MODELLING ASPECTS OF TERRESTRIAL ECOLOGY IN AN ITALIAN ENDEMIC SALAMANDER, *SALAMANDRINA PERSPICILLATA*

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RÉSUMÉ. – *Modélisation d'aspects de l'écologie terrestre d'une salamandre endémique italienne,* Salamandrina perspicillata.– La densité et d'autres aspects de l'activité terrestre ont été étudiés dans une population de *Salamandrina perspicillata* du centre de l'Italie (parc naturel de Vejo, province de Rome). La densité des salamandres a été établie par la méthode des line-transects avec le logiciel Distance. La distance à l'eau de chaque individu a également été mesurée ainsi que les corrélations entre densité de population, distance à l'eau et diverses variables de l'habitat. Au total, un échantillon de 227 captures a été obtenu et analysé. La distance à l'eau s'est avérée croître significativement avec le temps (nombre de jours à partir du début de l'étude, c-à-d. le 13 avril), que l'on prenne tant comme variable indépendante la distance moyenne des individus établie chaque jour du suivi que les distances individuelles de toutes les salamandres enregistrées durant l'étude. Après subdivision du cours d'eau en secteurs classés en fonction de leur morphologie et de leurs variables d'habitat, un modèle général linéaire a montré que la distance à l'eau variait de manière significative entre les secteurs, avec aussi un effet temps écoulé depuis le premier jour de suivi et un effet secteur x temps. La densité estimée variait de manière remarquable de 0 à plus de 55 individus/ha selon le jour de suivi. La densité moyenne était de 24,6 ± 14,7 individus/ha, similaire à celle de beaucoup d'autres espèces de salamandres étudiées jusqu'à présent. Tant des analyses multivariées que des modèles de régression logistique ont montré que deux variables d'habitat (l'inclinaison des pentes entourant le cours d'eau et le type de bord du cours d'eau) affectaient de manière significative la densité de population.

SUMMARY. – Density and other aspects of terrestrial activity were studied in a population of *Salamandrina perspicillata* from central Italy (Vejo Natural Park, province of Rome). Salamander density was studied by line-transect methodology with Distance modelling procedures. Linear distance of each salamander from water was also measured, as well as the correlations between population density, distance of salamanders from water, and some habitat variables. In total, a sample of 227 captures was collected and analysed. The distance of salamanders from water increased significantly with time (number of days after the beginning of the study, i.e. 13 April), considering either as dependent variable the mean distance of salamanders on each day of survey or the individual distances recorded for all the salamanders captured during the present investigation. After subdividing the stream into various sectors classified on the basis of their morphological and habitat variables, a General Linear Model (full factorial design) showed that the salamander distance from water varied significantly among sectors of the stream, with also an effect of time elapsed since the first day of survey and an effect of stream sector × time. Estimated density varied remarkably with day-of-survey, ranging from 0 to over 55 individuals × ha^{-1}. The mean density of salamanders was 24.6 ± 14.7 individuals × ha^{-1}, similar to that of many other salamander species studied so far. According to both multivariate analyses and logistic regression models, two habitat variables (inclination of the slopes surrounding the stream and type of stream banks) significantly affected the population density.

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European salamanders (Amphibia : Salamandridae) are generally characterized by a prolonged phase of terrestrial activity and a reduced phase of aquatic activity, generally confined to the larval stage and the period of oviposition by females (Halliday & Adler, 2005). This general rule is valid for all species except for the alpine black salamanders (*Salamandra atra* and *Salamandra lanzai*) that are live-bearing and give birth to fully terrestrial newborns (e.g., Thiesmeier, 1992 ; Luiselli *et al*., 2001). The majority of the species is also live-bearing, but give birth to fully aquatic larvae (e.g., *Salamandra salamandra ;* see Halliday & Adler, 2005), whereas the small-sized salamanders endemic to Italy (*Salamandrina perspicillata* and, probably also *S. terdigitata*) attach their eggs to stones and other underwater objects, and are terrestrial for the rest of their lives (Della Rocca, 2002 ; Della Rocca *et al*., 2005 ; Angelini, 2006).

