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European Plethodontid Salamanders on the Forest Floor: Testing for Age-Class Segregation and Habitat Selection

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Abstract.—**Spatial distribution of animals is affected by environmental and social factors, acting both at inter- and intraspecific levels, and generating patterns of segregation or aggregation. Several studies investigated age-class segregation of the European Cave Salamander *Speleomantes strinatii*, in underground environments, showing a clear spatial segregation. We investigated the spatial distribution of S. strinatii on the forest floor, on 111 plots surveyed three times/season for two consecutive seasons, in northern Italy during autumn 2017 and spring 2018. We analyzed count data to model co-abundance of adults and juveniles, using a conditional two-species N-mixture model, incorporating environmental covariates. In contrast with what was observed in underground environments, we recorded no spatial segregation between juvenile and adult of *S. strinatii* on the forest floor. Instead, we found that adults and juveniles showed different responses to environmental features.**

Spatial distribution of animals is affected by many environmental and social factors, which lead to particular and different population patterns (Fretwell and Lucas, 1970). In order to achieve their ecological optimum (e.g. reduced predation risk, access to shelters, resources, or mates), organisms develop behavioral adaptations, such as segregation or aggregation of individuals at the inter- or intra-specific level (Wertheim et al., 2000; Formica et al., 2004, Morales et al., 2012; Benson and Patterson, 2013). Considering the intraspecific level, these patterns may be achieved at multiple levels, e.g. age-classes, sexes, and familiarity (Jaeger, 1981; Catterall and Poiner, 1983; Ruckstuhl and Festa-Bianchet, 2001; Main, 2008). Moreover, the influence of environmental factors has repercussions also on habitat selection and on the home ranges of individuals. In fact, climatic conditions are constantly changing among seasons or years, forcing animals to constantly relocate themselves to maintain their physiological optimum (e.g., Feder, 1983; Seebacher and Alford, 1999, Lunghi et al., 2015). For this reason, it is important to understand how environmental conditions influence the spatial organization and the microhabitat selection of individuals within populations.

Among amphibians, lungless salamanders belonging to the family Plethodontidae are strongly dependent upon environmental conditions with high air humidity and reduced temperature variations (Feder, 1983; Feder and Londos, 1984). Moreover, terrestrial plethodontids generally have low dispersion capacities and relatively high site fidelity (Gergits and Jaeger 1990; Smith and Green 2005; Salvidio 2013; Mori, 2016), thus entailing an increase of possible intraspecific interactions. In some cases, different strategies may exist even within the same species. For example, the Eastern Red-Backed Salamander *Pletodon cinereus* shows variable behavior patterns depending on social and environmental conditions (Jaeger et al., 2016). Adults of the Eastern Red-Backed Salamander may exhibit aggression or tolerance towards conspecific individuals, depending on multiple factors such as sex, age, familiarity, and availability of shelters and trophic resources (Jaeger et al., 1995; Liebgold and Cabe, 2008).

Several studies investigated population structure and the spatial organization of the European Cave Salamander *Speleomantes strinatii* (Aellen, 1958; e.g., Salvidio, 1993; Lindström, 2010; Ficetola et al,. 2012). This species is a fully terrestrial plethodontid found in northwestern Italy and southern France on the forest floor, in the talus, along small streams, on humid rock faces, and inside underground habitats such as natural caves, man-made tunnels, or dry-stone walls (Lanza, 2007). In underground habitats, several studies showed a clear spatial segregation related to age, with juvenile salamanders always aggregating in the more external sectors, while adults were dispersed along the subsequent parts of the cave, with high abundances in the intermediate parts (Salvidio and Pastorino, 2002; Ficetola et al., 2013; Salvidio et al., 2020). Researchers gave various explanations for the reasons of this arrangement, e.g., prey distribution, social processes, microhabitat selection, but none completely explained the causes of this evident spatial segregation (Salvidio and Pastorino, 2002; Ficetola et al., 2013).

In any case, the aforementioned research has been conducted only in underground habitats, which are quite stable and resource-poor, in comparison with adjacent surface environments (Poulson and White, 1969; Culver and Pipan, 2014). Indeed, only one study analyzed the microhabitat selection of European plethodontid salamanders in woodlands (Costa et al., 2016), and without specifically analyzing spatial segregation patterns existing among different age-classes.

In this study, we investigated the spatial distribution of *S. strinatii* on the forest floor, starting from these hypotheses: 1) that age-related habitat segregation was present in populations inhabiting the forest floor, as already described in different underground populations (Salvidio and Pastorino, 2002; Ficetola et al., 2013), and 2) that this segregation could be due to different responses of juveniles and adults to different environmental variables (Ficetola et al., 2013), or to intraspecific competition or interference (e.g., Mathis, 1990).

