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LIFE HISTORY OF THE EUROPEAN PLETHODONTID SALAMANDER *SPELEOMANTES AMBROSII* (AMPHIBIA, CAUDATA)

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ABSTRACT

The biology of a *Speleomantes ambrosii* population inhabiting interstitial habitats was studied during two consecutive years in north-western Italy. Surface activity was highest in late spring and early fall and was positively correlated with monthly rainfall. The population structure was analysed on the basis of polymodal size frequency distributions. *S. ambrosii* demographic structure was composed of two juvenile size classes and a mixed component in which subadult and reproductive salamanders were present. Males became sexually mature when >50 mm and females when >58 mm SVL. Estimated age at first reproduction was 3.5 years for males and 5 years for females. Juvenile growth rates, during the first two years of life, ranged from 10 to 13 mm/yr.

INTRODUCTION

European plethodontid salamanders belong to the genus *Speleomantes* (Dubois, 1984) and are found from south-eastern France to central Italy and on the island of Sardinia (Thorn, 1969). To date, six species of *Speleomantes*, two continental and four insular, have been recognized on the basis of morphological and biochemical data (Lanza, Nascetti & Bullini, 1986). All European plethodontids are fully terrestrial; they lay egg clutches in humid rock crevices or in soil, and they have direct development (Stefani & Serra, 1966; Durand, 1967*a*,*b*).

The Northern Appennine species *Speleomantes ambrosii* (Lanza, 1955) ranges from the French Maritime Alps to eastern Liguria (NW Italy). This species is found in natural and artificial caves and in moist habitats along streams. Some aspects of the biology of this species are already known: thermoregulation (Cherchi, 1952), oviposition, embryogenesis (Durand, 1967*a*; 1967*b*) and diet (Morisi, 1981; Salvidio, 1992). On the other hand, many aspects of life history and population ecology are poorly documented.

The aim of this study was to elucidate the population structure, reproduction and growth rates of a *S. ambrosii* population inhabiting interstitial habitats along a NW Appennine stream.

MATERIALS AND METHODS

THE STUDY AREA

The study site was located in the Bisagno Valley near the village of Davagna, about 15 km NE of Genoa (central Liguria), north-western Italy, at an elevation of 380 m. *S. ambrosii* samples were collected on calcareous rock-faces, in the talus and beneath leaf litter along a 100 m section of a small tributary of the Bisagno river.

The dominant vegetation of the valley is sweet-chestnut woodland (*Castanea sativa*), and a hygrophilous vegetation (*Alnus glutinosa, Ostrya carpinifolia, Fraxinus ornus*) borders the streams. The vegetation cover is thick and the forest soil is moist and rich in organic materials (Montanari, 1988). The climate of the region is submediterranean with relatively high rainfall both in spring and autumn (total rainfall averages and often exceeds 1500 mm per year). The rainfall data utilised in this study were obtained from the pluviometrical station of Scoffera, 5 km north of the sampling area.

SAMPLING

Speleomantes ambrosii seasonal activity was studied from May 1988 to April 1989, except for November and February. A total of 41.5 hours were spent searching for salamanders in the study area, and a standardized index (number of salamanders/hour of search) was used to compare monthly activity patterns.

Monthly samples were collected (in May, October, December 1988 and in May and in October 1989) within 12 days, and were largely non-destructive (Bruce, 1988; 1989). Salamanders were held ventral side up against a transparent plastic ruler and body-size was measured, from the edge of the snout to the posterior end of the cloaca (SVL), to the nearest millimetre. A sample of 36 salamanders was dissected in the laboratory to determine reproductive status. In males the left testis and in females oocytes were counted and measured under a dissecting microscope. Mature males were recognized in the field as they possess a well-developed mental (= chin) gland, the site of production of courtship pheromones. In addition some gravid females were identified without dissection in October and December collections.

Because no egg clutches were found during the study, the time of hatching and body size of new born individuals were inferred from Durand's works (1967*a*; 1967*b*; 1973) on oviposition and embryogenesis of *S. ambrosii* in semi-natural conditions. Correspondence between age and body-size classes was estimated only for immatures, because in sexually mature plethodontids there is high overlap in body size between age classes (Houck & Francillon-Vieillot, 1988).