The terrestrial activity phase of most species (e.g., those of the genus *Salamandra*) has been well studied (e.g., Degani & Warburg, 1980 ; Andreone *et al*., 1994 ; Joly *et al*., 1994 ; Luiselli *et al*., 2001), but the two *Salamandrina* species are very little known, particularly their ecology during the terrestrial activity phase (e.g., Utzeri *et al*., 2004 ; Angelini, 2006). In particular, there is no extensive information on the population density and activity patterns of these species (but cf. Angelini, 2006 for some preliminary data on other aspects of activity) and a short list of food items of *S. perspicillata* is given in Utzeri *et al*. (2004).

Several studies have shown variation in the demography of birds and mammals correlated with geographic location (e.g., Sanz, 1998 ; Ferguson & McLoughlin, 2000 ; Ferguson, 2002), and Brown (1984) suggested that population densities of species decline when one moves from the core to the periphery of their distribution, making them more likely to go extinct (Curnutt *et al.*, 1996). Therefore, understanding the population ecology of a species throughout its geographic distribution, including the peripheral regions, is particularly relevant to its conservation (Bury, 2006). In our study case, we are confident that a detailed knowledge of the terrestrial phase of the two *Salamandrina* species may help considerably in achieving a reliable conservation strategy for these salamanders that are indeed vulnerable in most of their natural habitats in Italy (Della Rocca, 2002). In this paper we offer quantitative data on the population density and some aspects of terrestrial activity in a free-ranging population of *Salamandrina perspicillata* from central Italy, and apply, for the first time with this species, an analysis based on sophisticated statistical and modelling procedures (cf. Burnham *et al*., 1980 ; Burnham & Anderson, 2002).

MATERIALS AND METHODS

Study area

The field study was carried out during the period April-June 2007 in a small stream valley (named 'Valle dell'Inferno') situated inside the protected territory of the Vejo Natural Park, central Italy. 'Valle dell'Inferno'is a tufaceous valley linked to the main valley of the River Cremera, one of the main water bodies of the study area. The study stream is situated between N 42° 06' 30.91 – 12°24' 24.07 and N 42° 06'27.2 – E 12°06'29.46, at altitudes ranging from 215 to 246 m a.s.l.

The study area is characterized by a narrow, mostly seasonal (i.e. desiccating for a great part during summertime) stream. The mean water depth varies between 30 to 50 cm, and the bed of the river is mainly muddy with sparse stones. The surroundings of the stream are covered with a mixed, shady, oak forest (*Quercus cerris* being the dominant species, and *Acer campestre, Ostrya carpinifolia, Celtis australis, Fraxinus ornus, Castanea sativa,* etc. being other common tree species), with large amounts of stones, rocks and cut tree-trunks.

Protocol

The study area was divided into seven sectors based on their own topographic characteristics (Fig. 1). In each sector the presence and relative abundance of five independent habitat variables were evaluated : (i) average percent canopy (established by visual inspections of the canopy at random sites within each sector ; CAN), (ii) inclination of the slopes of the valley in the adjacent area of the stream banks (with three categorical types : flat, sloped, extremely sloped ; INC), (iii) type of stream banks (with two categorical types : covered by vegetation or by rocks ; BAN), (iv) relative percent abundance of three substratum types on the slopes of the valley (i.e., stones, rocks with cavities where salamanders can hide [hereby defined 'rocks'], or logged tree-trunks ; SUB), (v) diversity index of substratum types (calculated by Simpson's (1949) diversity formula ; DIV). The length (in m) of the line-transect lying along each stream sector was also measured with a tape (precision to ± 1 m).

Sampling was carried out two days per week all throughout the study period. In each day of survey we explored the whole study area, catching salamanders active in the open and also inspecting cover objects, stones, etc., in order to find individuals hidden under surface objects. Each salamander captured in the field was individually identified by taking a digital photograph of the ventral pattern, and a photographic database was prepared and later inspected to check for eventual recaptures. This method proved to work very efficiently with this amphibian species (Della Rocca *et al.*, 2005). Using an electronic calliper (resolution 0.01 mm) we measured the body length, from apex of head to middle of cloaca (MCL) of each specimen (Della Rocca *et al.*, 2005). For each salamander, we measured with a tape its linear distance from the closest water basin (to 1 m precision), as well as its perpendicular distance from the line-transect. Salamanders were not sexed because it is nearly impossible to correctly identify the sexes based on external morphological characters (Brizzi *et al*., 1989). Indeed in the field, only the (ovipositing) female can be identified reliably (Della Rocca, 2002 ; Angelini, 2006).