Materials and Methods

Study Framework.—To test our hypotheses, we selected three sampling sites of the focal species, and randomly placed 26 to 57 permanent plots in each site, under a metapopulation design (Royle, 2004; Kéry and Royle, 2010). We counted salamanders in all sites during three repeated surveys over a short period. We sampled the same plots during two consecutive seasons: autumn and spring, given that, in the study region, Cave Salamanders

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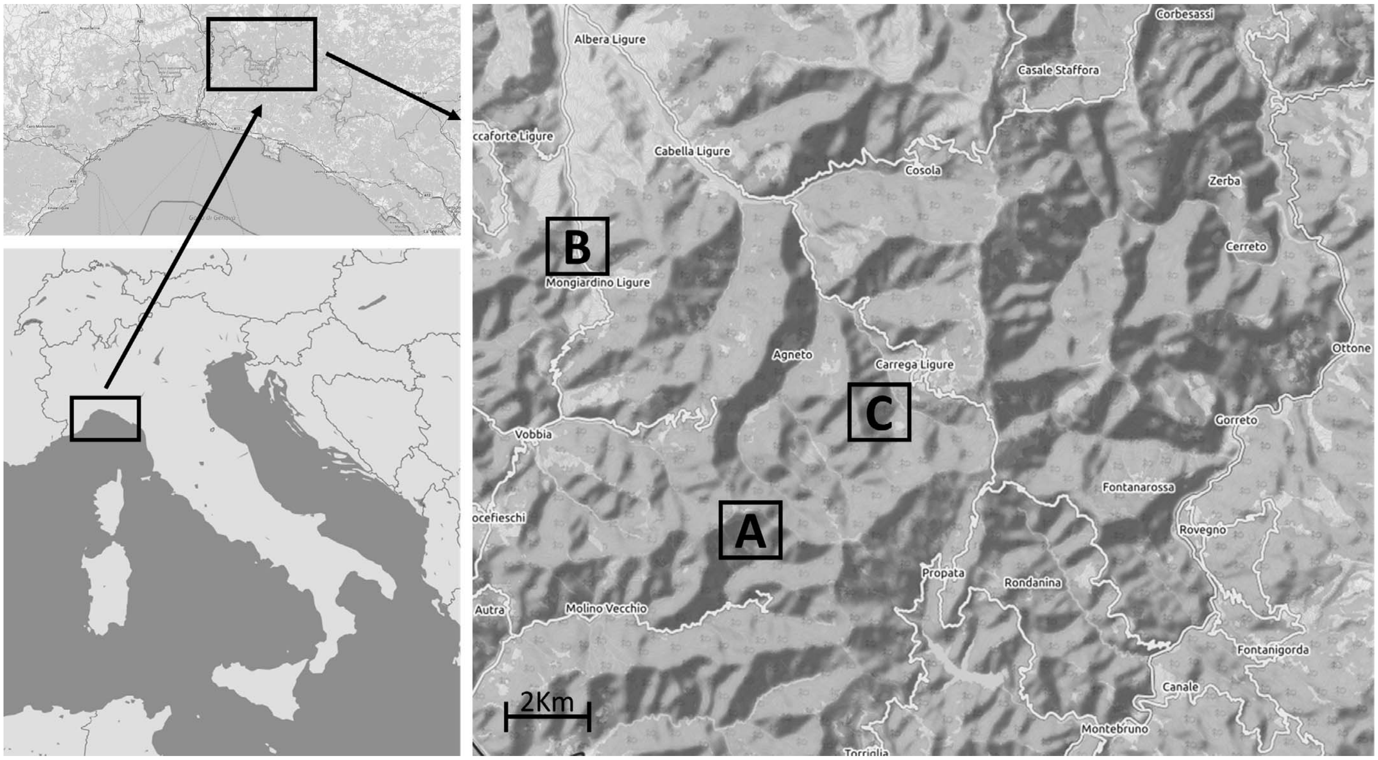

FIG. 1. Map representing locations of sampling sites. On the left, the lower panel shows the study area location in Italy, upper panel shows the study area in northern Italy. On the right, panels A, B, and C represent the location of sampling sites.

display a bimodal activity pattern and show a strong seasonality (Costa et al., 2021a), with high surface activity during rainy and moist periods (i.e. during spring and autumn months), while they retreat underground during summer and winter, which are the drier and coldest seasons of the year, respectively (Salvidio, 1993). We then employed count data to model co-abundance of adults and juveniles in the studied populations, using a conditional two-species N-mixture model (Royle, 2004), while incorporating environmental covariates (Waddle et al., 2010; Clare et al., 2016; Roth et al., 2016; Brodie et al., 2018).

