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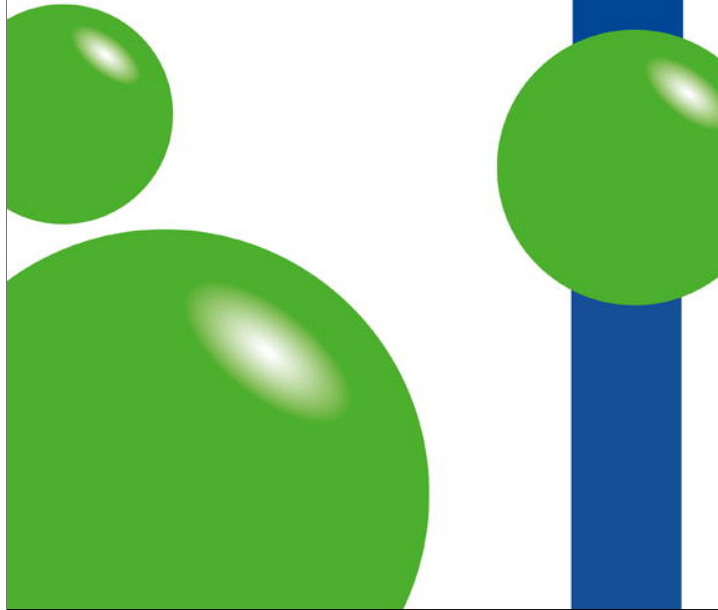# Acta Oecologica

Original article

Different season, different strategies: Feeding ecology of two syntopic forest-dwelling salamanders

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ABSTRACT

Trophic niche may be the most important ecological dimension for some vertebrate groups and in particular for terrestrial amphibians, that are important predators of soil invertebrates. In general, resource partitioning occurs between syntopic species with similar ecological niches, and coexistence patterns seem to be regulated by temporal resource variability. However most of the generalization on foraging strategies of terrestrial salamanders are extrapolated from studies on New World temperate species, thus we investigated the seasonal effect of resource variation in an European forest ecosystem, in which two ecologically similar but phylogenetically distinct salamander species are found. The diet of adult and juvenile cave salamanders (*Speleomantes strinati*), and of adult spectacled salamander (*Salamandrina perspicillata*) was obtained by stomach flushing, and results showed large seasonal changes both in prey availability and in salamander realised trophic niche. Values of trophic diversity were similar and niche overlaps were large among all salamander groups in spring, during high prey availability. Conversely in autumn, when a two-fold reduction in prey biomass was observed, there was a clear niche partitioning as the smaller *S. perspicillata* shifted from a generalist to a specialized trophic strategy. Juvenile *Speleomantes strinatii*, that largely overlapped in size with *S. perspicillata*, did not show any change in diet, suggesting that the feeding strategies were species-specific and not size-mediated. The observed patterns of variation in feeding ecology indicate that similar predators may react differently to changing prey availability to enhance niche partitioning. We also observed an increased energy intake during autumn for *S perspicillata* and *S. strinatii* juveniles, possibly related to differences in microhabitat use and activity patterns.

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1. Introduction

Generally, the relative importance of primary niche dimensions in ecological animal systems follows a particular pattern. Spatial dimensions are commonly the most important niche axes, followed by trophic niche dimensions, and finally temporal axes (Schoener, 1974; Pianka, 1975; Luiselli, 2008). However, some vertebrate groups do not conform to this model, and in some cases the trophic niche axis appears to be the most important. Such patterns are observed for some fish (Piet et al., 1999), for some amphibians (see Wells, 2007), and for snake communities worldwide (Luiselli, 2006).

Terrestrial amphibians play a key role in forest ecology because they regulate soil invertebrates which modulate the leaf litter turnover influencing important forest ecosystem functions, like nutrient storage and release (Hairston, 1987; Davic and Welsh, 2004; Walton, 2005). In fact in temperate forest ecosystems, terrestrial salamanders despite their relative small size, not only may be numerically dominant, but also may represent a significant component of vertebrate biomass and can be the main terrestrial predator group (Burton and Likens, 1975; Davic and Welsh, 2004).

Resource partitioning likely occurs between sympatric (or syntopic) populations of species with similar ecological niches, and temporal resource variability is supposed to shape the coexistence pattern of ecologically similar species (MacArthur and Pianka, 1966; Stephens et al., 2007). In particular in highly seasonal ecosystems, resources tend to fluctuate over time, and when they decrease below a threshold may become limiting. In this case, the theoretical expectation is that species should diverge in their resource use to limit competition (Lack, 1947). In the case of terrestrial salamanders, different ecological and behavioural mechanisms have been proposed (Hairston, 1987), but

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generalizations on ecological coexistence and in particular on foraging strategies were principally extrapolated from studies on North American forest plethodontids, while studies from different continents, and in particular from Europe, are scarce (Wells, 2007). In this study we focused on two endemic European terrestrial salamanders with similar small distribution ranges, the pletho-dontid *Speleomantes strinatii* (Aellen, 1958) and the salamandrid *Salamandrina perspicillata* (Savi, 1821). These salamanders are excellent subjects for the study of resource partitioning, interspe-cific competition, and niche shifts, because the adult of both species are syntopic and share similar habitat requirements. In addition, they are non-territorial, forage on forest floor invertebrates (Salvidio, 1992; Romano et al., 2010; Angelini et al., 2007 and reference therein), and show morphological convergence in rela-tion to feeding kinematics (Wake and Deban, 2000). At the study site, these species largely overlapped in two of the main niche dimensions (space and season of activity), therefore our main goal was to disclose if and by which mechanisms they differed in their feeding strategies, with emphasis on their seasonal resource use. Specifically we asked: *i*) do salamanders differ in their food use, being generalist or specialist predators? *ii*) is feeding ecology mainly shaped by the predator size, as it occurs in North American temperate salamanders communities (reviewed by Hairston, 1987) or is species-specific? *iii*) and, finally, are the two species less similar in diet in the season with less abundant prey, and which are the possible ecological or behavioural mechanisms that allow species coexistence in this particular context?