Statistical analyses

A line-transect, lying along the small valley of the study stream ('Valle dell'Inferno', see Fig. 1) was surveyed during several independent dates in order to catch salamanders (see above for details). Density estimates of salamanders were generated by 'distance sampling analysis', elaborating the data with Distance 5.0 (Buckland *et al.,* 2001 ; Burnham & Anderson, 2002), a dedicated software, utilized with free-ranging animal populations, e.g. by Katsanevakis (2006) and Luiselli (2006). Distance produces a detection function *g(x)* describing the probability of detecting an object (a salamander in our study case) located at distance *x* from the line-transect under survey (Buckland & Elston, 1993, and see the key and the series adjustment framework described in Buckland *et al.,* 1993, 2001).

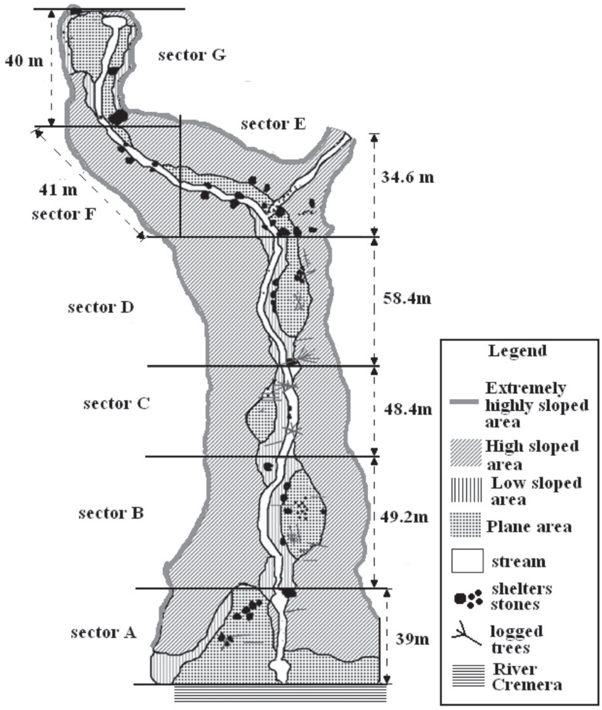


Figure 1. – Map of the study stream, including the main habitat characteristics.

The relationship between *g(x)* and *p* – the proportion of salamander individuals in area *A* that was actually detected – can be expressed as :

$$p = w^{-1} \int g(x)dx$$

where 2*w* is the width of the transect, while *d* represents the density of salamanders within a surface *A ;*

$$d = N (A \times p)^{-1} = N (2wL \times p)^{-1}$$

with *L :* length of the transect and *N :* number of detected individuals.

The detection function *g(x)* was modeled in the general form :

$$g(x) = \text{key}(x)[1 + \text{series}(x)] \times \{\text{key}(0)[1 + \text{series}(0)]\}^{-1}$$

where key(x) is the key function and series(x) is a series expansion used to adjust the key function. The uniform function, the 1-parameter half-normal function, and the 2-parameter hazard-rate function were considered as key functions ; the cosine series, simple polynomials, and Hermite polynomials were considered as series expansions (Buckland *et al*., 2001). The detection function was estimated both pooling data from the various sampling dates and separately for each sampling date, by considering all the combinations of the above key functions and series expansions, and the best eight dates in terms of survey results were chosen to generate an average estimate of density either for the study stream globally or for the various sectors of the study stream. The eight best dates were selected based on their relative Akaike Information Criterion corrected for small samples (AICc) that was used for model selection (Akaike, 1985) and computed for each candidate model. In our case, as model selection criterion we used the empirical rule of Richards (2005) that is based on the principle of parsimony (see also Corani & Gatto, 2007). The formula for AICc is as follows (see Sugiura, 1978 ; Mazerolle, 2006) :

$$\text{AICc} = -2 \text{ (log likelihood)} + 2K + 2K (K + 1) / (n - K - 1)$$

where n is the effective sample size, and K is the number of estimated parameters included in the model, i.e. the number of variables + 1, to include the intercept.