Study Sites.—The study area is located in northern Italy, across the Apennine mountain range of the Liguria and Piemonte regions, and consists of three sampling sites within the same mountain unit (Fig. 1). Sampling site A is located at an altitude of 800 m a.s.l. in the municipality of Valbrevenna (44°33′36″N; 9°07′48″E), sampling site B is located at an altitude of 600 m a.s.l. in the municipality of Mongiardino Ligure (44°38′24″N; 9°03′00″E), while sampling site C is located at an altitude of 900 m a.s.l. in the municipality of Carrega Ligure (44°36′00″N; 9°10′12″E). The maximum distance between sites is less than 8 km (Fig. 1). All sampling sites are crossed by a first order Apennine stream and characterized by a Supra-Mediterranean mixed deciduous forest, dominated by Chestnut (*Castanea sativa* Mill., 1768) and European Oak (*Quercus pubescens* Willd., 1805; Blondel and Aronson, 1999). We placed, individually marked, and GPS-positioned 111 square plots, measuring 30 m^2 (5.5-m sides), at a minimum distance from each other of 20 m, and so divided: 57 plots in sampling site A, 26 in sampling site B, and 28 in sampling site C.

Salamander Sampling.—During autumn (7–17 November 2017) and spring (16 April to 25 May 2018), the same observer visited all sites three times, during daytime, in favorable weather conditions for salamander activity (e.g., during or after light rain). During each survey, the observer searched each plot for 4 min (Romano et al., 2017), checking the leaf litter, inspecting rock crevices with an electric flashlight, and lifting rocks and deadwood shelters. The species demographic structure has been described on the basis of body-size polymodal distributions (Salvidio, 1998). Two juvenile size-classes are well-separated from all other cohorts. Reproductive males possess a conspicuous mental gland, but some overlap among large immatures (i.e. subadults) and small reproductive females lacking the gland are present. In any case, subadult salamanders display a spatial behavior more similar to adults than to juveniles (Salvidio and Pastorino, 2002; Salvidio et al., 2020). Therefore, we used a cutoff measure in the field to separate small immatures from all other individuals (Ficetola et al., 2013; Lunghi et al., 2015) and to give sound information about spatial and ecological requirements of juveniles versus adults and subadults. We considered as juveniles all individuals measuring less than 55 mm snout-to-vent length, and not displaying sexual characters, while we considered adults all the remaining (Ficetola et al., 2013).

Environmental Covariates.—On the field, using a digital soil moisture meter (Extech MO750), we performed five measurements of soil relative humidity within each plot at a depth of 20 cm, on the same day (April 2018), 4 days following a 50-mm rain. The average of these five measurements was considered a plot-specific proxy of the soil moisture retention potential (*MOIST*). From a Digital Elevation Model (DEM; 20-m mesh size) of the study area, we calculated two covariates: the duration of direct insolation (*INSOL*), expressed in hours, and the Topographic Position Index (*TPI*). This index expresses the topographic position of each cell within the landscape, assuming positive values for cells located on ridges or hilltops, and negative values for cells located in depressions (Guisan et al., 1999). Moreover, for each sampling session, we recorded the day of the year (*DAY*; i.e., the continuous count of the number of days beginning each year from 1 January). We obtained the temperature of the survey (*TEMP*) and the cumulated rain in the 72 h prior to sampling (*RAIN*), from local weather stations. We conducted terrain analyzes with software SAGA 7 (Conrad et al., 2015).

Data Analysis.—We analyzed our repeated count data of adult and juveniles *S. strinatii* separately for autumn and spring, using a co-abundance formulation of the static binomial N-mixture model of Royle (2004), for two species with directional interactions (Kéry and Royle, 2020). Binomial N-mixture models estimate latent abundance state N at site i (N_i), assuming $N_i \sim Poisson(\lambda)$, where λ is the expected abundance over all sites, by using repeated counts C at site i during survey j (C_{ij}) to estimate individual detection probability p, assuming $C_{ij} | N_i \sim Binomial(N_i, p)$. Both parameters can be modelled as a function of environmental covariates through a log or logit link, respectively. In order to model the co-abundance of *S. strinatii* adults and juveniles, we considered age-classes as two distinct species, by stacking two N-mixture models, and we used the latent abundance of adults as a covariate in the abundance model of juveniles (Clare et al., 2016; Roth et al., 2016; Brodie et al, 2018). Therefore, we added a co-abundance effect term (γ) to the model (Waddle et al., 2010) to estimate the overall effect of the abundance of adults on the abundance of juveniles (γ_0), along with an abundance effect on the relationship between the abundance of juveniles and k environmental features (γ_k; $k = 1, \ldots, K$; Kèry and Royle, 2020). Prior to building our model, we standardized covariates and checked them for collinearity separately for spring and autumn, considering a cutoff for inclusion of Pearson $r < 0.7$ (MacNally, 2002; Dormann et al., 2013). We modelled the detection process of both adults and juveniles as follows:

$$logit(p_{ij}) = \alpha_0 + \alpha_1 * DAY_{ij} + \alpha_2 * TEMP_{ij} + \alpha_3 * RAIN_{ij} + \delta_{ij}$$

where α_0 is the intercept, α_1–α_3 are covariate effects, and δ is a random effect, assuming normal distribution, to account for possible over dispersion in the detection process (Kéry and Schaub, 2011). For the abundance of adults and juveniles we built the following models:

$$log(\lambda_i^A) = \beta_0^A + \beta_1^A * MOIST_i + \beta_2^A * INSOL_i + \beta_3^A * TPI_i + \varepsilon_i$$

$$\begin{aligned} log(\lambda_i^J) = {} & \beta_0^J + \beta_1^J * MOIST_i + \beta_2^J * INSOL_i + \beta_3^J * TPI_i + \gamma_0 * N_i^A \\ & + \gamma_1 * MOIST_i * N_i^A + \gamma_2 * INSOL_i * N_i^A + \gamma_3 * TPI_i * N_i^A + \varepsilon_i \end{aligned}$$

where the superscript A and J in the formula stands for adults and juveniles, respectively, β_0 is the intercept, β_1–β_3 are covariate effects, $N^A{}_i$ is the latent abundance of adults at site i, γ_0 is the co-abundance effect of adults on juveniles, γ_1–γ_3 are covariate effects on the relationships between juveniles' abundance and environmental features and ε is a site-level random effect assuming normal distribution (Kéry and Schaub, 2011). We estimated model parameters using a Bayesian approach with Markov chain Monte Carlo methods, using uninformative priors. We ran three chains, each one with 350,000 iterations, discarding the first 50,000 as a burn-in and thinning by 100. We considered that chains reached convergence when the Gelman–Rubin statistic was <1.1 (Gelman and Rubin, 1992). We considered covariates on both abundance/detection and age-class interaction to have a significant effect when the 90% credible interval (CRI) of the posterior distribution did not cross the zero. The N-mixture model used here is derived from the static binomial N-mixture model proposed by Royle (2004), which shares the same assumptions and is prone to the same criticism on parameter identifiability, assumption violation, and overdispersion (e.g. Barker et al., 2018; Link et al., 2018; but see Kéry, 2018). Because of this, properly assessing model fit is of primary importance (Duarte et al., 2018; Knape et al., 2018; Costa et al, 2021b). For this purpose, we employed posterior predictive checks based on χ^2 statistics as a measure of the discrepancy between observed and simulated data and calculated a Bayesian *P*-value accordingly (Kéry and Schaub, 2011). Analyses were conducted calling program JAGS (V4.3.0; Plummer, 2003) from the R environment (R Core Team, 2014) with package "JagsUI" (V1.5.1; Kellner, 2019).

Results

During autumn, we obtained a total of 340 detections of salamanders, of which 278 were adults (mean count = 0.83; range = 0–12) and 62 juveniles (mean count = 0.18; range = 0–3). In spring, we obtained a total of 395 detections of salamanders: 248 of them adults (mean count = 0.74; range = 0–11) and 147 juveniles (mean count = 0.44; range = 0–6). After evaluating goodness-of-fit of our stacked N-mixture models by means of posterior predictive checks for both seasons, we recorded a good fit for adults (Bayesian *P*-value; autumn = 0.46, spring = 0.49; see Supplementary Figs. S1, S2) and juveniles (Bayesian *P*-value; autumn = 0.34, spring = 0.39; see Supplementary Figs. S3, S4). Convergence, assessed with R-hat value, was successful for all parameters monitored (maximum R-hat; autumn = 1.003, spring = 1.014). The complete list of parameters' estimates and their 90% CRI for both seasons are reported in Table 1, while graphical representations of covariates' effects are shown in Figures 2–3, for autumn and spring, respectively. Estimated per-site abundance of adults was slightly higher in autumn ($\lambda = 1.68$; 90% CRI = 1.15–2.50) than in spring ($\lambda = 1.24$; 90% CRI = 0.90–1.65). At the same time, juveniles' abundance was lower in both seasons (λ autumn = 1.07; 90% CRI = 0.42–2.47; λ spring = 0.56; 90% CRI = 0.31–0.92). *MOIST* had a significant positive effect on the site-specific abundance of both adults and juveniles, in all seasons. *TPI*, in turn, had a significant negative effect on the abundance of adults (Table 1).