2. Materials and methods

2.1. Study site: vegetation and climate

Salamanders and their prey were sampled along a first order Apennine stream in North-western Italy, Province of Genova (44°34′00″N; 9°08′10″E). The site, situated at about 900 m a.s.l., is a Supra-Mediterranean mixed deciduous forest (Blondel and Aronson, 1999) dominated by chestnut trees (*Castanea sativa*). This sub-Mediterranean region is characterized by a bimodal rainy pattern (autumn, and spring), with leaf growth and budburst occurring in spring (i.e. March—May), and leaf-falling in autumn [i.e. October—December, (Floret et al., 1989)]. Therefore, salaman-ders were sampled during humid periods, when surface activity is high. Conversely, surface activity is reduced during dry conditions (i.e. summer) and lacking in winter, when salamanders retreat underground to avoid freezing temperatures.

At the study site two salamander species were frequently observed, *S. strinatii* (family Plethodontidae) and *Salamandrina perspicillata* (family Salamandridae), while a third species the sal-amandrid fire salamander (*Salamandra salamandra*), was rarely observed.

2.2. Study species and their feeding mechanisms

S. strinatii is a completely terrestrial salamander, endemic to S France and NW Italy where it occurs on humid rock outcrops, in the leaf litter and in natural and artificial underground habitats (Lanza et al., 2005). *Salamandrina perspicillata* is endemic to central and northern Italy (Romano et al., 2009a) and occurs, along the Apen-nine, mainly in shady and damp but also in Mediterranean habitats. The adults are semi-terrestrial and only females go to the water to deposit their eggs (Lanza, 1983). *S. strinatii* and the terrestrial stages of *S. perspicillata* feed on a large variety of soil invertebrates (Vanni, 1980; Salvidio, 1992).

Plethodontids have a very specialised buccal anatomy, that allows the tongue to be projected outside the mouth to catch prey

far from the predator snout (Wake and Larson, 1987), while sala-mandrids usually have a fixed non-projectile tongue (Wake and Deban, 2000). However *Salamandrina*, in comparison to other sal-amandrids, has the ability to project the tongue up to 20% of snout-vent length (Miller and Larsen, 1990). Therefore, in this respect, *Salamandrina* may be considered convergent with plethodontid salamanders that have highly extensible tongues (Wells, 2007), although the mechanism of tongue projection is different (Wake and Deban, 2000). Salamanders with projectile tongues are lung-less (all plethodontids, Noble, 1931) or posses vestigial lungs (*Chioglossa* and *Salamandrina*, Anselmi, 1921). In these species the hyoid apparatus is not involved in respiration, which is accom-plished entirely through the gas exchange in the buccopharyngeal cavity and skin. As a result, all these salamanders require similar environmental conditions to perform the same activities.

2.3. Sampling predators and their prey

Sampling of both salamander species and their prey occurred, within an area of about 5000 m^2, in November 2008 and April 2009 during comparable humid periods (see Supplementary material S1), when the foraging of salamanders on the forest soil was not limited by drought. *Salamandrina* and *Speleomantes* occurred in the same microhabitats (i.e. under natural shelters or in the leaf litter) with the exception of small vertical rock-faces in which only *Spe-leomantes* were found. Salamanders were measured from the tip of the snout to the posterior end of the cloaca (SVL) and divided in three groups (Salvidio and Pastorino, 2002): juveniles (including subadults), adult males and females that were distinguished by the presence or absence of a mental gland. For *Salamandrina* we considered only a single group comprising adult males and females, sexed by the observation of the cloaca walls (Romano et al., 2009a). Salamanders were stomach flushed in the field and stomach contents stored in 70% ethanol (Salvidio, 1992). The ventral colour pattern of *Salamandrina* was photographed, while *Speleomantes* were toe-clipped to allow identification and to exclude recaptures from analyses.

Concerning prey availability, the main difference between the two seasons was assumed to be a higher spring invertebrate abundance, that in temperate forests peaks during the spring plant growing season (Wolda, 1988; Dajoz, 2000). In both seasons, ground-dwelling invertebrates were sampled by six pitfall traps (500 ml) and by two 1000 cm^3 soil cores and aerial invertebrates were captured with six transparent acetate sheets (21 × 29 cm) coated with entomological glue and fixed to the vegetation at about 1.20 m from the soil. Pitfall traps and soil samples yielded very similar assemblages (data not shown) and were pooled in analyses. The volume of intact prey items was calculated as a prolate spheroid, while incomplete items were assigned the taxon mean value.

2.4. Data analysis

Seasonal fluctuations in abundance and in volume of prey items among the three group of salamanders were examined using Kruskal—Wallis (KW) non-parametric analysis of variance. Pairwise comparisons, were performed using the non-parametric Mann—Whitney (MW) test, after Bonferroni correction (variances were not homogenous both for number and for volume of prey items, data not shown).

The within species sex differentiation in diet was analysed by means of analysis of similarity (ANOSIM), based on Bray—Curtis distance (Clarke, 1993). The diversity of prey taxa and volumes in salamander stomachs and in the environment were estimated through Simpson's index (1-D) and 95% confidence limits

calculated by bootstrapping (Magurran, 2004). Non-parametric multivariate analysis of variance (NPMANOVA, Anderson, 1991) analysed differences between species by season. All analyses were performed in the statistical package PAST (Hammer et al., 2001).

