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Fire salamander (*Salamandra salamandra*) males' activity during breeding season: effects of microhabitat features and body size

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Abstract. After metamorphosis, fire salamander is considered fully terrestrial, usually inhabiting wooded areas around aquatic habitats. It is often reported that only females go back to water for laying the larvae. The aim of this study is to assess if sites where males are active during the breeding seasons have specific features among microhabitat determinants and distance from the breeding sites. In the autumns of 2013 and 2014, we surveyed 26 transects and 72 plots around six isolated breeding sites in North-Western Italy. During rainy nights, we recorded males position and distance from breeding pools, while during daytime we characterized the environmental features of the plots. Males detection probability was relatively high (mean ± SE: 81.0 ± 4.3%). Several males (15% of the observations) were encountered inside breeding pools where females were laying larvae. Males occurrence was positively related to plots closer to breeding pools and higher leaf litter depth. Larger males were found closer to the breeding pools. This case study shows that the distribution of fire salamander males during the breeding season depends on the breeding sites.

Keywords. Breeding pond, ecology, mating behaviour.

INTRODUCTION

The assessment of ecological relationships between amphibians and their terrestrial habitat are very important to understand proper management actions and enhance conservation policies. Among European amphibians with extensive terrestrial habits there is the fire salamander, *Salamandra salamandra.* This is a widespread species in Europe, that has been extensively studied in its use of different breeding sites, while studies on terrestrial habitat requirements were less frequent (Denoël, 1996; Carafa and Biondi, 2004; Catenazzi, 2016). For breeding, *S. salamandra* is generally linked to small lotic environments (Manenti et al., 2009), but it can also use a wide variety of habitats like ponds (Egea-Serrano et al., 2006; Denoël and Winandy, 2014; Caspers et al., 2015) and hypogeous (i.e., subterranean) springs or pools (Ianc et al., 2012; Manenti et al., 2015). Moreover, some populations evolved complete viviparity, skipping the aquatic larval stage (Velo-Anton et al., 2007). Adults are strictly terrestrial and generally live in broadleaved forests (Joly, 1968). Even if it is generally reported that only females migrate to wetlands to give birth to the aquatic larvae while males do not go back to water after metamorphosis (Joly, 1968; Nöllert and Nöllert, 1992; Denoël, 1996; Lanza et al., 2009; Ficetola, 2012), it is known that the species lives around water bodies without strong displacements from them (Ficetola, 2012).

In general the species seems to prefer deciduous mixed woodlands, especially those mostly dominated by the common beech *Fagus sylvatica* (Lanza et al., 2009; Balogova and Uhrin, 2014). Studies performed in the Alps show that the fire salamander prefers areas which are characterized by a mean annual precipitation > 600

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mm (Schauer et al., 2012). Salamanders tend to be active at temperature as low as 1 °C, with a thermal optimum in terms of trade-off between thermoregulation and metabolic costs at 8 °C (Catenazzi, 2016). Estivation occurs at temperatures above 16 °C (Catenazzi, 2016). *S. salamandra* seems to avoid dry forests (especially spruce monocultures) and its ecology in floodplains and coniferous forests needs further studies (Lanza et al., 2009). Recent studies provided evidences of the importance that a complex ensemble of determinants, linked to both terrestrial and aquatic habitats, plays in allowing the occurrence of stable populations (Ficetola et al., 2011). However few studies are available in terms of microhabitat use in the forest environment. These data could allow to gain a better knowledge on proper forests habitat management for conservation purposes.