Detection probability for adults remained almost constant (*P* = 0.27; 0.31 for autumn and spring, respectively), while increased from autumn to spring for juveniles (*P* = 0.13; 0.33 for autumn and spring, respectively). In autumn, all covariates included in the detection model of adults had a significant effect: *DAY* had a negative effect, while *TEMP* and *RAIN* increased the probability of detection. For what concerns juveniles, in the same season, only *TEMP* and *RAIN* had a significant positive effect on *P*. During spring, all detection covariates on adult model remained significant, but *DAY* and *TEMP* shifted their effect on *P*, hence having a positive and negative effect on the detection process, respectively. Also, in spring only one covariate showed a significant effect on juveniles' detection probability: *RAIN* had a positive effect on *P*.

Finally, the co-abundance effect term (γ_0) was not significant in both seasons, indicating a lack of spatial segregation and an absence of relationship between the abundance of adults and juveniles.

Discussion

In the present study, contrary to our expectation and to what has been observed in cave populations, we recorded no spatial

TABLE 1. Co-abundance N-mixture model parameters' estimates for adults and juveniles *Speleomantes strinatii* in autumn 2017 and spring 2018. PD = probability of direction calculated from the posterior distribution; ESS = effective sample size. For model and parameter description see Materials and Methods section. *Indicates significance for covariate or co-abundance effect.

	Autumn				Spring			
Parameter	Estimate	90% CRI	PD	ESS	Estimate	90% CRI	PD	ESS
Adults								
Mean λ	1.68	1.15–2.50	–	5258	1.24	0.90–1.65	–	2034
β_0	0.49	0.14–0.91	–	5545	0.19	−0.09–0.50	–	3289
$\beta_{1\ MOIST}$	0.72*	0.50–0.94	1.00	7036	0.96*	0.76–1.16	1.00	5243
$\beta_{2\ INSOL}$	0.13	−0.09–0.33	0.83	9000	−0.20*	−0.38–−0.02	0.97	9000
$\beta_{3\ TPI}$	−0.20*	−0.40–−0.01	0.95	7129	−0.15*	−0.31–0.00	0.95	9000
Mean p	0.27	0.17–0.38	–	3198	0.31	0.21–0.41	–	1183
α_0	−0.99	−1.58–−0.49	–	4230	−0.81	−1.30–−0.36	–	1156
$\alpha_{1\ DAY}$	−0.32*	−0.61–−0.03	0.97	9000	0.32*	0.08–0.56	0.99	6707
$\alpha_{2\ TEMP}$	0.46*	0.22–0.72	1.00	9000	−0.71*	−1.05–−0.41	1.00	9000
$\alpha_{3\ RAIN}$	0.34*	0.08–0.63	0.99	9000	0.27*	0.04–0.51	0.97	6275
Juveniles								
Mean λ	1.07	0.42–2.47	–	2074	0.56	0.31–0.92	–	908
β_0	−0.09	−0.87–0.90	–	6841	−0.64	−1.17–−0.08	–	1470
$\beta_{1\ MOIST}$	0.86*	0.34–1.42	1.00	3000	1.05*	0.57–1.51	1.00	4076
$\beta_{2\ INSOL}$	0.05	−0.50–0.59	0.56	7532	0.06	−0.32–0.45	0.60	6909
$\beta_{3\ TPI}$	−0.37	−0.81–0.07	0.92	9000	−0.13	−0.48–0.22	0.73	2823
Mean p	0.13	0.04–0.23	–	9000	0.33	0.21–0.45	–	1154
α_0	−2.02	−3.06–−1.19	–	5221	−0.71	−1.32–−0.19	–	999
$\alpha_{1\ DAY}$	0.35	−0.07–0.79	0.91	8850	0.11	−0.17–0.40	0.75	9000
$\alpha_{2\ TEMP}$	0.43*	0.09–0.78	0.98	6088	−0.21	−0.58–0.13	0.84	9000
$\alpha_{3\ RAIN}$	0.45*	0.01–0.92	0.95	7845	0.43*	0.13–0.75	0.99	9000
γ_0	−0.04	−0.17–0.09	0.74	9000	0.15	−0.07–0.38	0.85	9000
$\gamma_{1\ MOIST}$	−0.04	−0.17–0.06	0.73	9000	−0.08	−0.20–0.04	0.87	9000
$\gamma_{2\ INSOL}$	−0.11	−0.27–0.03	0.90	8426	−0.03	−0.11–0.03	0.80	9000
$\gamma_{3\ TPI}$	0.06	−0.03–0.17	0.86	2653	0.02	−0.05–0.09	0.71	9000