Distance data were not combined with mark-and-recapture data (Alpizar's method, see Alpizar-Jara & Pollock, 1996) because there were too few recapture instances to build a consistent database. All other statistics were computed by means of SPSS (version 11.0) and Statistica (version 6.4) PC packages, with all tests being two-tailed and α set at 5 %. Non-normal variables were normalized by log-transformation ; parametric tests were used when variables were normal or normalized, whereas non-parametric tests were used when variables were neither normal nor normalizable. Levene's test was used for assessing normality of variables. Pearson's moment product correlation coefficient was used to correlate the distance from water of salamanders with time (number of days elapsed since 13 April). A cluster analysis (single linkage amalgamation model, with Euclidean distance standardized to 100 %) was performed for investigating the similarities among stream sectors in terms of habitat variables characteristics. A Principal Component Analysis (VARIMAX rotated model) was run to correlate in the multivariate space the occurrence of a high density of salamanders (> 20 ind. × ha^{-1}) with the relative position of the various habitat variables. A logistic regression analysis (forward stepwise conditional model) was run to predict whether high density of salamanders was affected by any of the five habitat variables. In this case, high versus low density of salamanders (i.e., high density was > 20 ind. × ha^{-1}) was the dependent variable, and the five habitat variables were the independent variables. To avoid pseudo-replication biases we used data from recaptured individuals only once; that is for homogeneity with those recorded the first time a given salamander was captured.

RESULTS

Similarity among sectors of the stream

The similarity among the different sectors of the stream, based on the measured characteristics of the five habitat variables considered, is given in Fig. 2. Based on this dendrogram, the closest clusters (thus showing the highest similarities) were between sectors A and B (and these with D), and between sectors E and G. Sector F was the most different among the various stream sectors, thus appearing clustered alone in Fig. 2.

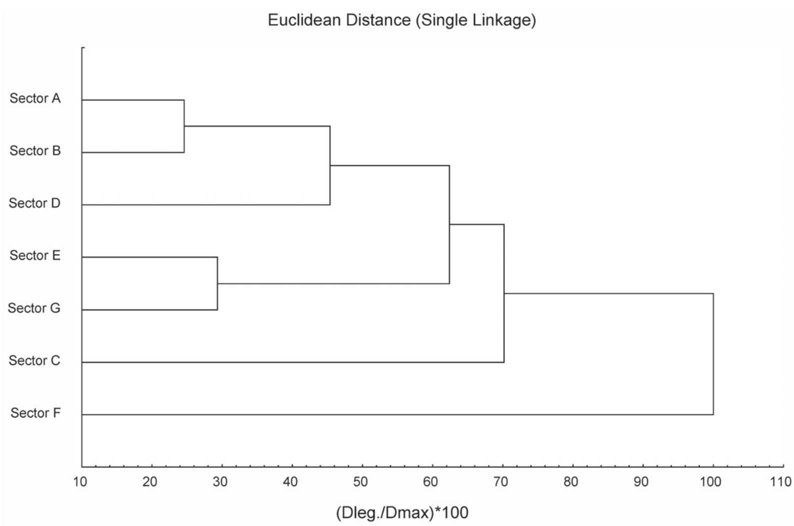
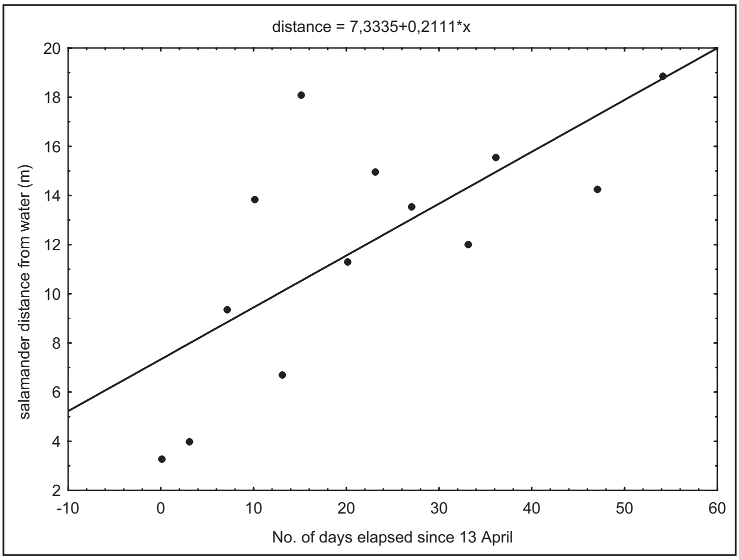