Adults are considered to be territorial even if some superimpositions of home ranges may occur (Lanza et al., 2009) and during winter individuals may aggregate in shelters (Baumgart, 1981; Balogova and Uhrin, 2014). The adult activity usually shows two peaks during the year, coinciding with high rainfall periods: one during spring, and one in autumn (Joly, 1968; Lanza et al., 2009). These are also the two seasons in which both mating and larvae laying occur, especially South to Alps (Romeo et al., 2015). Females usually lay larvae during night and may stay around their breeding sites for several nights, as females repeatedly give birth to only some of the larvae they retain (Joly, 1986); moreover in these occasions they likely mate for the following year's brood (Steinfartz et al., 2006). Mating happens on land habitats, most often in spring and in autumn months, and usually at night (Lanza et al., 2009). The reproductive males are reported to show a frequent posture during the courtship, in particular they rise on their anterior limbs and show a quick bucco-pharyngeal respiration. This posture can be frequently observed in the males of *S. salamandra* (Bruno, 1973; Catenazzi, 1998) and also in males of other congeneric species as *S. lanzai* and *S. atra,* also in absence of females and in more or less plane and open areas (Manenti and Pennati pers. obs.). In *S. salamandra* the display of this posture has been interpreted both as a territorial and competitive behaviour among males (Bruno, 1973), and as a strategy allowing a more effective perception or attraction of the females (Lanza et al., 2009). The advantage of an affective female detection could also favour a non-random choice by the males of the microhabitat where being active during the mating seasons. However, specific ethological and ecological studies are missing and, at present, it is impossible to say if males spatial patterns are linked to specific reproductive behaviours.

The general hypothesis of the present study is that, to increase their chances of mating, males should stay close to the females as soon as they are ready to mate, i.e., after they laid their larvae. Our specific hypotheses are that getting closer to the breeding ponds should be the most effective spatial strategy for males and that they should compete for the territory patches closer to the breeding sites. We therefore tested if the sites where males are active during the breeding seasons have specific features among some microhabitat determinants and distance from the breeding site. Moreover, we want to assess if male size (as a proxy of their reproductive quality) have a role in determining the location of activity sites. These information could increase our understanding of the spatial and reproductive ecology of *S. salamandra* and confirm that males compete for the occupancy of some sites/microhabitats and could be useful to perform further ethological studies on their reproductive and territorial behaviour.

MATERIAL AND METHODS

During the months of October and November 2013 and 2014, we performed surveys around 6 distinct breeding sites of the fire salamander located in the districts of Lecco and Monza e Brianza, Lombardy, North-western Italy (Fig. 1). The study area is characterized by hilly reliefs with a good cover of broad-leaved woodlands dominated by *Castanea sativa* and *Quercus robur*. It is crossed by a dense hydrographic network characterized by different typologies of water bodies such as creeks, streams, brooks, resurgences and rivers. Breeding sites were characterised by isolated pools, fed by small springs, with an area ranging from 5 to 15 m^2. Each isolated pool corresponded to a different locality. The maximum distance between the 6 sites studied was 14 Km (average 6.9 Km).

Linear transect surveys

We looked for fire salamander males during night surveys in rainy nights (between 9:00 pm and 12:00 pm), during which we also check for larvae depositions by females. These surveys were performed along 26 linear straight transects (4 linear transect around 4 pools and 5 linear transect around other two pools) beginning at distances comprised between 110 and 75 m (average ± SE: 97.2 ± 5.3 m) from the breeding sites and ending in them. The starting positions of the transects were randomly chosen during the daytime of the first field survey, and distinctive marks were placed to distinguish them to each other. Then we walked in the direction of the breeding site measuring the covered distance with a measuring strip and tracking and mapping the transect with a GPS Garmin Eterx 10 (precision 3 m). The width of the surveyed area around the transect was 5 meters (2.5 m on each side). For each survey season (October-November 2013 and 2014), we performed at least two surveys