segregation or aggregation between juvenile and adult of *S. strinatii* on the forest floor. In fact, we did not observe any density-dependent effect of adults on juveniles during the two consecutive seasons of surface activity considered (Table 1). These findings are in good agreement with those on *Plethodon cinereus*, in which the distribution of juveniles does not appear to be strongly influenced (i.e. familiarity, kin discrimination, or competition) by the home ranges of adults after rainfall events (Liebgold and Jaeger, 2007). Furthermore, salamanders living on the forest floor are more tolerant to the presence of conspecifics, especially during favorable humid periods, in which food and shelters are not limiting resources and competition is reduced (Jaeger, 1980, 1981). Furthermore, both abundance and activity of juvenile and adult salamanders seemed to be affected in different ways, or with a different magnitude, by environmental features and climatic conditions, as observed by Ficetola et al. (2013). In particular, during both autumn and spring, *MOIST* was the only variable positively influencing the abundance of both adult and juvenile salamanders, indicating that all age-classes concentrated in the more humid and favorable habitat patches (Lunghi et al., 2015). In autumn, *TPI* negatively affected only adults' abundances, thus indicating that adult salamanders avoided habitat patches located on ridges and hilltops, while occupying those laying in valleys and topographic depressions: a pattern already observed for plethodontid salamanders and probably adopted to minimize water loss (Peterman and Semlitsch, 2013). The duration of insolation (*INSOL*) had a positive effect on adults' abundance in autumn and a negative effect in spring. Because in autumn temperatures are lower and the time of sunlight is shorter, salamanders seek the sunniest patches to maximize daily activity in order to forage or mate (Romano et al., 2017), while in spring they avoid them. However, although we found an 83% probability that *INSOL* positively correlated with abundance in autumn, the 90% CRI of the effect of *INSOL* overlapped the zero (Table 1), probably because it may be obscured by the influence of other more meaningful variables, i.e. soil moisture.

Detection probability for adults was quite constant between seasons, while for juveniles it increased from autumn to spring. As already observed for abundance, adults were more influenced by extrinsic conditions than juveniles. Indeed, the effect of all survey covariates on the detection probability of adults is significant in both seasons, while juveniles' detection probability is affected only by *TEMP* in autumn and *RAIN* in spring. This is probably due to the lower abundance of juveniles, which in turn implies a higher uncertainty in detection estimates. This confirms the difficulty of correlating salamander abundance and detection probability with individual microhabitat variables (Dodd and Dorazio, 2004), because a species or, in this case an age-class, may not be completely influenced by site covariates. For adults in both seasons, and also for juveniles in autumn, detection probability was higher in correspondence with considerable cumulated rain. After or during rainfall there is always a consequent increase of humidity, therefore influencing salamander activity (Salvidio, 1993). By contrast, the effect of *DAY* had a different direction, depending on the season, on the detection probability of adults. In autumn, with the progression of the sampling season, suitable environmental conditions tend to decrease and so does the detection probability (i.e. negative effect of *DAY*), while during spring the opposite occurs (i.e. positive effect of *DAY*). For the variable *TEMP* we also observed a shifted effect between seasons: in late autumn, when temperatures are lower and forest-floor daily activity is usually reduced (Romano et al., 2017), adults tend to be more active during warmer days (i.e. positive effect of *TEMP*), while the opposite occurs in spring (i.e.