DATA ANALYSIS

Polymodal body-size distributions of corresponding periods were compared by means of Kolmogorov-Smirnov test for large samples (Sokal & Rohlf, 1981), to determine if the observed differences were statistically significant: then they were pooled and analysed using the maximum likelihood computer program MIX (Ichthus Data System). This method resolves mixed distributions providing estimates of proportions, means and standard errors of the different components present in the sample. It also evaluates the fit between the observed and theoretical distributions by a chi-square goodness of fit test (Macdonald & Pritcher, 1979; Bruce, 1988).

RESULTS

SEASONAL ACTIVITY

Monthly above-ground activity of the study population varied greatly over the year. Salamanders were most abundant during late spring and early autumn when temperatures were moderate and rainfall was abundant (Fig. 1). Activity decreased in winter when temperatures were low, and during summer when night temperature were >19°C and atmospheric humidity was <75%. Seasonal activity was positively correlated with monthly rainfall: Spearman's rank correlation coefficient r_s=0.66, n=10, P<0.05.

POPULATION STRUCTURE

The SVL distributions of 415 salamanders measured from May 1988 to October 1989 are shown in Fig. 2. The smallest individuals, ranging from 19 to 23 mm SVL, were observed in December. Since hatching begins in September (Durand, 1967*b*), this size class was undoubtedly composed of newborn individuals, about three months old.

May and October samples from successive years did not differ significantly (Kolmogorov-Smirnov D=0.190, P>0.05; and D=0.165, P>0.05 respectively). Thus, corresponding collections were pooled to obtain samples large enough to be analysed. Both spring and autumn SVL distributions were polymodal and were satisfactorily resolved into three normal

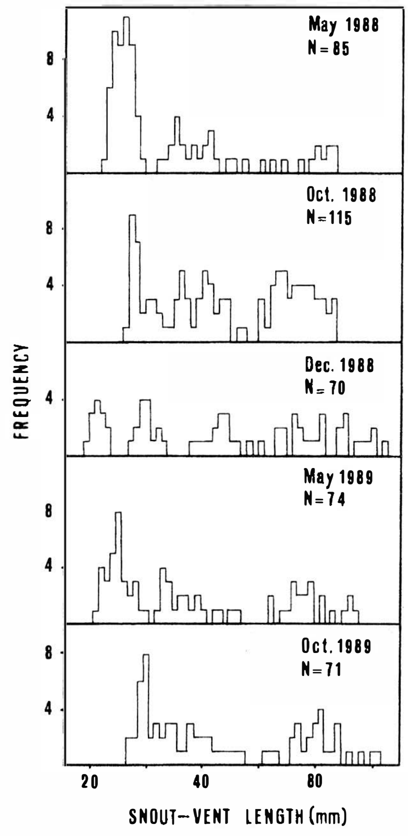

FIG. 2. Snout-vent length (SVL) distribution of 415 *Speleomantes ambrosii* sampled in May, October and December 1988 and May and October 1989.

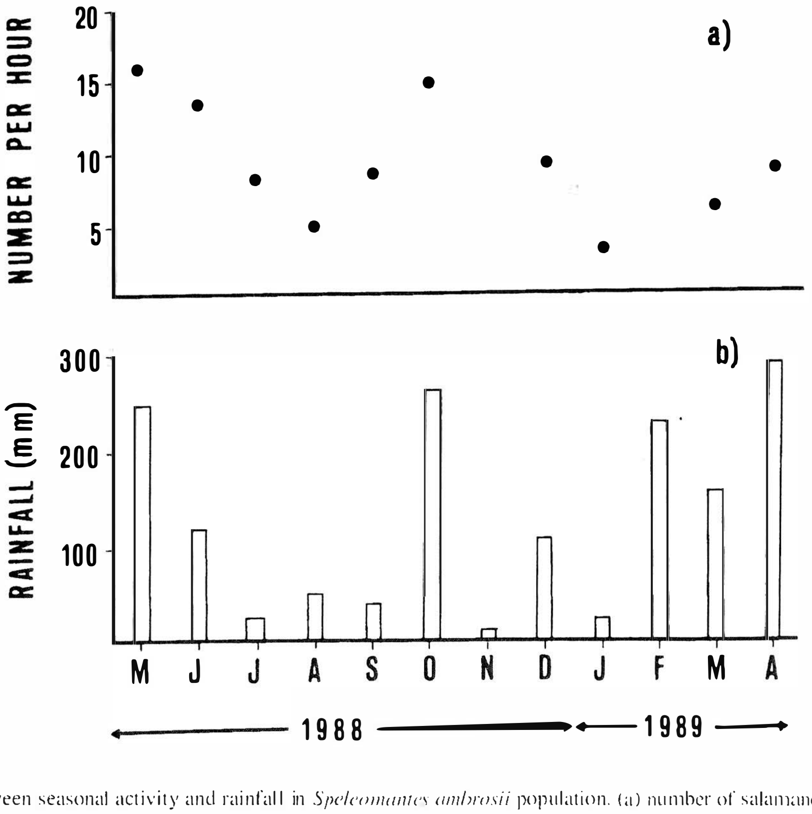

FIG. 1. Relationship between seasonal activity and rainfall in *Speleomantes ambrosii* population. (a) number of salamanders per hour of search. (b) monthly rainfall in mm.