Figure 2. – Dendrogram (single linkage amalgamation model, with Euclidean distance standardized to 100 %) showing the affinities among the different sectors of the study stream in terms of terrestrial habitat characteristics. Habitat characteristics in each sector of the stream were evaluated by means of eleven independent habitat variables (see methods for more details).

Sample size and distance of salamanders from water

Overall, we captured and individually identified 227 individuals, out of which 18 were recaptured at least once. The distance (in m) of salamanders from water increased significantly with time (number of days after the beginning of the study, i.e. 13 April 2007). This was evident considering either as dependent variable the mean distance of salamanders in each day of survey ($r = 0.714$, adjusted $r^2 = 0.465$, $F_{1,11} = 11.429$, $P = 0.006$; see Fig. 3A) or the various individual distances recorded for all the salamanders captured during the present study ($r = 0.373$, adjusted $r^2 = 0.136$, $F_{1,245} = 39.607$, $P < 0.00001$; see Fig. 3B).



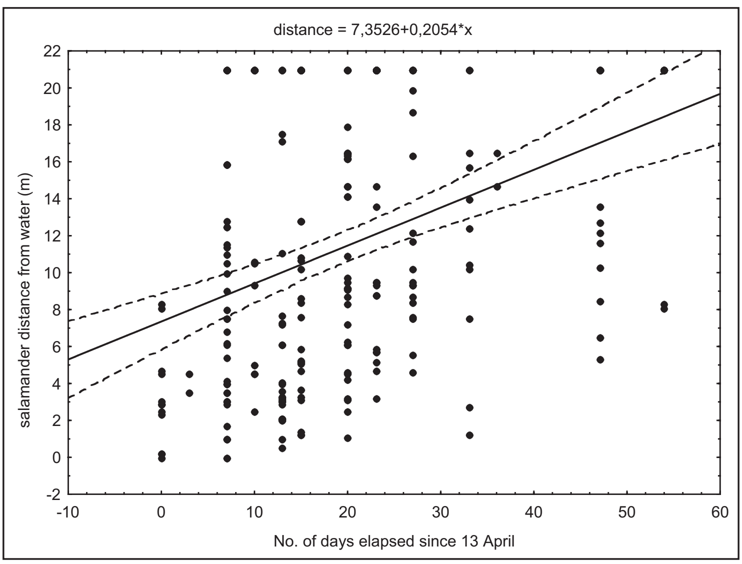


Figure 3. – Positive correlation between number of days elapsed since the 1st day of survey and the distance from water at which salamanders were found. In the upper graphic the mean distance from water on each day of survey is represented, whereas in the down graphic the distances of every salamander are represented. All distances are in m. For statistical details see the text.

Overall, the same trend was very clear also when considering the various stream sectors separately : indeed, distance of salamanders from water increased significantly with time in the stream sectors B ($r = 0.239$, adjusted $r^2 = 0.046$, $F_{1,84} = 5.084$, $P < 0.03$), D ($r = 0.328$, adjusted $r^2 = 0.089$, $F_{1,50} = 6.038$, $P < 0.02$), G ($r = 0.366$, adjusted $r^2 = 0.107$, $F_{1,32} = 4.942$, $P < 0.04$), and E ($r = 0.408$, adjusted $r^2 = 0.127$, $F_{1,21} = 4.123$, $P = 0.05$), whereas the same relationship was not significant in sector C ($r = 0.641$, adjusted $r^2 = 0.313$, $F_{1,6} = 4.184$, $P = 0.087$). Distances were not calculated for sector F because no salamanders were captured in this stream sector.

