Trophic niche of cave populations of *Speleomantes italicus*

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**Abstract**

This paper investigates the trophic niche of a poorly studied cave salamander, *Speleomantes italicus*. We examined Central Appennine hypogean populations that inhabit seven caves situated in three limestone areas in Umbria Region (Italy). Adults displayed feeding activity from May to December and the Vacuity Index analysis revealed a discontinuous trophic activity pattern throughout the year related to prey phenology. According to the qualitative analysis of the trophic spectrum, the populations in question can be defined as euryphagous, while the quantitative analysis (in terms of number and volume of preyed taxa) revealed a specialist strategy with a clear preference towards Diptera Limnobiidae. Both sexes presented similar trophic niche breadth and a high diet overlap, showing no intersexual differences. The hypogean populations of *S. italicus*, similarly to *S. strinatii*, showed a narrower trophic niche than epigeans of the same species, probably due to the limited food availability in the cave habitat.

**Keywords:** Central Italy, Amphibia Salamander, Speleomantes italicus, trophic niche

**Introduction**

*Speleomantes italicus* (Dunn, 1923) is a member of a plethodontid genus endemic to northern Italy and southern France (three species), and to Sardinia (four species) (Lanza et al. 1995). All other plethodontids occur in North, Central, and South America (Frost 2004), except for a recently described species from Korea (Min et al. 2005). The distribution of this family represents one of the most interesting examples of fragmented ranges (e.g. Wake et al. 1978). European Tertiary and Quaternary fossils were discovered in SE France, Italy, and Sardinia (Delfino et al. 2005), and recently in Slovakia (Venczel and Sanchiz 2005). *S. italicus* is a monotypic species (the previous subspecies *gormani* Lanza, 1952 is a synonym), distributed from the Provinces of Reggio Emilia and Lucca southwards to the southeastern slope of the Gran Sasso Massif (Lanza et al. 1995, 2006; Scalera et al. forthcoming). It is a eurizonal species, distributed from 80 to 1600 m a.s.l., inhabiting clefts in mesic and hygrophilic habitats, though often colonizing caves and artificial cavities (Lanza et al. 2006). Only sparse information is available regarding the
ecology and ethology of this species (Casali et al. 2005; Pastorelli et al. 2005), as well as for other species in the genus.

As far as the trophic niche of the Italian species is concerned, data on epigean and hypogean populations of S. strinatii (Aellen, 1958) have been published by Morisi (1981, quoted as italicus: study of faeces), by Salvidio (1990, 1992, 1996, quoted as ambrosii: examination of stomach contents from both dissected and flushed animals), and by Salvidio et al. (1994, quoted as ambrosii: examination of stomach contents). Lanza (1947) and Bruno (1973) cited qualitative data about ingesta, respectively, of epigean and hypogean Tuscan populations of S. italicus (both as subspecies gormani Lanza, 1952). No data at all exist for any Sardinian species. Cimmaruta et al. (1999) and Oneto and Salvidio (2005) studied the potential prey availability in epigean and hypogean populations of S. strinatii and S. ambrosii. The aim of this paper is to examine the trophic niche of S. italicus and to compare it with that of S. strinatii.

Study area
The research was carried out on Central Appennine hypogean populations of S. italicus, in three limestone zones belonging to a homogeneous geomorphological unit (the “Central Umbrian Valley”; see Martelli 1994 for a geological outline of this area): (a) the Monte Cucco Regional Park (near Costacciaro and Scheggia, Perugia Province—PG, Umbria Region—U) on Monte Cucco itself, which extends for about 20 km along the boundary between the Umbria and Marche Regions (maximum elevation 1566 m a.s.l.) (Cava di Valdorbia, 600 m a.s.l.; Cava Motette, 540 m a.s.l.; Grotta Ferrata 406 U/PG, 1010 m a.s.l.; Grotta del Fricchettone di Montagna 446 U/PG, 1010 m a.s.l.; Buca di Faggeto Tondo 400 U/PG, 1200 m a.s.l.; Buca del Ferro 24 U/PG, 1370 U/PG; Buca della Sorgente 348 U/PG, 1385 m a.s.l.); (b) at the base of Monte Ingino near Gubbio in the same province and region (Grotta del Diavolo a M. Ingino 150 U/PG, 645 m a.s.l.; Grotta Preistorica 126 U/PG, 630 m a.s.l.); (c) on the western slope of Monte Nerone Massif (near Cagli, Pesaro and Urbino province—PU, Marche Region—MA) (Grotta delle Nottole 44 MA/PU, 700 m a.s.l.). The climate is subcontinental-temperate at the valley bottom and subcontinental in the mountain areas. Annual average temperatures vary from 6 to 11°C (Menichetti 1987) and rainfall from 900 to 1440 (1900 at high altitudes) mm per year.