		COMPONENTS									Goodness of fit		
		1			2			3					
Sample	n	%	$\bar{x}$	SE	%	$\bar{x}$	SE	%	$\bar{x}$	SE	χ^2	df	P
May	159	50.4	25.1	0.2	26.6	36.3	1.1	23.0	58.0	1.0	26.8	40	0.94
October	186	23.4	28.7	0.3	34.6	37.9	0.9	42.1	57.2	0.7	28.4	38	0.87

TABLE 1. Composition of May and October *Speleomantes ambrosii* pooled samples provided by the maximum likelihood routine program MIX (Ichthus Data System).

Life-history stage	May SVL	May growth increment	October SVL	October growth increment
hatchlings	-		16	
		-		+13
1 yr juveniles	25		29	
		+11		+9
2 yr juveniles	36		38	

TABLE 2. Mean snout-vent length (SVL) and body growth increments (in mm) of juvenile *Speleomantes ambrosii* life-history stages. SVL of hatchlings was obtained from Durand (1973).

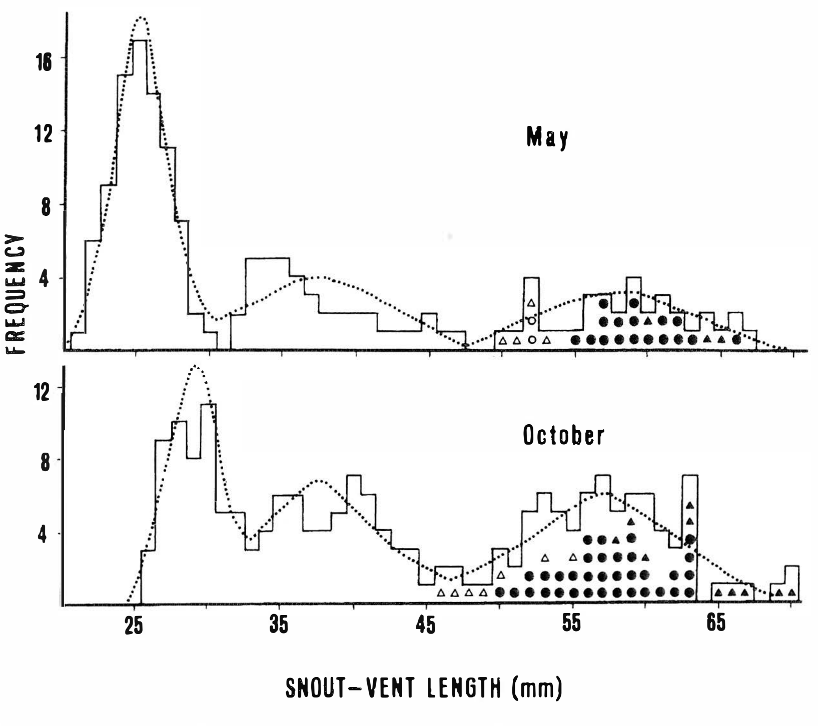

FIG. 3. Snout-vent length (SVL) distribution of May and October *Speleomantes ambrosii* cumulative samples. Open squares represent unsexable individuals, closed circles mature males, open circles immature males, closed triangles mature females, and open triangles immature females. The dotted curves represent theoretical distributions obtained by MIX computer routine program.

components by MIX computer program (Table 1). The analysis of dissected salamanders (see below) indicates that the two smallest body-size classes were composed of immature specimens. An additional subgroup of immature salamanders was included in the larger size class, together with breeding individuals (Fig. 3). In May, when mating occurs, this subsample was composed of subadults of both sexes while, in October, it was made up of subadult individuals in addition to some small mature males.

In autumn, when hatchlings are still underground, the smallest SVL class is about 1 year old, the intermediate juvenile class 2 yr, subadults 3 yr, and the larger mature individuals 4 yr or older.