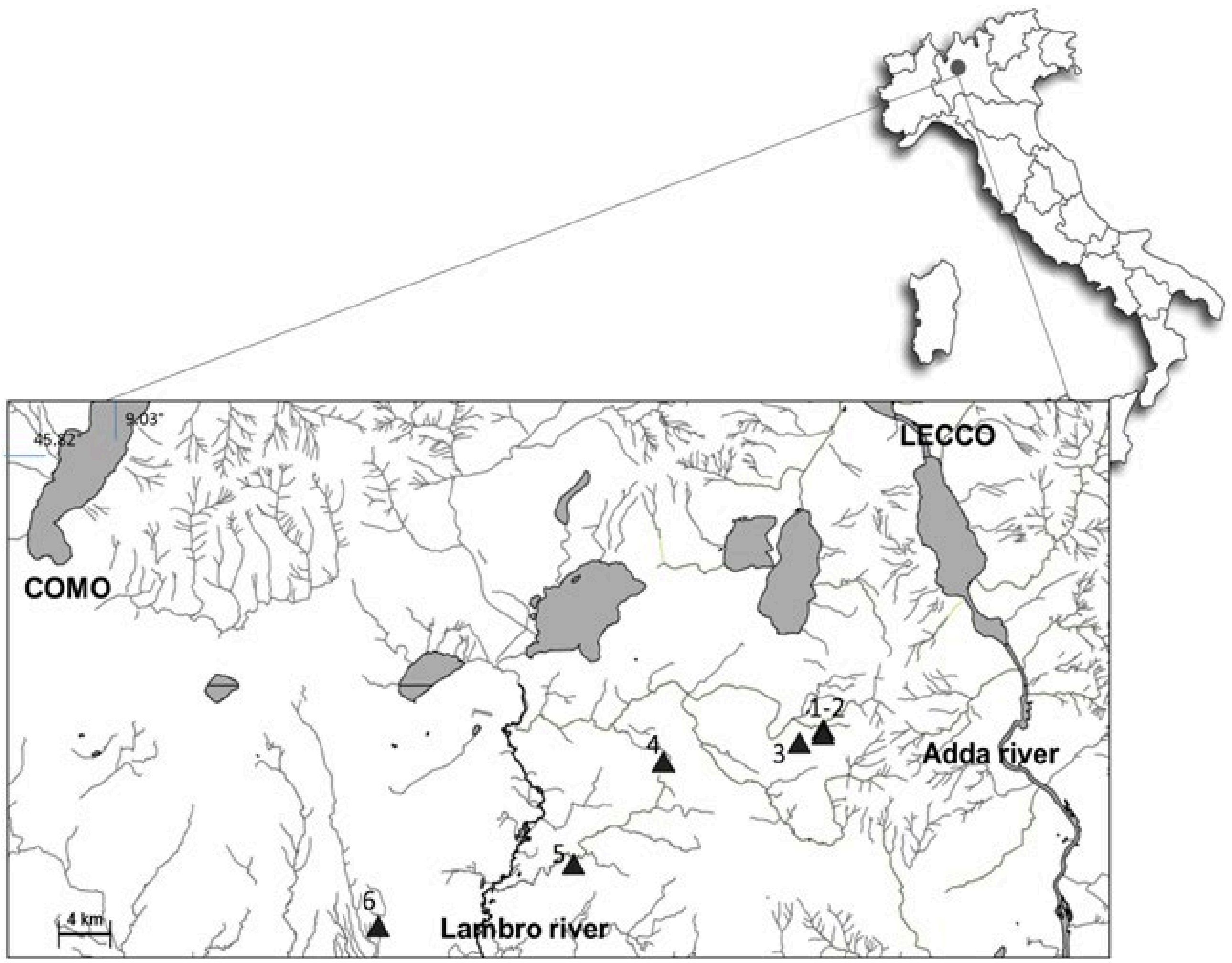

Fig. 1. Localization of the breeding sites (triangles) of fire salamander around which we positioned linear transects and plots .Numbers indicate the site ID; some of the sites are superimposed due to geographic proximity.

for transect (range 2-4 surveys per transect, average ± SE: 2.76 ± 0.11 times). Surveys for each transect lasted from 30 to 45 minutes. During night surveys, we caught all the fire salamanders that we encountered. We placed the individuals in small holed bags in the same point of observation following protocols used for other salamanders (Lunghi et al., 2015) in order to do the measures successively, without affecting the position of the individuals occurring in the successive parts of the transect. The point of encounter was registered with the same GPS Garmin Etrex 10. At each survey we re-recorded the starting point of the transects and the pool position, tracking all the transects length. After the capture of all the observed individuals we took a picture of each individual and registered their position. Each individual was photographed on a plastic millimetre paper to allow successive accurate measures of the total length, and weighed with a precision dynamometer PESOLA (precision ± 0.1 g). The total lengths (precision ± 1 mm) of the males was obtained through the software "ImageJ". In 2014 we also took a picture of the dorsal patterns to allow the individual identification of the salamanders. For each salamander, we used GPS data to record the distance from the pool, and we measured the maximum slope inclination of the capture point with a digital inclinometer Digital Angle Bevel Box 360 (precision ± 0.2°) placed over the middle of a flat wooden board of 10 × 10 cm. Sex determination was performed on the basis of their cloaca features. As males develop a swollen cloaca when they are sexually mature (Raffaëlli, 2007), the individuals shorter than the smallest recognizable male were considered juveniles.

