Ital. J. Zool., 66: 45-49 (1999)

A montane amphibian and its feeding habits: *Salamandra lanzai* (Caudata, Salamandridae) in the Alps of northwestern Italy

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ABSTRACT

Feeding habits in a population of *Salamandra lanzai* were studied at an Alpine meadow at 2020 m a.s.l. in the Cottian Alps, NW Italy. Adult specimens underwent stomach flushing was applied to in June and September 1992, and in July 1993. *Salamandra lanzai* proved to be an opportunistic predator, feeding on invertebrates within a broad range of categories and sizes. Ground-dwelling insects (especially carabids) constituted the main part of the diet. Although *S. lanzai* is commonly believed to be a completely terrestrial species, some individuals were observed to feed on aquatic Trichoptera larvae. The utilization of prey taxa by number of specimens consumed and volume consumed varied seasonally. Mean ingested volume per salamander averaged 173.76 ± 449.31 mm^3, i.e., about 1.39% of the average salamander mass (12.56 ± 3.43 g; range 6.0-22.5 g). Prey mass and predator mass were positively correlated in males, which most likely are more active than females. The prey mass to predator mass ratio was not significantly correlated with log predator mass, neither for males nor for females.

KEY WORDS: *Salamandra lanzai* - Salamandridae - Stomach content - Diet - Ecology - Seasonal variation - High altitude.

ACKNOWLEDGEMENTS

We wish to thank all the people who helped us in the course of this research. In particular we acknowledge the useful suggestions given by C. Miaud, R. Guyetant, A. Riberon, and R. Sindaco. The capture and study of the salamanders was authorized by the "Regione Piemonte". R. A. Griffiths kindly revised an earlier draft of this paper, and gave useful suggestions. An anonymous referee made useful criticisms.

(Received 14 September 1998 - Accepted 20 October 1998)

INTRODUCTION

Among the European amphibians, the genus *Salamandra* includes two strictly montane species, *S. atra* Laurenti, 1768 and *S. lanzai* Nascetti, Andreone, Capula & Bullini, 1988. They have disjunct distributions: *S. atra* is widespread in the central-eastern Alps with some isolated areas in the Dinaric Alps, while *S. lanzai* is distributed within a narrow area of the French and Italian Cottian Alps (Andreone & Sindaco, 1989, Gasc *et al.*, 1997). Both these salamanders exhibit common characters, such as blackish colouration, terrestrial life and aplacentar viviparity.

Despite the biogeographic interest of *S. lanzai*, the existing information about its ecology is scanty, with the exception of some data on a French population (Riberon *et al.*, 1996) and on spatial preferences (Andreone *et al.*, 1996). During the years 1992 and 1993 field research was carried out to investigate some aspects of *S. lanzai* natural history. One of the most interesting traits is its feeding habits, since in most of the sites where *S. lanzai* occurs it is the most abundant terrestrial amphibian, and possibly also one of the most abundant vertebrates. The aim of this paper is therefore (1) to describe the trophic spectrum within this Italian *S. lanzai* population, (2) to analyse the changes in diet throughout its active life, and (3) to evaluate the differences in feeding habits between males and females.

MATERIALS AND METHODS

Study site and period

The research was carried out in the Upper Po Valley (Cuneo Province, NW Italy), at an altitude of about 2020 m a.s.l.. The habitat is the Alpine meadow typical of the Alps above the tree line. Large boulders are present within the area, thus creating a system of crevices which are utilized as refuges by salamanders. The territory is covered by snow from October-November to the end of April.

Taking into account the low vagility of salamanders (Riberon *et al.*, 1997; pers. observ.) the study was limited to an area of about 16000 m^2. Salamanders were studied over two years: 16 days in June 1992, 14 days in September 1992, and 9 days in July 1993. The study was not extended to August since in this month the pressure of tourism is very high (Andreone, 1992).

Capture, sexing, and niche analysis

Animals were searched for both by day and night on wet Alpine meadows, in crevices, under stones and in other refuges. In adult specimens, sex was determined by analysis of external secondary sexual characters. Males are characterized by the presence of small granulations along the vertebral column and have a prominent cloaca, while females are slightly longer than males and are also heavier and fatter. Gentle palpation of the belly was used to determine whether females were at the end of their pregnancy. The presence of developed embryos at this stage was confirmed by x-ray. Throughout the text, we refer to non-gravid females or to females with embryos in early stages of development as 'females', while gravid females at the end of gestation are named 'pregnant females'. The juveniles are smaller individuals (SVL < 60 mm) which do not exhibit external secondary sexual characters.