The use of prey types in relation to their abundance in the environment was estimated by means of Vanderploeg and Scavia (1979) relativized electivity index (E^*) which is strongly supported by comparative evaluations (Lechowicz, 1982):

$$E^* = (Wi - 1/n)/(Wi + 1/n),$$

where $Wi = (ri/pi)/(\Sigma ri/pi) - 1$, and ri is the relative abundance of prey i in the diet, pi is the relative abundance of prey i in the environment, and n is the number of prey types. This index ranges from +1 (positive selection) to −1 (avoidance), while $E^* = 0$ indicated that prey items were consumed according to their availability. The threshold electivity value (u) for each prey type with more than 4 trapped individuals was calculated as the 5th percentile of the absolute values of E^* (Ramos–Jiliberto et al., 2011).

To assess dietary importance, we also used the index of relative importance (IRI $= [N + V]^*FO$) of prey taxa, expressed as a percentage [%IRI] (Cortes, 1997). IRI combines the numerical (N), volumetric (V) and frequency of occurrence (FO) value of each prey type, and thereby reduces bias towards large-sized or rare prey items (Pinkas et al., 1971).

The diet overlap between salamander groups was analysed by means of Pianka's index ($O_{jk} = \sum p_{ij}^* p_{ik}/[\sum p_{ij}^2 * \sum p_{ik}^2]^{1/2}$, where pi is the frequency of occurrence in samplings of prey item i in the diet of species j and k (Pianka, 1973). O_{jk} varies from 0 (total separation) to 1 (total overlap).

The trophic strategy of the two species was also analysed with a modification of Costello's (1990) graphical representation (Amundsen et al., 1996). According to this method, each prey category is plotted on a graph in which the X axis is the prey frequency of occurrence (FO), and the Y axis is the prey-specific abundance (Pi), defined as the proportion of prey items (i), considering only all the prey items found in the individuals that consumed that specific prey type (Amundsen et al., 1996). This graphical approach gives insights on the population feeding strategy: specialized (when some prey taxa have high Pi values and are projected in the upper part of the plot) vs. generalist (when all prey taxa have low Pi values and are projected in the lower part of the plot).

3. Results

3.1. Prey availability: abundance and biomass

During this study 1411 invertebrates were captured, of which 406 (29%) in autumn and 1005 (71%) in spring (see Appendix). The total prey biomass ranged from 13.08 to 23.30 mm³ in autumn and spring, respectively. In the study habitat, the diversity of prey taxa and volumes remained similar between seasons (see Appendix) but, as expected, there were about 2.5 times more invertebrates

and about twice the prey biomass during spring, which is the main plant growing season in temperate European forests.

3.2. Body size in salamander groups

A clear gradient in mean body size was present in the five groups of salamanders. Male and female *Salamandrina* (mean SVL = 34.97 mm ± 2.01 s.d., $n = 29$ and SVL = 37.29 mm ± 2.31, $n = 22$, respectively) were the smallest, while male and female *Speleomantes* (54.586 ± 3.43, $n = 51$ and 60.26 ± 2.72, $n = 40$, respectively) the largest groups. Juvenile *Speleomantes* (SVL = 44.69 ± 4.89, $n = 41$) were intermediate in size between the adults of the two species and largely overlapped with *Salamandrina*. All the pairwise comparisons between salamander groups indicated that the means SVL's were significantly different (Kruskal–Wallis ANOVA, $P < 0.05$, after Bonferroni correction).

3.3. Sexual differences in diet

Overall, 132 *S. strinatii* (41 juveniles, 51 males and 40 females) contained at least one prey in their stomach (see Appendix). The ANOSIM using as variables both taxa and volume categories showed no sexual or age differences within season (ANOSIM, $P > 0.05$, in all cases), but males in spring were significantly different from both males and juveniles in autumn ($P < 0.01$ after Bonferroni correction, in both cases).

Concerning *Salamandrina*, 51 individuals (29 males and 22 females) contained prey in their stomach (see Appendix). The ANOSIM considering taxa and volumes indicated that sexes were similar within seasons ($P > 0.10$, in both cases), but differed between autumn and spring both in taxa and volumes ($P < 0.03$ in both cases, after Bonferroni correction).

According to these results, sexes within the same species were pooled by season, but juvenile *Speleomantes* were maintained as a separate group to facilitate a direct comparison with the similar-sized *Salamandrina* and to test prediction iv (see Introduction).

3.4. Prey number and prey volume

The mean number of prey ingested was 6.05 ± 5.98 s.d., ($n = 19$), 4.09 ± 2.99 ($n = 22$), 4.37 ± 3.32 ($n = 47$) in spring, and 13.09 ± 12.27 s.d ($n = 32$), 4.84 ± 2.93($n = 19$), 6.48 ± 3.82($n = 44$) in autumn for *Salamandrina*, adult and juvenile *Speleomantes*, respectively. The number of prey items per stomach among the three groups of salamanders was not significant in spring (KW, $H = 0.63$, $P > 0.1$) but was significantly different in autumn (KW, $H = 20.38$, $P < 0.001$). The pairwise comparisons indicated that *Salamandrina* consumed significantly more prey items than both adult and juvenile *Spelomantes* ($P < 0.001$, in both cases), which did not differ between them ($P > 0.1$).