Sample areas/plots surveys

Along each transect, we chose a total of 72 circular plots with a 2.5 m ray, separated each other by at least 5 meters, and placed within 30 m from the breeding pools (average number ± SE of plots per transect was 2.7 ± 0.2, range: 2-5). The number of plots was chosen to specifically cover the part of the transects placed closer to the breeding sites, and their position was randomly chosen within a buffer of 30 m around each breeding site to gather detailed information on the microhabitats. In these plots, we recorded five environmental variables during daytime surveys: litter leaf depth, maximum slope inclination, number of trees with a diameter > 50 cm, distance from the breeding pool, bush cover. Leaf litter depth may be linked to shelter availability, humidity level of the soil and prey availability: it was measured placing a rigid ruler in the point of the plot with the maximum litter depth and measuring its height from the soil. Maximum slope may be important to explain salamander distribution (Manenti et al., 2011; Werner et al., 2014): inclination was measured placing digital inclinometer over a rigid wooden board (20 × 20 cm) in the point of the plot with the maximum inclination. The trees diameter was assessed using a measuring strip: all the trees with a diameter > 50 cm occurring in the plots were counted, in order to detect the possible effect of the occurrence of large and old trees that are often shelters for salamanders (Apodaca and Godwin, 2015). The distance of the plot from the breeding sites was assessed using measuring strips with a precision of 0.01 m. The bush cover was estimated following the point-intercept method described by Dodd (2010), using a 2 m long pole placed vertically in the plot center and numbering the times it intercepts any piece of vegetation. The position of each plot was recorded through GPS and each plot was marked with small, temporary but visible during night marks over trees or rocks.

Statistical analyses

Linear transect surveys

We built a Linear Mixed Model (LMM) to assess factors influencing the distance from the breeding sites at which males were found during night samplings. We limited this analysis to the males observations of 2014 (n = 80), because the identification of each individual (based on their dorsal pattern) was performed only in the second year. We added the males square-root transformed total length as dependent variable, and log-transformed distance from the breeding site, and log-transformed slope inclination as independent variables. As we found recaptures, we added the individuals identity as random effect. Variables transformation was performed to increase normality (tested through a Shapiro test). Since there is a strong exponential linear dependence between weight (W) and total length (L) of males ($W = 0.02\ L^{2.67}$; $R^2 = 0.82$), we considered only total lengths to analyse the effects of male size on their distribution. The variables significance was assessed through a Wald F test (Bolker et al., 2008).

Sample areas/plots surveys

We used PRESENCE 5.5 to assess in each plot the probability of detection per visit of males and females (Hines, 2006). Accounting for the probability of detection it is important because a non-detection record (equivalent to a recorded absence) represents a lack of evidence that the species occurs in a specific site (Gomez-Rodriguez et al., 2012). We used multiple season models (MacKenzie et al., 2003) to understand the predictors (survey and environmental variables) that satisfactorily described the collected records while accounting for imperfect detection (MacKenzie et al., 2002). Meaning that we considered the story of detection and non-detection per visit per plot considering both Autumn 2013 and Autumn 2014. On the basis of this history, PRESENCE returns a probability to have correctly assessed the presence/absence of the species in the plots, such as a probability of occurrence (MacKenzie et al., 2003). To disentangle the role of the predictors it is necessary to build models comprising all their possible combinations and to select the best reliable model. We used the Akaike's information criterion (AIC values) to select the best model explaining males probability of occurrence in the plots (Rolls, 2011; Lele et al., 2013). The model with the lowest AIC and the highest weight was considered the best model describing species detectability (Burnham and Anderson, 2002). Since a model with no covariates for neither occupancy nor detectability (model $\psi(.)\ p(.)$) showed that the detection probability of males was relatively high (mean ± SE: 81.0 ± 4.3%), when building the other occupancy models, we only varied the predictor variables for occupancy and always used a model with constant detection probability (i.e., model ψ(predictor variables) $p(.)$).