Eight caves were studied, five of them situated on Monte Cucco, two on Monte Ingino, and one on Monte Nerone; three additional artificial cavities were examined in the Monte Cucco Regional Park.

Material and methods
Caves were sampled monthly from November 2003 to December 2004 except when adverse weather conditions occurred. Within the caves, salamanders were sampled (authorization from the Italian Ministry for the Environment, DPN/2D/2006/10441) by Visual Encounter Surveys (VES) (Heyer et al. 1994) and caught by hand, then sexed, weighed, and measured (from the end of the snout to the posterior end of the cloaca) with an electronic balance (0.01 g) and an electronic calliper (0.01 mm). These biometric features will be used in a further study on population dynamics (F. Caldera et al., unpublished); individual weight is here compared with prey size. Digital photos were taken of the dorsal and ventral colour patterns of salamanders to allow individual identification
(Heyer et al. 1994; Salvidio et al. 1994). Individuals smaller than the smallest captured male with evident mental gland (typical of reproductive males) were considered juveniles, because this sexual dimorphic hedonic gland is used by plethodontids during courtship (Lanza 1959).

The Vacuity Index—the ratio between the number of empty stomachs and the total number of analysed stomachs—was calculated monthly for both sexes. Adults, immediately after capture, were subjected to the non-destructive and harmless procedure of stomach flushing (Fraser 1976; Legler and Sullivan 1979) previously used for Speleomantes ambrosii (Salvidio 1992), by means of a 20 ml syringe filled with water joined with a silicon catheter (1.5 mm diameter). They were then released in the same location where they were captured. The flushing procedure was repeated until no further prey items were ejected. Data from recaptured specimens were not considered in the analysis. The stomach contents were preserved in ethanol (70%). Juveniles, more vulnerable than adults (Salvidio 1992), were not subjected to flushing, to avoid any harm. No mortality was observed during or after stomach flushing and recaptured specimens showed normal feeding activity. Food items were recognized using a stereomicroscope and identified at the class level for some groups (non-parasitic Nematoda, Gastropoda, Oligochaeta, Copepoda, Chilopoda, and Diplopoda), or at the order level for the remaining prey, except the most common Diptera and Hymenoptera, which were determined at family level.

Food items were photographed using a stereomicroscope with a digital camera and analysed by IMAGE TOOL software (UTHCSA 3.00 version 2002), measuring the total length and the width. Most of the adult prey volumes were calculated with the spheroid volumetric formula: \[ V = \frac{4}{3}\pi \left( \frac{\text{length}}{2} \right) \left( \frac{\text{width}}{2} \right)^2 \] (Dunhan 1983); the volume of Nematoda, Oligochaeta, Pseudoscorpiones, Chilopoda, Diplopoda, and larvae of Hexapoda was calculated from the formula for a cylinder \[ V = \text{length} \left( \frac{\text{width}}{2} \right)^2 \pi \]. Following Hyslop (1980), both numerical and volumetric data were used to assess the trophic niche. Cumulative curves of food items of males and females were constructed and showed that data collected with the stomach-flushing technique were representative of the trophic spectrum. The trophic strategy of cave salamanders was determined for both sexes using Costello’s (1990) graphic visualization modified by Amundsen et al. (1996). This graphic technique relates the prey-specific abundance to the frequency of occurrence. The distribution of the food items in the plot is related to three directrices, allowing three aspects of the trophic niche to be assessed: (1) alimentary strategy (specialization versus generalization—the vertical axis represents predator strategy going from generalist to specialist); (2) prey importance (dominant versus rare—first diagonal axis (/) represents abundance increase along with prey importance); (3) niche breadth (high diversity among individuals versus high diversity within an individual and tendency towards the same resource use—second diagonal axis (\)) represents resource use changing from BPC (Between Phenotype Component, among individuals of population) to WPC (Within Phenotype Component—tending towards the same resource use) (Amundsen et al. 1996). In Costello’s graphic visualization, the prey specific abundance \( P_i \) is plotted against the frequency of occurrence:

\[
P_i = \left( \frac{\sum S_i}{\sum S_n} \right) \times 100,
\]

where \( P_i \) is the prey-specific abundance expressed in numeric and volumetric data; \( S_i \) is the abundance of the prey \( i \) in the stomachs and \( S_n \) is the total abundance of prey in the stomach of those specimens that contain the prey \( i \). Mann–Whitney \( U \) test was applied to
the volumes of all the prey for both sexes, in order to evaluate differences of volume prey selection in the diet of both males and females.

To compare our results to those in the literature on cave salamander species, both Schoener (1968) (C) (2) and Pianka (1973) (O) (3) Indices were applied to analyse the degree of overlap of the trophic niche in both sexes.

\[
G = 1 - 0.5 \left( \sum_i |p_{xi} - p_{yi}| \right)
\]

\[
O_{xy} = \frac{\sum_{i=1}^{n} p_{xi}p_{yi}}{\left( \sum_{i=1}^{n} p_{xi}^2 \sum_{i=1}^{n} p_{yi}^2 \right)^{1/2}},
\]

where \(p_{xi}\) is the proportional utilization of prey \(i\) by form \(x\) and \(p_{yi}\) is the proportional utilization of prey \(i\) by form \(y\). Both indices range from 0 (no prey in common in diet spectrum) to 1 (same diet spectrum).

Because of limitations of niche overlap indices for arbitrary cutoffs (Feinsinger et al. 1981), we also compared the observed overlap values to an appropriate null model. The distribution of the null model was created by using Ecosim software (version 7.68) (Gotelli and Entsminger 2001) elaborating two simulations with 1000 randomized replications of the data set. The simulations were generated using two randomization algorithms, the RA2 (Niche breadth relaxed/Zero States retained) and the RA3 (the “scrambled-zeros” randomization algorithm proposed by Winemiller and Pianka 1990). Statistical significance was determined by comparing the observed overlap value to the null distribution; an observed value greater than 95% of the simulated values indicates significant overlap at the <0.05 level (Winemiller and Pianka 1990).

The Levins (1968) Index (4) and its standardized variant (5) (Hurlbert 1978) were utilized to calculate the width of the trophic niche:

\[
B = \frac{1}{\left( \sum_{i} p_{ji}^2 \right)}
\]

\[
B_A = \frac{(B-1)}{(n-1)},
\]

where \(p_{ji}\) is the proportion of use of the trophic niche by \(j\) sex that consists in the \(i\) trophic resource; \(n\) is the total number of trophic categories. \(B\) minimum value is 1, when the species utilizes a unique resource and it increases with number of types of utilized resource. When the resources are equally utilized \(B\) is maximum. \(B_A\) ranges between 0 and 1.

**Results**

A total of 129 adult specimens (65 males and 64 females) was examined; no adults were found in January, February, and March. In the examined caves, the first feeding activity was recorded in May and ended in December, although only a few specimens were observed in the last mentioned. Monthly and total Vacuity Index (VI) of adults (both sexes), with number of specimens examined, are reported in Table I. The total VI of males
Table I. Vacuity Index in all caves and number of flushed individuals (n).