BODY SIZE AT MATURITY

All dissected specimens smaller than 45 mm (n=10) had small undifferentiated gonads. The smallest male with a swollen mental gland (SVL = 50 mm) and the smallest dissected mature male (SVL = 52 mm) were measured in October. In dissected males (n=10), testes begin to enlarge as the mental gland becomes clearly evident, and the testicular volume was positively correlated with SVL (r=0.79, n=10, P<0.01).

All dissected females 46<SVL<57 mm (n=11) had small translucent follicles (0.2-0.6 mm in diameter) and therefore were not yet mature. In October, a gravid female of 58 mm SVL was measured in the field, and a reproductive female (SVL=59 mm) possessing maturing oocytes was dissected. The mean clutch size, estimated from the number of yolk-filled oocytes observed in mature females, was 13.80±2.05 (n=5, range 12-17).

In May, there were no gravid females, whereas they represented 48% of reproductive females in October (10 of 21) and 58% (7 of 12) in December.

SEXUAL DIMORPHISM

All individuals larger than 58 mm SVL and not possessing the mental gland were considered adult females. The average body length of reproductive females was 64 mm (range 58-72), while mature males average only 58 mm (range 50-67). Only females exceeded a body-length of 68 mm, and the largest individual ever caught was a gravid female (SVL=72 mm, total length *in vivo* = 116 mm). Student's t-test indicates that the observed differences in SVL between sexes were statistically significant in all sampled months (P<0.01 in all cases).

JUVENILE GROWTH RATES

Juvenile growth rates of *S. ambrosii* were estimated indirectly from the mean SVL of different size classes defined by MIX computer routine (see Table 1). Body size of new-born salamanders was obtained comparing their total length (24 mm) reported by Durand (1973) with the smallest individual measured in December collection (SVL= 19 mm, total length = 29 mm). Annual growth rates of juvenile SVL classes were estimated to vary from 13 to 10 mm during the first two years of life (Table 2).

DISCUSSION

Two peaks in seasonal activity were observed for the European plethodontid *S. ambrosii*. The first peak occurred during spring (May) when mating takes place, the second during autumn (October). The overall pattern in surface activity was related to monthly rainfall. During the study period, rainfall distribution was consistent with the general trend observed in the region over a 30 yr period (data from the Regional Meteorological Service, 1951-1981).

In the study population, body size frequency distributions were constant over two successive years. Thus, the population structure appeared stable and was suitable for a demographic and ecological study.

In plethodontid salamanders, estimates of age from size-frequency data for juvenile life-stages are accurate if there is no large overlap between size-classes (Houck, 1982; Bruce, 1990). *S. ambrosii* population structure was composed of two distinct juvenile age classes and a mixed component in which large juveniles and adult salamanders were present. In this latter group, an additional age class (subadults), not well defined by size, could be recognized on the basis of sexual immaturity. In autumn, the two small immature classes were made up by individuals aged about 1 and 2 yr respectively, and subadults were 3 yr old. Since breeding occurs during spring, males could be able to reproduce for the first time at an estimated age of 3.5 yr. On the other hand, females were about 8 mm larger than males at sexual maturity, and probably will be able to mate only a year later; thus they will likely deposit their first egg clutches, in winter at an age of 5. That females reproduce for the first time at a larger body-length and at an older age than males is a quite common pattern in plethodontids (Houck, 1982; Herrington & Larsen, 1987; Bruce, 1988, 1989; Ovaska & Gregory, 1989). This seems to be the case in the study *S. ambrosii* population, even if growth differences between males and females could contribute to some of the difference.

Breeding individuals were in their fourth year or older. Because of the wide overlap in SVL of successive age groups, it was impossible to detect discrete classes within the reproductive component. This superposition was probably due to lower adult growth rates and to higher variance in individual growth. In any case, it was impossible to estimate, even roughly, the average age and the oldest age reached by adult *S. ambrosii*.

Juvenile growth rates were estimated to vary from 10 to 13 mm/yr during the first two years of life after hatching. These values fall within the reported range (10-21 mm/yr) for temperate plethodontid salamanders, according to many authors (Houck 1982; Hairston, 1983; Semlitsch & West, 1983; Bruce, 1988, 1990).

This study showed that, apart from a relatively long period of embryonic development (Durand, 1967*b*), the *S. ambrosii* life-history pattern is comparable to those observed for Nearctic plethodontid salamanders that have direct development. Indeed, the population structure, size and age at sexual maturity and juvenile growth rates appear to be consistent with those characterising many new world temperate species.

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