Specimens were anaesthetized by immersion in a 0.5% MS 222 Sandoz solution and individually marked by toe-clipping. Phalanges were later utilized for skeletochronology (Miaud *et al.*, 1997). Snout-vent length (SVL, at 0.1 mm) and mass (at 0.1 g) were also taken.

Stomach-flushing analysis was performed only on adults, since juveniles were rather small and delicate. This technique was derived from Legler & Sullivan (1979), and Salvidio (1992): a 10-ml syringe equipped with a plastic tube covering the needle (2 mm wide; length 60 mm) was utilized; the covered needle was gently inserted through the mouth and into the stomach, and about 5 ml of water was injected. The stomach contents were flushed out, stored in 70% ethanol, identified under a binocular microscope, and classified.

The linear dimensions of the intact items were measured to the nearest 0.1 mm. Fragments were counted when they allowed the determination of a precise number of prey. The volume of each item was then calculated using the cylinder formula $[2a(\pi b^2)]$ for Oligochaeta, Myriapoda, larvae of Insecta and Mollusca, and hemi-ellipsoid $[0.5(4\pi ab^2/3)]$ for Arachnida and metamorphosed Insecta. Prey usage is expressed as both the total number and total volume. When finished the anaesthesia effects the salamanders were immediately released in the same place of capture. A small number of salamanders was taken into captivity after stomach flushing to verify any possible negative effect. However, no ill-effects were apparent and specimens already analysed and later recaptured were all in good health. The trophic spectrum is given separately for males, non-pregnant, and pregnant females, while the niche analysis was carried out on males and females (non pregnant and pregnant females pooled together).

Trophic niche breadth and overlap was calculated on the basis of the volumes of the following invertebrate categories: Mollusca, Oligochaeta, Arachnida, Myriapoda and Insecta. Niche breadth was calculated as $B = 1/R \cdot \Sigma p_i^2$ (Levins, 1968), where p is the proportion of the prey i taken by the salamander, out of all the R prey types used; this index may range from 1/R (lowest breadth, only one resource used) to 1 (all resources used in equal proportions). Overlap in resources was calculated by Pianka's (1973) symmetrical index as $O_{xy} = \Sigma P_{ij} \cdot P_{ik} / \Sigma P_{ij}^2 \cdot \Sigma P_{ik}^2$, where O_{xy} is the index for the overlapping between the categories x and y, and P_{ij} and P_{ik} are the frequencies of utilization of the ith category by the jth and the kth categories. This index is symmetrical, meaning that the overlapping between the groups A and B is the same as that between B and A. Its range goes from 0 (no common utilisation of the resources) to 1 (complete overlapping).

RESULTS

Body size, diet composition, and trophic utilization

In the overall study period, 209 salamanders were marked by toe-clipping: 91 males, 88 females, 16 pregnant females, and 14 juveniles. Males had a SVL of 82.2 ± 5.4 mm, and females of 84.4 ± 7.3 mm. The percentage of pregnant females was stable throughout the study: 16.9% in June, 10.0% in July, and 16.0% in September; these values did not differ significantly (χ^2= 0.57; P > 0.05).

Stomach flushing was carried out on a total of 53 salamanders in June, 32 in July and 36 in September. The diet composition in males, non-pregnant females, and pregnant females is given in Figure 1. The percentage of animals that apparently contained empty guts in June, July, and September was 24.5%, 12.9% and 5.6%, respectively (Table I).

In total, 690 specimens of Insecta, representing 87% of the overall diet, were identified in the food of *S. lanzai*. Of these, 327 were adult Insecta, and constituted