The mean prey volume (mm³) was 286.61 ± 415.45 s.d., ($n = 19$), 141.89 ± 145.95 ($n = 22$) and 195.05 ± 310.07 ($n = 47$) in spring, and 804.61 ± 845.05 s.d ($n = 32$), 156.27 ± 111.39 ($n = 19$) and

Table 1
Results of NPMANOVA. P values for comparisons, after Bonferroni corrections, are given above the diagonal for prey taxa, and below the diagonal for volume categories.

	S. perspicillata autumn	S. perspicillata spring	S. strinatii adults autumn	S. strinatii juv. autumn	S. strinatii adults spring	S. strinatii juv. spring
S. perspicillata autumn	–	0.000	0.000	0.000	0.000	0.000
S. perspicillata spring	0.006	–	0.002	0.044	0.507	1.000
S. strinatii adults autumn	0.000	0.000	–	1.000	0.000	0.498
S. strinatii juv. autumn	0.000	0.102	1.000	–	0.035	1.000
S. strinatii adults spring	0.000	0.114	0.000	0.012	–	1.000
S. strinatii juv. spring	0.000	1.000	0.029	0.705	0.665	–

331.41 ± 267.93 (n = 44) in autumn for *Salamandrina*, adult and juvenile *Speleomantes*, respectively. Prey volume per stomach did not differ in spring (KW, H = 0.84, P > 0.1), but was significantly different in autumn (KW, H = 34.92, P < 0.001), and the three salamanders groups differed in all pairwise comparisons (P < 0.05). At the intra-specific level, the prey volume was significantly higher in autumn than in spring, both for *Salamandrina* and for juvenile *Speleomantes* (MW U = 111 and 549 respectively, P < 0.0001 in both cases). These results suggest an increased energy intake in autumn for *Salamandrina* and for juvenile *Speleomantes*, while adults of the latter species maintained constant energy requirements in different seasons.

3.5. Niche overlap, trophic strategy and prey selection

In general, *Speleomantes* showed relatively similar diversity indices of both prey taxa and prey volumes, in both seasons (see Appendix). Conversely, *Salamandrina* showed a dramatic seasonal change: in the spring it displayed relatively high diversity values (1 − D = 0.82 and 0.61, for taxa and volumes respectively), but in autumn these values were significantly lower (1 − D = 0.50 and 0.29, for taxa and volumes respectively, see Appendix). The results of NPMANOVA using both prey taxa and prey volume corroborated these observations (Table 1). The diet of *Salamandrina* in autumn differed from all the others groups (P < 0.001), but in spring there were no differences among *Salamandrina* and *Speleomantes*. Concerning *Speleomantes*, adults and juveniles were similar within each season, but there was a significant difference in adult diets between spring and autumn (Table 1). The highest diet overlap values were observed between adult and juvenile *Speleomantes* in both seasons, while the lowest value was recorded in autumn between adult *Speleomantes* and *Salamandrina* (Table 2).

Considering Amundsen' plot, both adult and juvenile *Speleomantes* adopted a typical generalized feeding strategy (Fig. 1A, B, C and D) since all values of taxa and volume categories had Pi values ≤0.60, and were thus projected in the lower half of the plot (see Amundsen et al., 1996 for details). Conversely, *Salamandrina* in autumn appeared highly specialized toward the smallest prey size category (Pi = 0.86), represented in their stomachs mainly by springtails (Pi = 0.72, Fig. 1E). In spring, *Salamandrina* displayed no evident pattern (Fig. 1F) and there was a general similarity among all salamanders (Fig. 1B, D and F).

In autumn, the %IRI showed that the prey importance in the diet of adult *Speleomantes* was evenly divided among spiders, millipeds, adult flies and bugs (see Appendix), and E^* indicated that the large-sized millipeds and centipedes were positively selected. A similar pattern was observed in juveniles *Speleomantes* that showed high %IRI values for spiders millipeds and fly larvae and positive selection for the large-sized millipeds and centipedes. *Salamandrina* had high %IRI values for both springtails (E^* = 64,73, which is the highest %IRI value obtained in this study) and adult flies, but selected springtails over other available taxa (Fig. 2A).

In spring, both adult and juvenile *Speleomantes* displayed high %IRI values for adult flies (see Appendix). The pattern of feeding selection appeared more complicated, although in general concordant between adult and juvenile *Speleomantes* that

Table 2
Trophic niche overlap (O_{jk}) in autumn (above diagonal) and in spring (below diagonal).

	S. perspicillata	*S. strinatii* adults	*S. strinatii* juveniles
S. perspicillata	–	0.48	0.63
S. strinatii adults	0.71	–	0.74
S. strinatii juveniles	0.67	0.81	–

displayed high E^* values for spiders, unidentified insects, and millipeds (Fig. 2B). The spring diet of *Salamandrina* was characterised by a high %IRI contribution of springtails and adult flies, with a positive selection for spiders, unidentified insects, and woodlices.

4. Discussion

Relatively few works compared prey abundance obtained from terrestrial salamander stomachs and prey availability in the environment (but see Maiorana, 1978; Sites, 1978; Jaeger, 1980; Greene et al., 2008). Terrestrial salamanders are usually classified as generalist predators (Maiorana, 1978; Sites, 1978; Wheeler et al., 2007; Wells, 2007), but these data are based on North-American terrestrial salamander communities in which several plethodontid species live in syntopy (e.g., Fraser, 1976; Adams and Rohlf, 2000). Conversely, there is a surprising scarcity of data on the feeding ecology of terrestrial or semi-terrestrial European salamanders, in particular in relation to the seasonal variations in their trophic resources. In forest ecosystems, if salamanders display overlap in size and food is a limiting resource, their trophic interactions appear mainly shaped by the body-size gradient existing among species and among age groups within the same species (Fraser, 1976; reviewed by Hairston, 1987). As expected in temperate environments, we found that the prey availability was significantly higher in spring than in autumn, being more related to the vegetation growth period, rather than to rainfalls, contrary to what it is observed in tropical and subtropical rainforest (Toft, 1980). In this regard, our study greatly improved the knowledge of the realized trophic niche of *S. strinatii* (cf., Salvidio, 1992) and, in particular, of *Salamandrina perspicillata* for which only scanty data are available (Utzeri et al., 2004; see also Angelini et al., 2007).