| Month | January | February | March | April | May | June | July | August | September | October | November | December | Whole year |
|-------|---------|----------|-------|-------|-----|------|------|--------|-----------|---------|----------|----------|------------|
| Adults| VI      | –        | –     | –     | 1.00| 0.75 | 0.48 | 0.42   | 0.25      | 0.57    | 0.28     | 0.20     | 0.50       | 0.47      |
| n     | 0       | 0        | 0     | 2     | 12  | 25   | 19   | 8      | 28        | 18      | 10       | 4        | 129        |
| Males | VI      | –        | –     | –     | 0.71| 0.38 | 0.67 | 0.50   | 0.50      | 0.38    | 0.14     | 0.67     | 0.48       |
| n     | 0       | 0        | 0     | 0     | 7   | 13   | 9    | 4      | 14        | 8       | 7        | 3        | 65         |
| Females| VI    | –        | –     | –     | 1.00| 0.80 | 0.58 | 0.20   | 0.00      | 0.64    | 0.20     | 0.33     | 0.00       | 0.47      |
| n     | 0       | 0        | 0     | 2     | 5   | 12   | 10   | 4      | 14        | 10      | 3        | 1        | 64         |
was very similar to that of females (0.48 and 0.47, respectively) and the average annual values of both sexes showed no statistically significant differences (mean VI<sub>males</sub>=0.494, SD=0.193; mean VI<sub>females</sub>=0.417, SD=0.356; t=0.545; df=15; P=0.594; t test). An analysis made on the caves in which at least five specimens of <i>S. italicus</i> were found showed no correlation between the VI of each cave and its altitude (r<sub>Spearman</sub>=−0.27, n=9; P=0.471).

The analysis of stomach contents revealed the presence of 464 prey belonging to 25 food categories (Table II). Costello’s graphic visualization showed similar feeding strategies for males and females. Diptera Limnobiidae were the dominant prey for both sexes and most of the remaining food categories represented a marginal fraction of the diet spectrum (see Figure 1); males then preyed on Isopoda to a much lesser extent, while females preyed on other adult Diptera (though neither Limnobiidae nor Sciaridae). As concerns trophic resources, Limnobiidae apart, females were slightly more generalist than males. The analysis of numeric and volumetric data for both sexes showed a tendency towards a pattern characterized by a high diet diversity among individuals. The volume of the prey items in males (VM) and females (VF), although greater in the latter, did not differ significantly (mean VM<sub>191</sub>=6.74 mm<sup>3</sup>, SD=7.63; mean VF<sub>273</sub>=9.39 mm<sup>3</sup>, SD=18.99; U=25631; P=0.7566; Mann–Whitney U test). A positive correlation between adult body mass and volume of prey was observed (r<sub>Spearman</sub>=0.298; n=55; P<0.05), though no correlation was found between weight and number of prey or food categories per stomach. No differences were found between sexes.

The observed diet overlaps were relatively wide using the Pianka (O) and Schoener (C) Indices and gave higher values considering numeric rather than volumetric data (O<sub>num</sub>=0.857, O<sub>vol</sub>=0.8; C<sub>num</sub>=0.692, C<sub>vol</sub>=0.595). The observed overlaps evaluated with the Pianka Index based on numeric and volumetric data resulted in statistically significant differences (P<0.05). Both sexes showed a similar trophic niche breadth using numeric data; volumetric analysis showed an overall niche slightly wider in females than in males (males: B<sub>Anum</sub>=0.22, B<sub>Avol</sub>=0.125; females: B<sub>Anum</sub>=0.26, B<sub>Avol</sub>=0.29).

**Discussion**

Our study of the trophic niche of the hypogean adults of <i>Speleomantes italicus</i> confirms the euryphagy of this species, as previously shown in the literature, but only in terms of the number of prey taxa (Lanza 1947; Bruno 1973). The *ingesta* cited by Bruno seem to represent only the list of some cave-dwelling invertebrate species of the Tuscan Apennine caves and are not assessable to analyse the trophic niche. The composition of the diet includes more trophic categories than those observed in other studies on both hypogean and epigean populations of <i>S. strinatii</i> (Salvidio 1992). A wide trophic spectrum has been observed for epigean cave salamander populations of both <i>S. italicus</i> and <i>S. strinatii</i> (Lanza 1947; Salvaidio 1990, 1992; Salvaidio et al. 1994). Adults of the hypogean populations showed a variable trophic strategy in <i>S. strinatii</i> (Morisi 1981; Salvadiio et al. 1994), which presented a high tendency to forage outside the cave as well; in <i>S. italicus</i> (present research) prey items represent both troglophilic and trogloxene species that were observed living in the cave. The hypogean populations of both <i>S. strinatii</i> and <i>S. italicus</i> showed a narrower trophic niche than epigean populations. This different pattern of trophic strategy could be due to limited food availability in cave habitats (Salvidio et al. 1994).