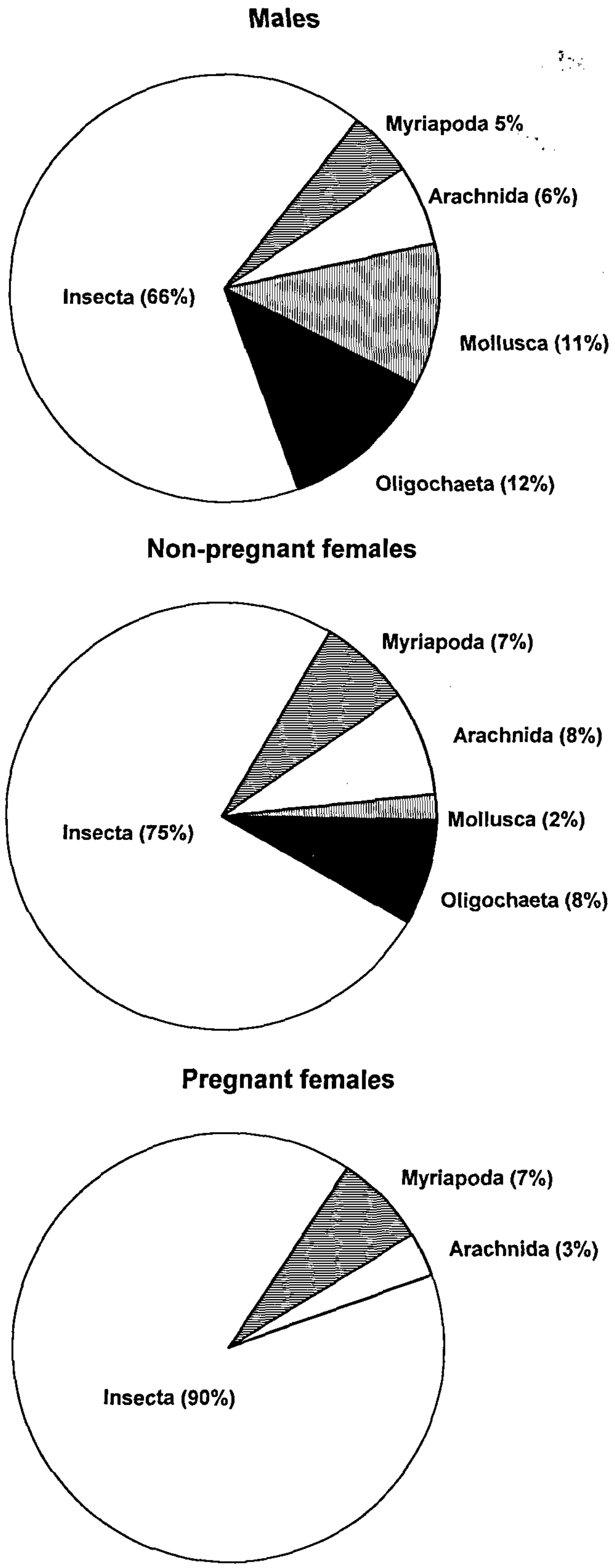

Fig. 1 - Numerical percentage of the prey items found by means of stomach flushing in *Salamandra lanzai* individuals from the Upper Po Valley, NW Italy; **A,** males (analysed food items, *n* = 336); **B,** non-pregnant females (*n* = 398); **C,** - pregnant females *n* = 62). Data for the three analysed periods (June, July, and September) have been pooled.

TABLE I - Salamandra lanzai *individuals collected in three periods and found with and without stomach contents.*

	with stomach content	without stomach contents
June		
Males	20	7
Females	18	3
Pregnant females	2	3
Total	40	13 (24.5%)
July		
Males	13	2
Females	13	1
Pregnant females	2	1
Total	28	4 (12.5%)
September		
Males	10	1
Females	20	1
Pregnant females	4	0
Total	34	2 (5.6%)
Overall total	102	19 (15.7%)

The percentage refers to the number of salamanders found without gut contents within each month compared to the total number found in that period (males, females and pregnant females pooled).

47% of the total intake. It must be pointed out that a large number of Insecta (245) were represented by larvae of Diptera, most likely predated by a few salamanders (8) from carrion. Excluding this 'anomalous' food (determined by the predation of only a few individuals), Insecta comprised 445 items with adults representing 73% of the diet. Coleoptera (in particular Carabidae) formed the bulk of the diet, constituting 30% of all the Insecta (adults and larvae) and 41.3% of the adult Insecta. Larvae of Lepidoptera were the most frequently predated larvae: 20% in June, 63% in September, and 13% in July in terms of numbers.

Volumes and numeric abundance of all the prey are shown in Table II. They comprise invertebrates only, with a large proportion consisting of arthropods (Insecta, Arachnida, Myriapoda), Mollusca, and Oligochaeta. Insects in different phases of their life cycle represented 87% of the diet (larvae = 54.3%; nymphs = 0.3%; adults = 45.4%). Adult Coleoptera were the most important prey in June, since they constituted 37.8% by number and 16.9% by volume. In July larvae of Diptera were the most abundant prey, being 73.3% (number), but Oligochaeta were the most important volumetric item (22.6%). Oligochaeta were only rarely found in the diet, although in volumetric terms their presence was consistent: in July, for instance, over a total of 323 prey items, only six were Oligochaeta: however they constituted 22.6% of the total volume of the stomach contents. After these two prey categories the next largest volumetric percentage in this study was larvae of Trichoptera (14.0%). In September the larvae of Lepidoptera constituted 24.3% by number and 48.6% by volume. The volumetric contribution of Orthoptera was important in September (14.5% of the total volume of prey, and 3.6% by number). The volumetric percentage of Araneae was steady during the three periods (with a minimum of 2.2% in July and a maximum of 4.4% in June). The other Arachnida were only rarely predated. Myriapoda (Diplopoda and a few Chilopoda) varied from 8.6% in June to 1.0% in July.