4.1. Are Speleomantes strinatii and Salamandrina perspicillata generalist or specialist predators?

Adult and juvenile *Speleomantes* adopted a generalist feeding strategy both on taxa and volumes with relatively little seasonal variations, while *Salamandrina* was clearly specialized on the smallest-sized prey items (i.e. springtails and mites), especially in autumn (Fig. 1E, F). However, if we consider also prey availability (Fig. 2), both species showed some positive selection towards certain taxa and avoidance of others. In spring the prey categories positively selected were, on the whole, concordant between the two species, while in autumn they differed substantially. In particular during autumn, *Salamandrina* shifted from a generalist feeding strategy towards a highly specialized diet, in response to some environmental or behavioural factor. This seasonal variation in feeding habits within the same population suggests that studies conducted over a single season may not be sufficient to correctly describe the diet of salamander populations, in particular if prey availability and food habits of other syntopic species are not considered. Indeed in autumn, the foraging behaviour of *Salamandrina* was specialised on small-sized prey (Fig. 1E), and moreover higher prey numbers and volumes per individual were foraged to increase energy intake (Table 1; see also the results on prey and volumes per stomach). The higher foraging rate of *Salamandrina* and juvenile *Speleomantes* and the concomitant reduction in prey availability observed in autumn, strongly suggest that this season may correspond to a high competition period for the salamanders at the study site. Indeed, it was during this season that the smaller values in trophic niche overlap between all pairs of salamander groups were observed, corroborating the expectation (see below).