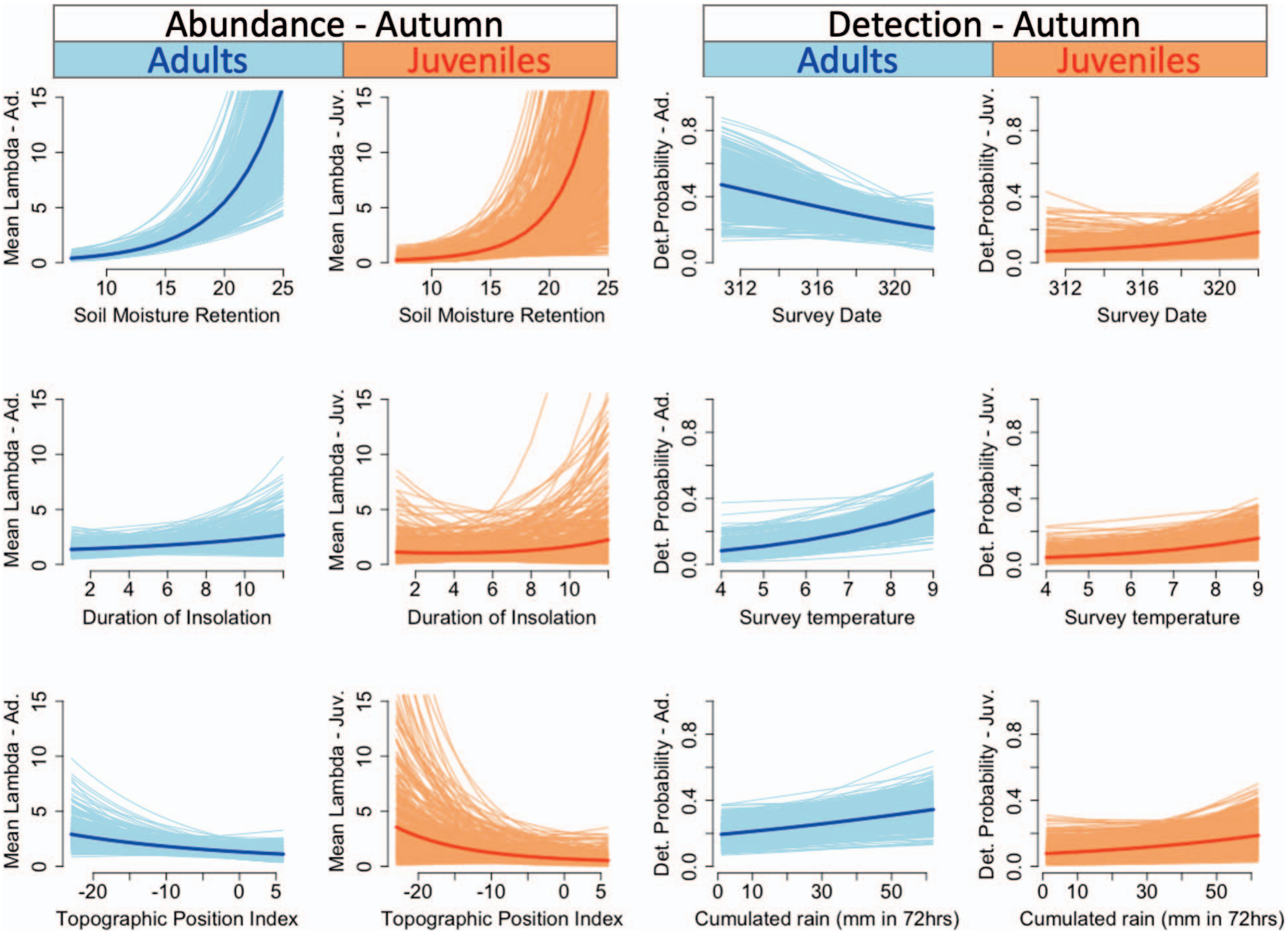

FIG. 2. Plots showing the relationships between covariates and abundance/detection probability of adults (blue) and juveniles (red) *Speleomantes strinatii* in autumn 2017. Narrow lines represent a random sample of 500, drawn from the posterior distribution, while the thick line represents the mean of the posterior distribution.

negative effect of *TEMP*). Plethodontids could display behavioral thermoregulation within the range of ambient temperatures, in order to control their body temperatures in response to internal and environmental cues (Spotila, 1972; Feder, 1982).

Contrary to our findings, in underground environments *S. strinatii* shows a clear age-class segregation (Salvidio et al., 1994; Ficetola et al., 2013; Salvidio et al., 2020). Juvenile salamanders concentrate near the entrance of the cave and occupy the twilight zone, displaying an aggregate distribution (Salvidio and Pastorino, 2002), while subadults and adults disperse in the inner cave, where absence of light is permanent and climatic conditions are more stable, daily and seasonally (Ficetola et al., 2013; Salvidio et al., 2020). However, when environmental features are accounted for, juvenile and adult Cave Salamanders may show a positive abundance relationship (Ficetola et al., 2013), suggesting that co-occurrence of these age-classes is positively affected by an unmeasured environmental factor or some kind of social interaction (Ficetola et al., 2013). Observed differences in the spatial distribution in caves could be caused by the presence of an environmental gradient, in which illumination, temperature, and relative humidity are all strongly autocorrelated (Ficetola et al., 2020). In fact, all these variables show directional gradient from the surface to the inner parts of the underground environment (Tobin et al., 2013; Mammola and Isaia, 2018).