A quantitative analysis of the food items revealed a specialist strategy in the studied populations of <i>S. italicus</i>. In both sexes, Diptera Limnobiidae were the dominant prey
Table II. Total prey items recorded from stomach contents analysis in adults, males and females of *Speleomantes italicus*.

|          | Adults |          |          |          | Males |          |          |          | Females |          |          |          |
|----------|--------|----------|----------|----------|-------|----------|----------|----------|---------|----------|----------|----------|
|          | Proportion of N | Frequency | Volume (mm³) | Proportion of volume | Proportion of N | Frequency | Volume (mm³) | Proportion of volume | Proportion of N | Frequency | Volume (mm³) | Proportion of volume |
| Nematoda | 1      | 0.0022   | 0.015    | 0.28     | 0.0001 | 1        | 0.0052   | 0.029    | 0.28     | 0.0002 | –         | –         | –         |
| Gastropoda | 3     | 0.0065   | 0.04451  | 84.59    | 0.022  | 3        | 0.0157   | 0.088    | 84.59    | 0.0656 | –         | –         | –         |
| Oligochaeta | 2    | 0.0043   | 0.015    | 44.23    | 0.0115 | 2        | 0.0105   | 0.029    | 44.23    | 0.0343 | –         | –         | –         |
| Acari     | 13     | 0.0280   | 0.103    | 1.66     | 0.0004 | 5        | 0.0262   | 0.088    | 0.2      | 0.0002 | 8         | 0.029    | 0.118     |
| Araneae   | 34     | 0.0733   | 0.265    | 371.92   | 0.0965 | 14       | 0.0733   | 0.265    | 56.88    | 0.0441 | 20        | 0.073    | 0.265     |
| Opiliones | 1     | 0.0022   | 0.015    | 2.33     | 0.0006 | 1        | 0.0052   | 0.029    | 2.33     | 0.0018 | –         | –         | –         |
| Pseudoscorpiones | 11 | 0.0237 | 0.118    | 13.6     | 0.0035 | 1        | 0.0052   | 0.029    | 1.3      | 0.0010 | 10        | 0.036    | 0.206     |
| Copepoda  | 2      | 0.0043   | 0.015    | 1.34     | 0.0003 | 2        | 0.0105   | 0.029    | 1.34     | 0.0010 | –         | –         | –         |
| Amphipoda | 8      | 0.0172   | 0.044    | 131.6    | 0.0342 | –        | –        | –        | –        | –       | 8         | 0.029    | 0.088     |
| Isopoda   | 52     | 0.1121   | 0.294    | 567.11   | 0.1472 | 28       | 0.1466   | 0.294    | 189.7    | 0.1472 | 24        | 0.088    | 0.294     |
| Chilopoda | 2      | 0.0043   | 0.029    | 16.09    | 0.0042 | 1        | 0.0052   | 0.029    | 2.1      | 0.0016 | 1         | 0.004    | 0.029     |
| Diplopoda | 11     | 0.0237   | 0.103    | 68.81    | 0.0179 | 9        | 0.0471   | 0.147    | 41.4     | 0.0321 | 2         | 0.007    | 0.059     |
| Collembola | 20   | 0.0431   | 0.132    | 12.25    | 0.0032 | 9        | 0.0471   | 0.118    | 2.33     | 0.0018 | 11        | 0.04     | 0.147     |
| Coleoptera (adults) | 15 | 0.0323 | 0.147    | 176.7    | 0.0459 | 5        | 0.0262   | 0.118    | 63.9     | 0.0496 | 10        | 0.036    | 0.176     |
| Coleoptera (larvae) | 9  | 0.0194  | 0.059    | 158.65   | 0.0412 | 2        | 0.0105   | 0.059    | 28.56    | 0.0222 | 7         | 0.026    | 0.059     |
| Diptera (adults) | 84 | 0.1810 | 0.25     | 215.44   | 0.0559 | 18       | 0.0942   | 0.176    | 71.07    | 0.0551 | 66        | 0.242    | 0.323     |
| Diptera (larvae) | 9   | 0.0194  | 0.049    | 46.23    | 0.012  | –        | –        | –        | –       | –       | 9         | 0.033    | 0.059     |
| Diptera | 126     | 0.2716   | 0.5      | 1185.53  | 0.3077 | 63       | 0.3298   | 0.471    | 592.77   | 0.4599 | 63        | 0.231    | 0.529     |
| Limnobiidae |          |          |          |          |        |          |          |          |          |         |          |          |          |
| Diptera Sciariidae | 24 | 0.0517 | 0.235    | 98.25    | 0.0255 | 14       | 0.0733   | 0.206    | 54.39    | 0.0422 | 10        | 0.037    | 0.265     |
| Hymenoptera | 10   | 0.0216   | 0.103    | 10.36    | 0.0027 | 2        | 0.0105   | 0.059    | 1.49     | 0.0012 | 8         | 0.029    | 0.147     |
| Hymenoptera | 10    | 0.0216   | 0.147    | 38.49    | 0.01    | 6        | 0.0314   | 0.176    | 9.7      | 0.0075 | 4         | 0.015    | 0.118     |
| Formicidae |          |          |          |          |        |          |          |          |          |         |          |          |          |
| Homoptera | 7       | 0.0151   | 0.044    | 25.12    | 0.0065 | 2        | 0.0105   | 0.059    | 7.26     | 0.0056 | 5         | 0.018    | 0.029     |
| Lepidoptera (larvae) | 4 | 0.0086  | 0.059    | 319.18   | 0.0828 | 1        | 0.0052   | 0.029    | 2        | 0.0016 | 3         | 0.011    | 0.088     |
| Orthoptera | 3      | 0.0065   | 0.044    | 38.73    | 0.0101 | 2        | 0.0105   | 0.059    | 30.98    | 0.0240 | 1         | 0.004    | 0.029     |
| Trichoptera | 3     | 0.0065   | 0.044    | 224.41   | 0.0582 | –        | –        | –        | –       | –       | 3         | 0.012    | 0.088     |
| Total     | 464     | 3853     | 191      | 1288.82  | 273    | 2564.18  |          |          |          |         |          |          |          |