Thanks to the relative small number of variables considered, we were able to test all the possible combinations among them. In order to reduce the retention of overly complex models we excluded from the candidate set those models that were more complicated versions of any model with a lower QAIC value (Richards et al., 2011). This approach reduces model uncertainty, and improves the performance of model selection (Richards et al., 2011). We present all the candidate models with some supporting information, e.g. delta-AIC < 4, QAIC weight > 0.1. To assess the relative role of the variables composing the best model we used a Wald F test (Bolker et al., 2008) with "car" package in R environment.

To asses which environmental factors affect males sites choice, we preferred to use the estimates of males probability of occupancy at a given plot (calculated with

PRESENCE) rather than the observed "naïve" absence/presence. We considered this value as the dependent variable of a Generalized Linear Mixed Model (GLMM) with a quasi-binomial error distribution using the log-transformed microhabitat features recorded in the plots as independent variables. We included pool locality as random factor, to account for the fact that several plots can surround the same pool. All the analyses were performed by R software using the packages "lmerTest", "lme4" and "car" (R Development Core Team, 2013).

RESULTS

Linear transects surveys

During the two sampling seasons, we caught 213 salamanders 147 of which were males. Males total length was 17.1 cm on average (maximum 21.6 cm, minimum 8 cm, SD = 2.39), while weight was 32.5 g on average (maximum 45 g, minimum 4 g, SD = 10.0). Females were 17.5 cm long on average (maximum 21.2 cm, minimum 8.5 cm, SD = 3.3) and weighed 43.4 g on average (maximum 78 g, minimum 6 g, SD = 18.7). In 67% of night surveys, we observed ponding females near the pools borders or on floating elements in the pools. The 15 % of the observed males were encountered inside breeding pools where females were laying larvae. Average males distance from the pools was 21.2 m (maximum 106 m, minimum 0 m, SE = 3.44). We detected a significant effect of males size on their distribution. In particular, on average, longer males were closer to the breeding pools (Table 1).

Sample areas/plots surveys

Detection probability on the surveyed plots was higher for males (p = 0.81 ± 4.3% SE) than for females (p = 0.54 ± 6.2% SE). The plots in which males were encountered showed a higher mean litter depth (1,5 cm ± 0.2 SE vs. 0.9 cm . ± 0.1 SE), slower slope inclination (5.48° ± 1.2 SE vs. 9.25° ± 1.7 SE) and lower number of trees (1.46 ± 0.2 SE vs. 2.63 ± 0.3 SE).

The best occupancy model was that including distance to breeding pools, slope inclination, number of trees and leaf litter depth (Table 2). The occupancy probability of males was higher in plots closer to breeding pools (F = 22.29; P < 0,001) and with higher leaf litter depth (F = 10.11; P < 0,01). There was a non-significant negative tendency to both slope inclination and trees density.

Table 1. Results of LMMs analysis showing the relationship between the size of the encountered males considered as dependent variable and, slope inclination and distance from the breeding pools of the encountering point considered together as independent variables (NumDF = degrees of freedom in the numerator; DenDf = degrees of freedom in the denominator).

Variable	Estimate	NumDf	DenDf	F	*P*
Distance from the breeding site	-0.29	1	67	11.2	**0.001**
Slope inclination	0.03	1	67	0.17	0.68

DISCUSSION

Our results provide novel data on the fire salamander males spatial activity around breeding sites. In particular, our study provides evidence that during the breeding season males use microhabitats with specific features like deeper leaf litter and closer to breeding sites. Generally the use of terrestrial habitats by the salamanders of the genus *Salamandra* has been investigated to study their site fidelity to a restricted area and their relatively small home ranges (Schulte et al., 2007; Ficetola, 2012). Most of the information about the use of the terrestrial environment is at the landscape scale and underlines the importance of suitable woodland habitats in riparian, mountainous and agricultural areas (Manenti et al., 2009; Tanadini et al., 2012; Manenti et al., 2013); while studies on terrestrial microhabitat preference in the genus *Salamandra* are lacking.