In order to evaluate whether the mean distance of salamanders from water varied among stream sectors, we could not calculate the mean distance observed in each date of survey because, as already mentioned, this varied significantly with time. So, we had to take into account the daily variation of distance when making an inter-sector analysis. Sectors A and F were removed from this analysis due to too few individuals observed. A GLM (full factorial design) gave a significant model ($F_{31,204} = 9.646$, $P < 0.00001$), and revealed that the salamander distance from water varied significantly among sectors ($F_{4,204} = 32.301$, $P < 0.00001$), with also an effect of time elapsed since the first day of survey ($F_{7,204} = 2.296$, $P < 0.03$), and an effect of sector × time ($F_{20,204} = 1.939$, $P < 0.013$). Once the time elapsed since the first day of survey is taken into account, the greater mean distances from water were of salamanders in sector E and D, and the least for salamanders in sector C (all these sectors being significantly different from others in post-hoc pairwise comparisons).

Salamander density

Salamander density was calculated for each independent date of survey, including the upper and lower limits of confidence for its estimate (Tab. I). Density varied remarkably with day-of-survey, ranging from 0 individuals × ha^{-1} to over 55 individuals × ha^{-1}. The mean density of salamanders, calculated on the basis of the eight 'best dates-of-survey', was 24.56 ± 14.74 individuals × ha^{-1}.

TABLE I

Density estimates of salamanders at the study area, calculated for each day of survey by DISTANCE procedure applied to the whole transect length

Date of survey	AICc	ESW	D	DLCL	DUCL	DCV
13 April	52.14	6.42	30.135	18.35	49.46	0.228
16 April	8.02	4.5	7.16	0.027	19.37	0.463
20 April	245.26	19.1	33.77	25.65	44.47	0.137
23 April	87.25	21	10.75	7.33	15.76	0.178
26 April	159.52	8.17	55.252	34.28	89.07	0.235
28 April	178.58	21	22.27	16.48	30.08	0.148
03 May	215.12	21	26.88	18.82	38.38	0.177
06 May	172.49	21	21.5	16.69	27.69	0.124
10 May	129.87	21	16.129	11.22	23.17	0.175
16 May	68.98	21	8.44	4.46	15.98	0.292
19 May	13.21	16.5	1.95	0	0	0.411
30 May	81.16	21	9.98	6.28	15.87	0.215
06-June	75.07	21	9.21	6.53	12.99	0.157

Symbols : AICc = small sample AIC (Akaike Information Criterion) ; ESW = Effective Strip Width ; D = density (per ha) ; DLCL = lower confidence limits of the density ; DUCL = upper confidence limits of the density ; DCV = density coefficient of variation.

Daily density of salamanders, as modelled by DISTANCE, was not correlated significantly with time elapsed since the first date of survey ($r = -0.211$, adjusted $r^2 = -0.042$, $F_{1,11} = 0.511$, $P = 0.489$). However, a General Linear Model procedure showed that mean salamander density varied significantly among stream sectors ($F_{6,49} = 7.120$, $P < 0.0001$; Fig. 4). In particular, the sectors B and G had significantly higher salamander densities than the other sectors in post-hoc pairwise comparisons, whereas the sectors A and F had the lower densities (Tab. II).

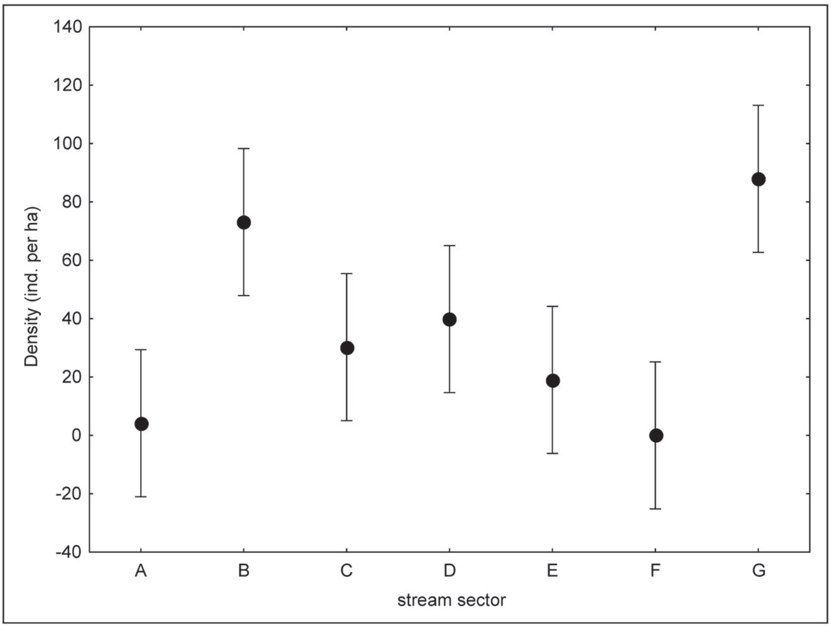


Figure 4. – Variations among sectors of the density of *Salamandrina perspicillata,* modelled by DISTANCE, at the study stream. For more details, see the text.