In conclusion, in the present study, we expanded the knowledge on the age-class relationships occurring within *S. strinatii* populations, by extending the study of spatial segregation from a simplified and gradient-dominated environment (i.e. caves) to a more complex and patchy one (i.e. forest floor), in part confirming and in part rejecting our starting hypotheses. Our findings suggest that the observed pattern of spatial distribution of adults and juveniles is affected by a complex interaction of environmental and social factors (Ficetola et al., 2013). For this reason, to better understand the arising of age-class segregation and which factors affect spatial distribution and habitat selection of Strinati Cave Salamander, it will be necessary to carry out further investigations, using methods that retain individual identity, and focusing on the effect of fine-scale habitat features, trophic availability, and site fidelity.

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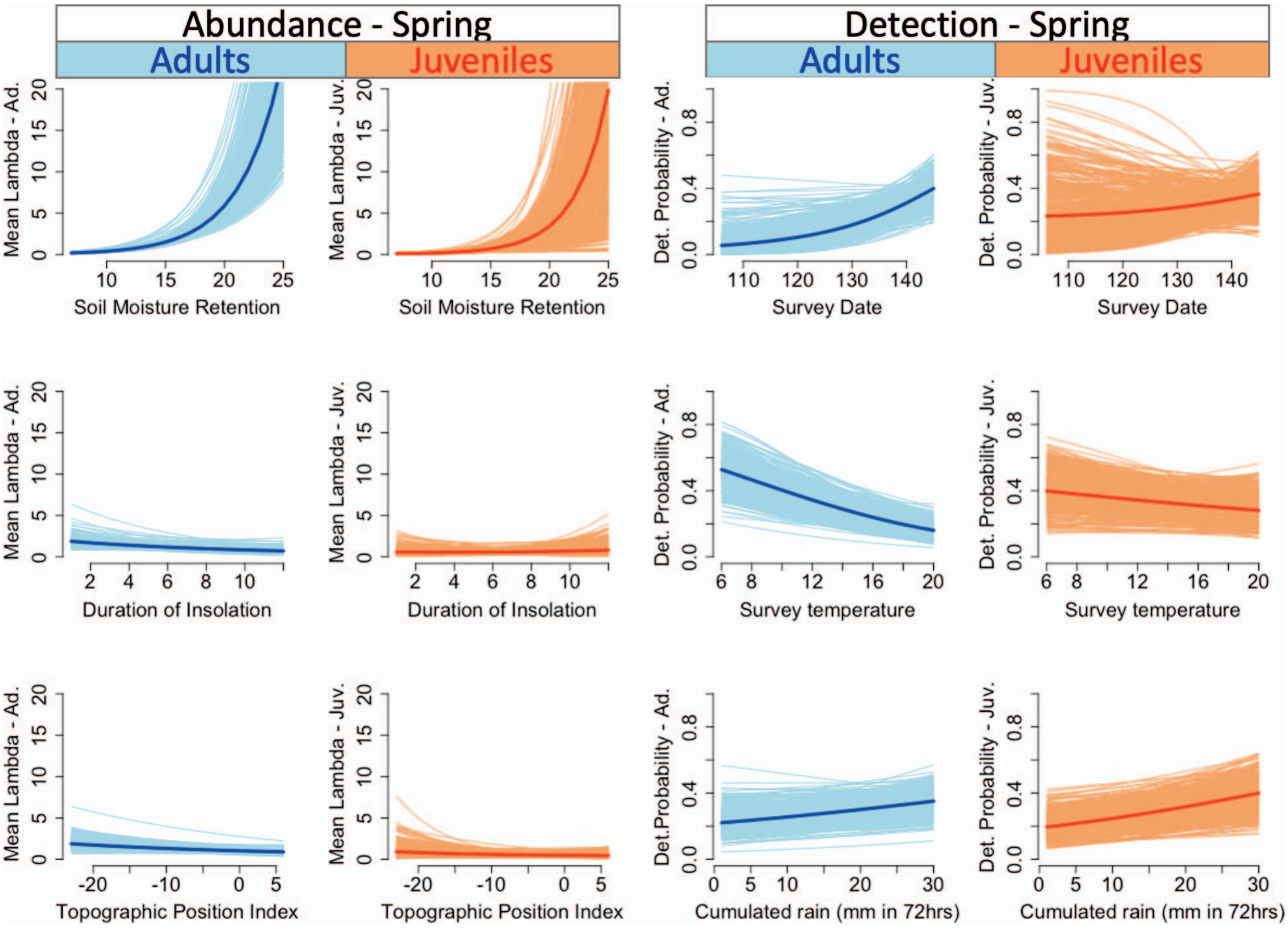

FIG. 3. Plots showing the relationships between covariates and abundance/detection probability of adults (blue) and juveniles (red) *Speleomantes strinatii* in spring 2018. Narrow lines represent a random sample of 500, drawn from the posterior distribution, while the thick line represents the mean of the posterior distribution.

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Supplementary Data

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