Predator-prey size relationship and niche

Adult males and non-pregnant females preyed upon the same groups (Fig. 1), and differences were significant (χ^2 = 30.77, df = 4, P < 0.01). Pregnant females did not feed on several groups: neither Oligochaeta nor Mollusca were found, the diet being based almost entirely (90%) on Insecta, with a lower contribution of Myriapoda (7%) and Arachnida (3%).

Mean ingested volume per salamander was 173.76 ± 449.31 mm^3 (range: 2.83-3718.96, n = 96), representing about 1.39% of the average salamander mass (12.56 ± 3.43 g; range: 6.0-22.5 g). The prey mass/predator mass percentage averaged 1.41 ± 3.54 (range: 0.04-23.83). In males there was a significant positive correlation between log prey volume and log predator mass (r = 0.435, adjusted r^2 = 0.169; n = 42, ANOVA: $F_{1,40}$ = 9.341, P = 0.004), while in females (including pregnant individuals) there was no relationship (r = 0.231, adjusted r^2 = 0.035; n = 54, ANOVA: $F_{1,52}$ = 2.920, P = 0.093). However, the mass of the total ingested preys: predator mass ratio was not significantly correlated with log predator mass, either in males (r = 0.122, adjusted r^2 = 0.000; n = 42, ANOVA: $F_{1,40}$ = 0.608, P = 0.440), or in females (r = 0.088, adjusted r^2 = 0.000; n = 54, ANOVA: $F_{1,52}$ = 0.407, P = 0.526). This is an indication that, with respect to smaller salamanders, larger ones did not tend to feed upon larger prey (relative to their own size), or to feed more, than smaller salamanders.

Values for trophic niche breadth decline from June to September, ranging from 0.315 to 0.094 and from 0.267 to 0.131 (males). Overall female niche breadth was lower than that of males (0.139 in females and 0.227 in males). Niche overlap was observed in the trophic niche between male and female niches: O_{xy} = 0.86 (June), 0.93 (July), and 0.99 (September).

DISCUSSION

Authors who previously studied the feeding habits of *S. salamandra* (e.g., Fachbach *et al.*, 1975; Lizana *et al.*, 1986) found considerable importance of Oligochaeta and Gastropoda in its diet. Luthard & Roth (1983) explained this preference as the attraction of salamanders towards the slow movements of these invertebrates. In the diet of *S. lanzai,* Oligochaeta were rather scarce,

TABLE II - *Numerical (N) and Volumetric (V) percentage of prey of* Salamandra lanzai *in June, July and September (in parentheses number of analysed specimens).*

	June (*n* = 40)		July (*n* = 28)		September (*n* = 34)		Total (*n* = 102)	
Prey	N (%)	V (%)	N (%)	V (%)	N (%)	V (%)	N (%)	V (%)
Mollusca	1.19	9.77	0.30	0.39	3.60	2.15	1.51	4.42
Oligochaeta	1.19	9.72	1.85	22.61	1.35	4.03	1.51	8.36
Araneae	4.38	5.26	2.16	7.94	3.15	6.37	3.14	6.22
Pseudoscorpiones	0.00	0.00	0.61	0.11	0.00	0.00	0.25	0.01
Opiliones	0.00	0.00	0.00	0.00	0.90	0.13	0.25	0.07
Acari	0.00	0.00	0.00	0.00	3.60	0.20	1.01	0.11
Chilopoda	0.79	0.53	0.00	0.00	4.50	2.78	1.51	1.68
Diplopoda	4.38	5.88	0.92	1.72	8.55	2.55	4.15	3.54
Coleoptera	37.84	16.98	8.97	11.05	4.95	0.61	16.96	7.37
Coleoptera (larvae)	0.79	0.11	0.00	0.00	1.80	1.08	0.75	0.62
Collembola	2.39	0.24	0.00	0.00	1.80	0.07	1.26	0.11
Diptera	3.58	3.44	1.85	2.24	7.20	1.38	3.89	2.17
Diptera (larvae)	0.79	0.15	73.68	15.42	2.25	0.86	30.78	2.56
Ephemeroptera	0.00	0.00	0.00	0.00	0.90	0.28	0.25	0.15
Hemiptera	25.49	8.89	0.62	0.03	9.45	8.06	10.93	7.28
Hemiptera (nymphs)	0.00	0.00	0.00	0.00	0.90	0.44	0.25	0.24
Hymenoptera	1.99	1.01	0.92	0.98	4.50	0.69	2.26	0.83
Lepidoptera (larvae)	5.17	8.93	1.54	8.52	24.32	48.59	9.05	30.31
Orthoptera	1.99	3.11	0.30	0.00	3.60	14.50	1.76	8.86
Plecoptera	0.00	0.00	1.54	10.21	0.00	0.00	0.63	1.35
Trichoptera	0.39	0.03	2.16	13.96	5.40	0.21	2.51	1.97
Indeterminate insect	5.17	8.15	0.92	4.03	4.05	2.38	3.14	4.50
Indeterminate larvae	2.39	17.71	1.54	0.73	3.15	2.53	2.26	7.27
Total	251	8920	323	3601	222	14684	796	27205