TABLE II

Post-hoc pairwise comparisons of GLM *results on the salamander density variations among stream sectors*

	Sector B	Sector C	Sector D	Sector E	Sector F	Sector G
Sector A	**0.000305**	0.148153	**0.049704**	0.407072	0.814627	**0.000020**
Sector B		**0.019375**	0.066777	**0.003677**	**0.000144**	0.407810
Sector C			0.589579	0.529671	0.094529	**0.002072**
Sector D				0.245266	**0.029109**	**0.009252**
Sector E					0.288980	**0.000306**
Sector F						**0.000009**

Significance is in boldface. Note that sectors B and G had higher salamander density than nearly all the other stream sectors.

CORRELATIONS BETWEEN SALAMANDER DENSITY AND HABITAT VARIABLES

PCA analysis showed that factor 1 was positively correlated to DIV and negatively to INC, and factor 2 was positively correlated to BAN and negatively to SUB (Fig. 5). High density of salamanders proved to be positively correlated to BAN and negatively to INC (eigenvalues :

2.524 and 1.546 ; percent of variance explained by first two factors = 67.83 %). We also ran a logistic regression analysis (forward stepwise conditional model) to predict whether the high density of salamanders was affected by any of the five habitat variables. Although the overall model was not statistically significant ($\chi^2 = 9.540$, df = 6, P = 0.145), the logistic regression analysis revealed that the only variables significantly correlated to high density of salamanders were BAN ($\beta = 12.6$; rocks being the most important type of banks) and INC ($\beta = -15.7$), thus confirming and further extending results from PCA.

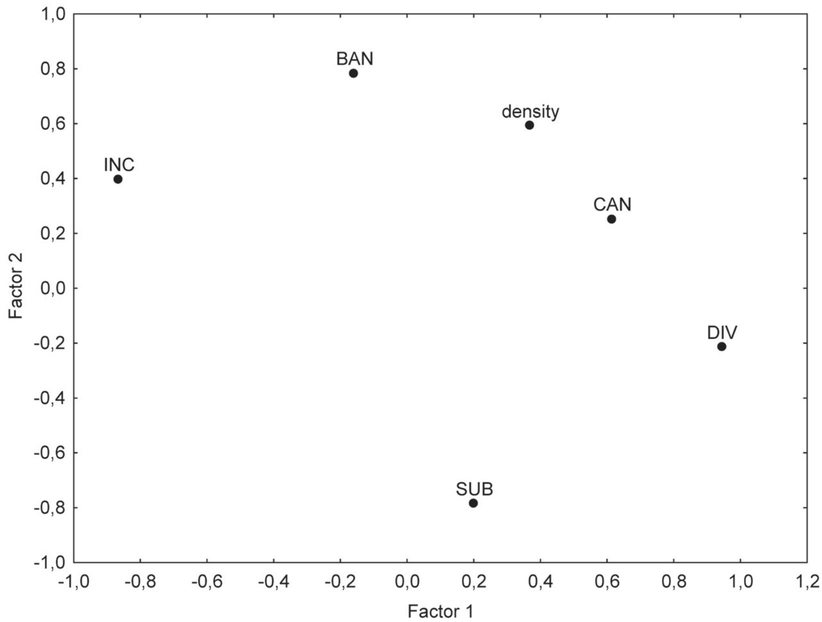


Figure 5. – Plot of loadings from a Principal Component Analysis highlighting similarity between high density of salamanders (i.e. > 20 individuals × ha^{-1}) and the various habitat variables. Note that factor 1 was positively correlated to DIV and negatively to INC, and factor 2 was positively correlated to BAN and negatively to SUB. For more details, and the meaning of the symbols, see the text.