Volumetric data per taxon, which is one possible measure of energy-gain, were not always reflected in abundance data, which indicated the cost of acquiring prey (compare prey abundance and
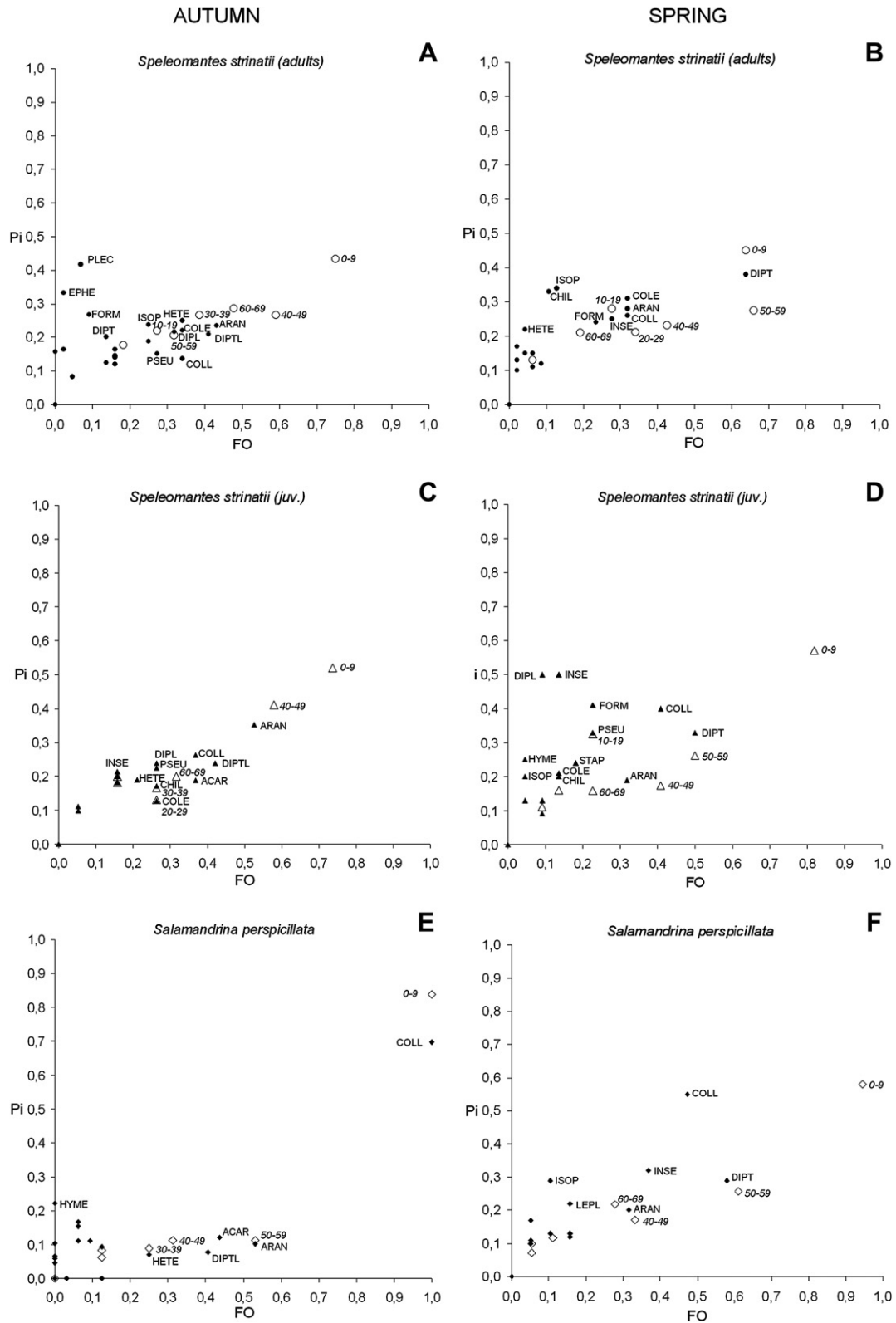
Fig. 1. Modified Costello plot (Amundsen et al., 1996), describing the trophic strategies of *Speleomantes strinatii* and *Salamandrina perspicillata* in autumn (A, left column) and spring (B, right column). Prey taxa are shown with black symbols and volume categories with white symbols. Pi = prey-specific importance (see text); FO = frequency of occurrence. Food categories with both values of Pi and FO lower than 0.2 are not shown. ACAR = Acarina, ARAN = Araneae, CHIL = Chilopoda, COLE = Coleoptera adults (not Staphylinidae), COLEL = Coleoptera larvae, COLL = Collembola, DIPT = Diptera adults, DIPTL = Diptera larvae, PLEC = Plecoptera, EPHE = Epemeroptera, FORM = Formicidae, HYME = Hymenoptera (not Formicidae), INSE = Undetermined insects, ISOP = Isopoda, LEPL = Lepidoptera larvae, PSEU = Pseudoscorpionida, STAP = Coleoptera Staphylinidae.
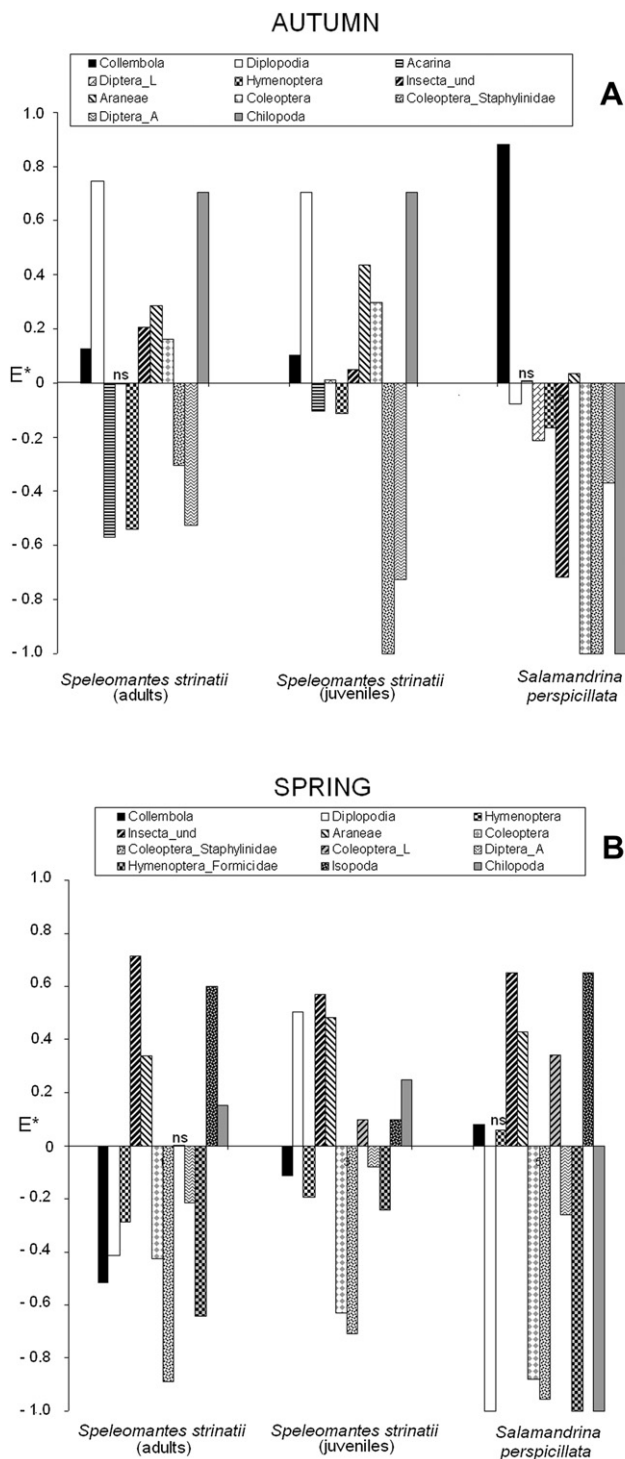
Fig. 2. Electivity index (E^*) for prey taxa selected by *Speleomantes strinatii* and *Salamandrina perspicillata* in autumn (A) and spring (B). ns = not significant (see text for threshold value definition).

%IRI in Appendix). In this respect, the less profitable prey items for all salamanders were springtails, mites and beetles (i.e. small prey items), while the most profitable ones were millipedes, woodlices, butterfly and fly larvae (i.e. large prey items). However, a large percentage of individuals of both species fed also on the smallest prey categories (see Fig. 1). According to Jaeger (1990) salamanders may select lightly armoured prey items, such as springtails, because

they are rapidly digested and maximize the net energy gain per time unit. Therefore, prey size did not appear to be the only selection criterion, but rather a shared criterion together with prey type, as emerged comparing the respective use by salamanders of prey taxa and volumes (Figs. 1 and 2).