Our study was carried out when females reach the breeding sites to lay the larvae and focuses on adult males, to understand their microhabitat choice when they likely look actively for mating. In the fire salamander, copulation may occur at almost any period of the year except during the winter (Francis, 2002); it hap-

Table 2. Model selection of the best fitted site-occupancy models (only models with ΔQAIC ≤ 4 are shown). The symbol (.) indicates a constant parameter with no covariate and *K* is the number of parameters in the model. ΔAIC is the difference between the QAIC score of the model and the best ranked model and *w* is the Akaike model weight.

Model	*K*	QAIC	ΔQAIC	*w*
ψ(distance + leaf litter depth + slope + n. of trees) *p*(.)	5	137.41	0.00	0.416
ψ(distance + n. of trees) *p*(.)	4	138.06	0.65	0.300
ψ(distance + leaf litter depth) *p*(.)	4	139.42	2.01	0.152
ψ(distance) *p*(.)	6	140.89	3.48	0.073

pens generally during night, and both in spring and autumn it is quite frequent (Rivera et al., 1999; Lanza et al., 2009). The higher probability of finding males was found in the plots where the trees were less numerous and slope inclination lower, even if the tendency was not significant. A similar result has been already reported by Denoël (1996) who observed a high encounter rate for footpaths and open areas. It is likely that this choice may be linked to the possibility to enhance mating opportunities through a more effective females detection. Some previous studies showed the existence of a role played by the slope inclination since the species generally visits more frequently sites with inclinations lower than 35° (Manenti et al., 2011; Werner et al., 2014) and, especially in mountainous landscapes, salamanders are active on paths and microhabitats with lower inclinations (Pantuso et al., 2015). We found males in plots with a lower mean slope inclination, and this variable was included in the best occupancy model. No information is available on the role played by leaf litter; even if its depth may be easily linked to prey occurrence, shelters availability and optimal humidity.

The sex ratio observed during our study (69% males) is similar to those found by Klewen (1985) and Schulte et al. (2007) in autumn. The observed differences between sexes are correlated with general differences in activity patterns (Schulte et al., 2007), with females that likely are less active outside shelters than males which probably remain active to maximize their mating opportunities.

Our results clearly show that males are more active in microhabitats close to the breeding sites. This fact may be incidental to the use of the breeding sites by females, with males exploiting the pools and their surroundings to enhance the probabilities to mate. Although other explanations may exist, as males could prefer the surroundings of the water bodies because humidity or prey availability could be higher.

This is the first report demonstrating that the activity of adult fire salamanders of both sex depends to the vicinity of the water, while it was generally believed that after metamorphosis only females go back to the water bodies (Lanza, 1983; Joly, 1986; Nöllert and Nöllert, 1992; Ficetola, 2012).

Moreover, our results reveal that there are differences among males in their distribution around the breeding sites. In particular, larger males exploit the microhabitats closest to the pools thus increasing their probability to meet the females. Thus, a competition and a territoriality for the sites is likely to occur. The existence of possible territoriality in *S. salamandra* at least during the breeding seasons has been reported (Catenazzi, 1998). Moreover in the close relative *S. algira* the existence of fights between males has been reported (Bogaerts and Donaire-Barroso, 2005). Males that are likely to be looking for mating display a typical posture rising on their anterior limbs; this position has also been reported as a fighting posture (Bruno, 1973) but may be interpreted as an olfactory strategy allowing a more effective perception of the females presence, or as a behavioural display to attract females, related to male quality (Wells, 2007; Lanza et al., 2009). We did not precisely quantified the males exhibiting this posture because we took any care to avoid disturb and fear responses but this aspect may be of particular ethological interest and further researches should be conducted to relate males behaviour and microhabitats choice; not only in the fire salamander, but also in its fully terrestrial congeneric species like *S. atra* and *S. lanzai* in which the same behaviour is very common (Andreone, 1992) and the knowledge of the ecological and ethological factors favouring active mate searching by males may be of importance for proper habitat managements.

In general our study underlines that factors facilitating females perception like vicinity to the breeding sites drive the male distribution patterns. The extensive exploitation of terrestrial habitats surrounding the breeding pools also has implications for planning proper conservation actions for *S. salamandra*, as the maintenance of favourable microhabitats allowing females perception may enhance mating possibilities for males. The terrestrial environment surrounding water bodies appears to play a fundamental role in the ecology and ethology of the fire salamander.

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