DISCUSSION

Compared to previous studies (Angelini *et al*., 2001, 2006 ; Della Rocca, 2002 ; Della Rocca *et al*., 2005 ; Angelini, 2006 ; Bovero *et al*., 2006), this study has allowed to collect detailed field data on previously unknown aspects of the population ecology of *Salamandrina perspicillata* during the terrestrial phase : (i) the modelled density (estimated by DISTANCE procedures, see Buckland *et al.,* 1993), (ii) the linear distance of salamanders from water in periods other than the reproductive season, and (iii) the relationships between density and distance from water and a set of habitat variables that were a priori selected. Notably, our study is based on a very large sample compared to previous studies (e.g., Della Rocca, 2002 ; Della Rocca *et al*., 2005 ; Bovero *et al*., 2006), despite it has been conducted over a shorter time-span than other studies did (Della Rocca *et al*., 2005 ; Angelini, 2006).

Concerning the distance of salamanders from water, we observed that the individuals tended to increase their distance from water with elapsing of time after the first day of survey (13 April). This pattern was evident both at the small scale of most of the stream sectors and at the overall stream scale. We consider this pattern being dependent on two main factors : (i) the hydric regime of the stream is irregular and the stream is mostly desiccated by June ; thus, the humidity level at the stream banks is high only in springtime, whereas the humidity level is low by late May, thus forcing the salamanders to escape from the too dry microclimate of the immediate surroundings of the stream ; (ii) Salamanders oviposit in early spring (Angelini *et al*., 2001) thus in spring several individuals may be found in close proximity of the stream banks because they have just oviposited or are going to do this.

Concerning the population density, our estimates are likely reliable because the collected sample size (over 200 different individuals) is much over the minimum required (i.e. about 40 to 60) for the DISTANCE methodology to be applied (Burnham *et al*., 1980). However, given the sizes of our sub-samples, it is more likely that our density estimates for the various sectors of the stream are somewhat underestimated rather than overestimated (for the limits and biases of DISTANCE methodology, see Barry & Welsh, 2001 ; Ramsey & Harrison, 2004). In any case it is very unlikely that the relative differences in salamander density among the various stream sectors are biased and do not reflect genuine patterns of relative density variations (Buckland *et al*., 1993). These estimates reveal that the salamander density is not homogenous along the various sectors of the stream, but varies remarkably from site to site. This indicates that the local density of the population is likely non-random, but depends on the relative adequateness for salamanders of the proximate external conditions of the various stream sectors. At the scale of the stream valley, our density data are in good agreement with data available for other salamanders (e.g., see Heatwole, 1962 (40 individuals × ha^{-1}) ; Burton & Likens, 1975 (30 individuals × ha^{-1}) ; Wyman & Jancola, 1992 (37 individuals × ha^{-1}) ; Petranka *et al*., 1993 (33 individuals × ha^{-1})). Overall, the complex of the habitat features of each sector of the stream did not influence the relative density of salamanders, as shown by the poor matching between the sector-by-sector habitat feature similarities (see Fig. 2) and the high-density (> 20 salamanders × ha^{-1}) sectors (Fig. 4). Indeed, the stream sectors with highest salamander density were B, C, D, and G, but these sectors were not clustered together in terms of habitat feature similarity (Fig. 2). Looking at the data in more detail, however, we demonstrated by both PCA and logistic regression analyses that two independent habitat variables strongly affected the salamander density at the local scale : the type of stream banks (BAN, with the presence of rocks being crucial in determining a high density of salamanders), and the inclination of the slopes of the valley in the adjacent area of the stream banks (INC), with flat and moderately sloped inclinations favouring a high density of salamanders. We hypothesize that these habitat features are explainable by some kind of anti-predatory reasons, because the presence of abundant rocks (that are associated to an area difficult to access) around the salamander valley is certainly discouraging for the presence of their natural predators, for instance the grass snakes (*Natrix natrix*). Indeed, these snakes are uncommon in the salamander valley (Filippi & Luiselli, unpublished data), whereas they are much more common in other areas of the river basin where there is no such rock component. At the same time, the local presence of moderately sloped areas is likely important because it ensures an abundance of stones and logged trees, thus permitting the salamanders to use a lot of refugia where to hide during the daylight hours.

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