4.2. The feeding behaviour of Speleomantes strinatii and Salamandrina perspicillatais species-specific

There were no sexual differences in diet within *Salamandrina* and *Speleomantes*, two sexually dimorphic species, in which females are larger than males (Salvidio and Bruce, 2006; Romano et al., 2009b). At the study site salamanders could be categorized in three well separated body size groups: adult *Salamandrina*, juvenile and adult *Speleomantes*, listed in increasing size order. Juvenile *Speleomantes*, which largely overlapped in size with *Salamandrina*, clearly exhibited a trophic strategy similar to (and largely overlapping with) conspecific adults, and significantly different from *Salamandrina*, suggesting that morphological feeding mechanisms were more important than body size. That is, for the salamanders we studied, the feeding ecology was species-specific and not body-size dependent. Moreover, the trophic strategy of *Speleomantes* was largely unrelated to the seasonal variation in available resources. These results corroborate the prediction that larger species tend to have broader trophic niches (Williams et al., 2010). In fact, in both seasons, there was a clear gradient in both prey taxa and volume diversity indices according to predator body size, with the smallest species (i.e. *Salamandrina*) always displaying the lowest diversity.

4.3. The possible mechanisms of species coexistence

Several mechanisms allow species coexistence such as selective predation, temporal changes in habitat quality (i.e. storage effects), and resource partitioning (reviewed in Chesson, 2000; and Kotler and Brown, 2007). In the case of our two-species community, we can rule out differential predation, because *Salamandrina* and *Speleomantes* do not share any specific predator (e.g. Lanza et al., 2005; Angelini et al., 2007). The possibility of storage effects can not be excluded, because long-term data on population dynamics of the two species coupled with habitat or resource fluctuations are completely lacking. However, this study demonstrated that different realised trophic niches characterised the two species in autumn, when trophic resources were low and salamanders where actively foraging with higher rates in comparison to spring, as shown by the higher prey number and prey volume per individual stomach. In this context of high foraging rate and low prey availability, juvenile *Speleomantes* and *Salamandrina* possibly experimented a high interspecific competition for food. Optimal foraging theory, and in particular the prey model predicts that, in ecological time, organism should expand their diet as food becomes scarce (MacArthur and Pianka, 1966; Stephens and Krebs, 1986). However, whereas *Speleomantes* apparently did not change the feeding strategy, *Salamandrina* did, decreasing its dietary diversity and becoming a specialist on small-sized prey items.

Two possible explanations are possible, the first that the two species in autumn were feeding in different microhabitats, where different prey groups were found, the second that *Salamandrina*, was more active, and for longer time periods, on the forest floor to feed. However the second hypothesis seems to be not corroborated by the data available on the daily activity pattern of *Salamandrina* which is mainly active, in a similar forest habitat, from dawn to early hours of the morning (Bruni and Romano, 2011) or from sunset to midnight in drier Mediterranean environments (Utzeri et al., 2004). The fact that in autumn also juvenile *Speleomantes*

consumed high prey volumes without evident changes in their diet, may be explained by their high energy investment in somatic growth and/or by the need of accumulating storage reserves for dispersal.

In any case, our findings confirm that, if syntopic species have similar ecological requirements and prey resources become limited, niche partitioning seems to play a key role in their long-term coexistence (Schoener, 1965; Moermond, 1979; Huey and Pianka, 1981; Alatalo and Moreno, 1987).

5. Conclusions

The present study showed that the sampled salamander food web was relatively complex, as already shown for temperate ecosystems with similar number of species (Fraser, 1976; Sites, 1978). Moreover, there were dynamic variations in both prey availability and in salamander trophic strategies, since the two predators showed different seasonal feeding patterns. In autumn, when a reduction in prey biomass was observed, the smallest species (*Salamandrina perspicillata*) shifted towards a highly specialized diet, an uncommon feature for terrestrial salamanders that are generally considered to be generalist predators (Maiorana, 1978; Wells, 2007; but see Sites, 1978). Conversely, there was no relevant variation in the trophic strategy of both adult and juvenile *S. strinatii*, which are larger and phylogenetic distinct. This finding has important ecological implications because the observed variation was not size-related but rather species-specific, and because intra-specific changes in diet and in foraging strategy over different seasons may also influence model testing.

The coexistence of similar animal species in ecological communities is one the most studied and perplexing problems in ecology (reviewed in Gordon, 2000 and Chesson, 2000). Variation in the use of food resources (but also of microhabitats and time) are the result of several interacting factors, such as competition, predation, morphology, physiological constraints and also phylogenetic history (Toft, 1985; Brooks and McLennan, 1991; Zimmerman and Simberloff, 1996). Although we observed, partic-ularly in spring, wide niche overlap values between all salamander functional groups, this pattern alone does not necessarily indicate possible competition, because if resources are not limiting, two or more organisms can share them without producing reciprocal negative impacts (Pianka, 1974). However when, in autumn, resources became less abundant we observed an abrupt change in the foraging behaviour of *Salamandrina*. This shift in resource use produced a clear seasonal niche partitioning among the two species. These data provide indirect evidence of competition for food resources, or possibly of behavioural interference between these species (e.g. Pimm et al., 1985; St-Pierre et al., 2006). In any case, our findings do not demonstrate that such interactions are important in determining the relative abundance or the patterns of resource use by individual species, but these two alternative hypotheses are testable in the in the field or laboratory by pro-grammed behavioural experiments (Jaeger, 1971, 1974).

The study of the feeding strategy and the prey availability of *Salamandrina* populations in similar habitats where *Speleomantes* are absent would better allow to distinguish the ultimate causes of the observed variations in feeding patterns. This topic would be of particularly interest to solve, since in natural assemblages of amphibians food competition appears to be an unusual event, which play a minor role in the structure and dynamics of the community (Kuzmin, 1995).