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category, similar to a Northern Apennine hypogean population of *S. strinatii* (Salvidio et al. 1994), though different from another subalpine cave population of this species (Morisi 1981) that feed predominantly outside the cave and display a more generalist strategy. During spring and summer, Diptera Limnobiidae aggregate on the cave walls, forming a rich and easily located trophic resource for cave salamanders. Sampled hypogean adults of *S. italicus* showed trophic activity from May although some specimens were recorded in activity in caves from April. Even if some food categories used by the examined population

Figure 1. Graphic representation of the diet strategy of the *Speleomantes italicus* studied population. Numeric and volumetric data are represented by solid and empty circles, respectively. The position of the prey taxa is interpreted considering three directrices in the plot: from top to bottom is the alimentary strategy (specialization versus generalization); the first diagonal (/) represents prey importance (dominant versus rare); on the second diagonal axis (\) niche breadth is displayed (high diversity among individuals versus high diversity within individual and tendency towards the same resource use). Some food categories with low values of Pi and frequency of occurrence are not labelled. ACA, Acari; AMP, Amphipoda; ARA, Araneae; CAD, Coleoptera (adults); CLA, Coleoptera (larvae); COL, Collembola; COP, Copepoda; DAD, other Diptera (adults); DIP, Diplopoda; DLA, Diptera (larvae); DLM, Diptera Limnobiidae; DSC, Diptera Sciaridae; GAS, Gastropoda; HFR, Hymenoptera Formicidae; HOM, Homoptera; HYM, Hymenoptera; ISO, Isopoda; LLA, Lepidoptera (larvae); NEM, Nematoda; OLI, Oligochaeta; ORT, Orthoptera; TRI, Trichoptera.
(Aranea and Isopoda) are available throughout the year, adult activity in the caves followed
Diptera phenology, as reported by Oneto and Salvidio (2005) for S. strinatii. The total
Vacuity Index did not differ between males and females, evidence of a similar rate of
alimentation.

The analysis of the trophic spectrum of adults showed a width overlap between males
and females, from both the numeric and volumetric analyses. As in other plethodontids,
particularly in the tribe Bolitoglossini (Salvidio and Bruce 2006), females of S. italicus are
significantly larger and heavier than males (F. Caldera et al., unpublished), and this
intersexual difference could be explained by the females selecting slightly larger prey than
those of males. Further, the trophic niche breadth on a volumetric basis is wider in females
than in males. This could be due to the need, for females, to feed on larger prey to sustain
the energetic effort of producing and caring for the eggs.

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