Total and monthly frequencies are shown by number and volume (in mm^3).

most likely due to their rarity at high altitudes or to their scarce epigean activity in this Alpine environment, and were found only in male guts. As males seem to be more active than females (Andreone, 1992) it is likely that their food intake is wider. The scarcity of these prey is also in agreement with data provided by Guerrero *et al.* (1990) in a study on the feeding habits of a montane subspecies of fire salamander, *S. salamandra almanzoris*: in this case too, the diet was mainly based on Coleoptera, Diptera, and on Insecta larvae.

In general, *S. lanzai* feeds on hard-bodied invertebrates, such as beetles, which are likely to be more abundant and encountered more often in the montane habitat where this population was studied. On the other hand, as stated by Griffiths (1986), for a study of the diet of *Triturus helveticus* and *T. vulgaris*, an assumption underlying this type of food analysis is that the rate of digestion is the same for all prey categories. It is possible that some invertebrates were digested much more quickly than those with chitinous exoskeletons, such as beetles and other adult insects. This may be another or a complementary explanation why some groups, such as Oligochaeta and Mollusca are so rare in the stomach contents of *S. lanzai.*

Being totally terrestrial and not dependent on free-standing water for reproduction, *S. lanzai* was expected to feed only on terrestrial prey. It is thus interesting that aquatic larvae of Trichoptera were present in the gut contents of salamanders, and that in July they represented 14% of the overall analysed prey volume. In fact in this month several salamanders were sometimes found half submerged in the small streams which cross the studied area. Possibly, salamanders moved closer to the water to thermoregulate during a period of high temperature and strong winds, and there they were attracted to water by the movements of Trichoptera larvae. This observation stresses the opportunistic nature of the feeding habits of *S. lanzai.*

A significant relationship between the size of the salamanders and that of the ingested food was observed in males: larger males tend to eat larger prey (for example, Orthoptera were ingested only by males with SVL > 8.5 cm). This relationship is not significant in females (either pregnant or non-pregnant), which may be explained by the fact that males are more active and may choose prey suitable for their size, while females, being less active, prey mainly on available invertebrates. In males, however, the visual cues may be more important in predation (and thus determine the size relationships), while females may depend more on olfactory cues and therefore the size of prey is not relevant.

Although the number of analysed pregnant females, was rather low, the absence of some invertebrate categories in their diet and the consequent larger percentage of Arachnida (2.91%) and Myriapoda (6.61%) might be interpreted in terms of habitat preferences, since pregnant females were found more frequently under rocks and in other refuges (Andreone *et al.*, 1996). The percentages of hidden salamanders were as follows: 26.1% pregnant females, 17.3% non-pregnant females, 8.3% males. Most likely, Arachnida and Myriapoda are more abundant under stones and may therefore constitute the main food item, while Mollusca and Oligochaeta are groups more easily found in open areas.

The analysis of niche breadth showed a general decrease from June to September, higher values in June indicating a more diverse diet. It is interesting to point out that in this month the number of salamanders found in refuges was also high (43 in June, as opposed to 16 in July, and seven in September). Since utilization of refuges may result in the increase in some taxa in the diet, in this month, the diet appeared more varied. In July, the below-surface activity of salamanders increased, mostly in relation to the climate which forced them into humid retreats. Moreover, it is likely that females which had already given birth became more active within the relatively homogeneous habitat of the Alpine meadows, where invertebrate diversity was lower, and the salamander trophic niche breadth decreased.

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