
N	17	20	19	8	2	17	15
S	2	4	3	1	4	1	—
L	—	3	1	—	—	—	1
Sun	2	17	2	—	—	2	—
Shade	17	10	21	9	6	16	16
January							
N	27	21	23	6	15	34	30
S	8	8	4	4	3	3	3
L	—	—	2	2	—	—	—
Sun	—	24	10	5	—	8	1
Shade	35	5	19	7	18	29	32
February							
N	6	10	6	2	12	8	5
S	—	—	—	2	1	—	1
L	—	—	—	—	—	—	—
Sun	1	7	1	1	4	1	1
Shade	5	3	5	3	9	7	5

TABLE IV

Distance and movement patterns in winter vipers. Sample size in parentheses.
[1]: movements observed during radio-racking days; [2]: this male moved during non radiotracking periods.

Viper #	Distance per movement	Distance between days	Days between movements	Distance per day[1]	# Movements
m 4	1 ± 0 (4)	0.5 ± 0.8 (16)	8.8 ± 9.3 (5)	0.3 ± 0.4 (16)	0.3 ± 0.4 (16)
m 22	3.3 ± 3.5 (7)	12.3 ± 20.5 (9)	4.4 ± 1.7 (9)	1.1 ± 2.9 (21)	0.3 ± 0.7
m 36[2]	6.7 ± 4.2 (3)	14.5 ± 6.8 (8)	5.6 ± 4.7 (7)	1.2 ± 3.3 (17)	0.2 ± 0.5 (17)
m 51	10.3 ± 8.1 (7)	17.3 ± 26.4 (8)	7.3 ± 9.5 (8)	9 ± 15.1 (8)	1 ± 1.1 (8)
f 10	0 (24)	7.6 ± 5.3 (6)	10 ± 16.3 (6)	1.6 ± 3.9 (24)	0 (24)
f 33	1.9 ± 1.7 (5)	2.2 ± 2.8 (17)	3.7 ± 3.2 (15)	0.5 ± 1.2 (18)	0.3 ± 0.5 (18)
f 52	4.6 ± 3.7 (6)	2.1 ± 3.2 (15)	9 ± 11.8 (7)	1.8 ± 3.4 (16)	0.5 ± 0.9 (16)

(Table II); male no. 4 and female no. 10 spent most of their time of inactivity (male 4: 83 % of a total of 60 fixes; female 10: 88.3 % of 34 fixes) in two areas of 4×3 m and 4×2 m, namely their refuges.

The winter activity recorded was characterized by a relative paucity of direct insight observations (38 days out of 116, 29,1 % of total days; Table II), and by a marked inter- and intra-sexual variability, more evident in males. We found that studied specimens displayed a relatively constant surface activity during the observation period, under dead leaves, bushes, and in grass, except for male no. 4 and female no. 10, which were normally very inactive. We also found that activity, mainly characterized by short and long movements, was more concentrated in December and January (in male no. 51 also in February), while females were active generally for two months, with no constant pattern.

DISCUSSION

There are two main costs for winter snakes associated with basking or moving. One of these is being captured by visually oriented predators (Saint Girons, 1994), and the other is the increase in metabolic energy costs during a non-feeding period, namely weight loss (Duguy, 1963; Aleksiuk, 1976). Different hypotheses suggest that the presence of winter basking activity in snakes "allows a continuation of gonadal activity" (Jacob & Painter, 1980), and may also anticipate the time of mating (Shine, 1979). Unfortunately, no other published study on winter viperids (Duguy, 1963) has been carried out in a Mediterranean ambience. Nevertheless, the whole topic as is activity and reproductive biology, could be considered throughout the whole year: multiple comparisons between different habitats and seasons, and different latitude populations (Duguy, 1963; Bonnet & Naulleau, 1996), and/or different species, could contribute to the comprehension of variability patterns of life history traits of our and of other related taxa (Martin, 1993; Luiselli, 1995). Generally speaking, food availability, fat accumulation, body size and climate can directly influence reproductive success in some snake species (Madsen & Shine, 1992; Martin, 1993; Luiselli, 1995; Bonnet & Naulleau, 1996); latitude can also be the modulating factor of some biological traits of snake life (Sexton *et al.*, 1992), as probably is the case of present study. Our results indicate quite clearly that activity patterns of *Vipera aspis*, but also probably of some other snake species of this area, could be extended to winter periods (Naulleau, 1992). The observed winter activity in the years of the study, was almost certainly due to temperate winters and to a mild climate. Both recorded air and surface temperatures were greater than 10 °C when snakes were active, and lower than 10 °C when snakes were inactive, suggesting such a temperature as the thermal threshold for activity/inactivity in Asp Vipers (Duguy, 1963); nevertheless this temperature can not allow digestion activity, at least in *Vipera aspis* (Saint Girons, 1978; Naulleau, 1983). In other reptile and snake species, warm winter temperatures have been presumed to cause interruption of winter dormancy (Gregory, 1982). In these cases, winter dormancy is not surely dependent on metabolic depression, and species in which hibernation is triggered by exogenous factors, are called facultative hibernators. Winter aphagia is related to relatively low temperatures, even if they were high enough to allow moving activity (Gregory, 1982). Winter period usually produces relevant variations in adrenal gland activity: in these cases, adrenal activity and secretion of adrenalin directly reflect increased glycemia during hibernation (Agid *et al.*, 1961).

As preliminarly observed (Zuffi, unpubl.), most females from coastal populations probably anticipate their parturition time; both sexes also increased the frequency of foraging and feeding activity from about 10 to 12 months (M.A.L. Zuffi, pers. obs.), according to a southward latitudinal gradient (Gregory, 1982, and reference herein). Winter movement capacity was surely dependent on suitable thermal environments. Movement pattern seemed to have followed the model known for most snake species, that is much more active males than females (Naulleau *et al.*, 1996). Such pattern is usually typical of the reproductive phase, during which gravid females carry additional mass and must limit the capacity of speed endurance and long distance movement. Our observations in winter can exclude that female low mobility is due to the reproductive status, but low mobility could be interpreted as a general adaptive behaviour to avoid predator pressure. In addition, male longer movements could be related to active search for suitable basking spots. This behaviour has been referred, for other species, to continuation of gonadal activity (Jacob & Painter, 1980).

As pointed out by Duvall *et al.* (1993), the reproductive success of female snakes is helped by efficient foraging and feeding. We found that most of the females collected, from 1990 to 1996, had very high body condition index values, as found by Bonnet *et al.* (1994) and reproduced every year, as already been observed in most Australian Elapid snakes (Shine, 1979). On the overall, we presume that the long feeding period, and the continuation of activity during winter have probably contributed to the maintenance of annual reproductive frequency (Zuffi *et al.*, in press).

ACKNOWLEDGEMENTS

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