Appendix A. Supporting information

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.actao.2012.05.001.

Appendix B

Prey seasonal variation in the diet of *Salamadrina perspicillata*, *Speleomantes strinatii* and in traps at the study site. The index of relative importance (%IRI) is given in bold for taxa with values ≥10%. Simpson's diversity indexes (1-D) with 95% confidence limits (CL) are shown.

| | *Salamadrina perspicillata* | | | | *S. strinatii* (adults) | | | | *S. strinatii* (juveniles) | | | | Traps (6 per type in each season) | | | |
| | Autumn (n = 32) | | Spring (n = 19) | | Autumn (n = 44) | | Spring (n = 47) | | Autumn (n = 19) | | Spring (n = 22) | | Autumn | | Spring | |
	n	%IRI	n	%IRI	n	%IRI	n	%IRI	n	%IRI	n	%IRI	Sticky	Pitfall	Sticky	Pitfall
Prey taxa																
Arachnida																
Acarina	28	2.53	6	0	16	0.99	12	0	10	6.95	11	0	0	59	0	260
Araneae	16	3.57	14	8.24	18	**14.14**	23	7.61	17	**31.46**	9	8.83	10	7	25	9
Opilionida	0	0	1	0.08	5	0.94	1	0.20	0	0	0	0	0	2	0	0
Pseudoscorpionida	6	0.17	0	0	17	2.70	2	0.06	7	3.60	6	2.69	0	0	0	0
Myriapoda																
Diplopoda	1	1.63	0	0	12	**14.98**	1	0.05	6	**16.89**	2	1.49	0	5	0	4
Chilopoda	0	0	0	0	12	7.89	9	1.28	6	7.89	3	1.69	0	5	0	11
Hexapoda																
Coleoptera-larvae	12	0.80	3	0.88	20	1.46	3	0.20	1	0.19	1	0.14	0	2	0	5
Coleoptera not Staphilinidae	0	0	2	0.32	13	1.32	26	7.02	5	3.39	4	1.32	34	12	1	73
Coleoptera Staphilinidae	0	0	1	0.13	11	2.37	5	0.58	0	0	4	1.32	8	11	26	135
Collembola	292	**64.73**	45	**27.96**	20	6.72	25	5.72	9	7.13	17	**13.65**	0	39	0	130
Diptera-larvae	17	1.69	18	0	19	9.11	49	0	12	**10.15**	21	0	0	56	0	12
Diptera-adults	26	**21.68**	26	**42.40**	11	**11.30**	58	**58.88**	4	3.95	21	**52.72**	129	38	83	21
Protura	2	0.03	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Ephemeroptera	0	0	0	0	15	0.03	0	0	0	0	0	0	1	0	1	0
Heteroptera	8	1.91	0	0	25	**11.70**	2	0.11	4	3.62	2	0.66	1	1	0	1

(continued)

	Salamadrina perspicillata				S. strinatii (adults)				S. strinatii (juveniles)				Traps (6 per type in each season)			
	Autumn (n = 32)		Spring (n = 19)		Autumn (n = 44)		Spring (n = 47)		Autumn (n = 19)		Spring (n = 22)		Autumn		Spring	
	n	%IRI	n	%IRI	n	%IRI	n	%IRI	n	%IRI	n	%IRI	Sticky	Pitfall	Sticky	Pitfall
Hymenoptera not Formicidae	2	0.03	3	0.73	2	0.04	3	0.16	1	0.14	1	0.11	5	2	4	4
Hymenoptrera Formicidae	4	0.28	0	0	19	1.90	17	3.74	4	1.93	13	8.13	0	3	0	130
Lepidoptera-larvae	0	0	5	6.40	8	0	0	0	1	0	2	2.86	0	0	0	1
Plecoptera	0	0	0	0	3	2.80	1	0	0	0	1	0	7	0	3	0
Trichoptera-larvae	0	0	1	0.12	8	0	0	0	0	0	0	0	0	0	0	2
Insecta indermined	1	0.04	7	6.28	8	3.73	18	6.81	3	2.44	3	1.74	4	1	12	1
Mollusca																
Gastropoda	1	0.03	0	0	9	0.46	1	0.03	1	0.25	0	0	0	1	0	0
Crustacea																
Isopoda	2	0.86	7	6.45	6	7.99	12	7.72	0	0	1	0.78	0	3	0	5
Annelida																
Lumbricidae	0	0	0	0	5	0.02	0	0	0	0	1	0.09	0	3	0	2
1-D (taxa) (95% CL)	0.50 (0.44–0.56)		0.82 (0.79–0.85)		0.95 (0.94–0.96)		0.88 (0.86–0.89)		0.90 (0.86–0.91)		0.89 (0.86–0.90)		0.84 (0.82–0.86)		0.84 (0.83–0.85)	
Prey volume categories (mm³)																
0–9	307		76		104		102		40		62		30	173	13	548
10–19	4		1		23		30		4		13		0	5	0	130
20–29	0		2		11		28		5		4		2	12	35	73
30–39	9		1		33		3		5		2		2	0	1	3
40–49	16		14		48		33		23		12		25	12	10	20
50–59	26		26		21		60		4		21		83	38	129	21
>60	4		12		34		16		7		6		3	8	7	10
1-D (volumes) 95% CL)	0.29 (0.23–0.35)		0.61 (0.53–0.66)		0.78 (0.75–0.81)		0.77 (0.74–0.79)		0.71 (0.62–0.76)		0.68 (0.59–0.74)		0.63 (0.59–0.66)		0.64 (0.61–0.66)	

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