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Fire salamander (*Salamandra salamandra*) in Larzac plateau: low occurrence, pond-breeding and cohabitation of larvae with paedomorphic palmate newts (*Lissotriton helveticus*)

Mathieu Denoël*, Laurane Winandy

*Laboratory of Fish and Amphibian Ethology, Behavioural Biology Unit, Department of Biology, Ecology and Evolution, University of Liege, 22 Quai van Beneden, 4020 Liege, Belgium. * Corresponding author.* E-mail: Mathieu.Denoel@ulg.ac.be

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Abstract. Alternative reproductive strategies are widespread in caudate amphibians. Among them, fire salamanders (*Salamandra salamandra*) usually rely on streams to give birth to aquatic larvae but also use ponds, whereas palmate newt larvae (*Lissotriton helveticus*) typically metamorphose into terrestrial juveniles, but can also reproduce in retaining their gills, a process known as paedomorphosis. Here we report repeated observations of an unusual case of coexistence of these two alternative traits in the same pond (Larzac, France). The prevalence of fire salamanders in Southern Larzac was very low (pond occupancy: 0.36%). The observed abundance of fire salamander larvae and paedomorphic newts was also low in the studied pond. On one hand, the rarity of this coexistence pattern may suggest that habitat characteristics may not be optimal or that competition or predation processes might be operating. However, these hypotheses remain to be tested. On the other hand, as this is the only known case of breeding in Southern Larzac, it could be considered to be at a high risk of extirpation.

Keywords. Pond-breeding, facultative paedomorphosis, syntopy, coexistence, conservation, fire salamander, palmate newt.

INTRODUCTION

Fire salamanders (*Salamandra salamandra*) typically give birth to gilled larvae in epigeous running waters such as streams throughout their widespread distribution range in Europe (Thiesmeier, 1994; Steinfartz et al., 2000; Manenti et al., 2009b; Ficetola et al., 2012). Some subspecies and populations have evolved differently, skipping the aquatic developmental stage (Buckley et al., 2007). Between these two extremes, fire salamanders have also specialized in using alternative aquatic habitats: epigeous stagnant waters such as ponds (Egea-Serrano et al., 2006; Schulte, 2008; Caspers et al., 2009) and hypogeous (i.e., subterranean) springs or pools (Manenti et al., 2009a; 2013).

Fire salamander larvae can coexist with other caudate species. This occurs frequently with newts in ponds and similar lentic water bodies (Wiestermann, 2004; Segev and Blaustein, 2007; Thiesmeier and Dalbeck, 2011). However, in running waters, they are more often the only caudate species present (Thiesmeier and Dalbeck, 2011). Exceptions remain, such as in the Pyrenees, where fire salamander larvae can be seen in the same streams as Pyrenean brook newts (*Calotriton asper*). However, even in this case, there is often spatial partitioning between the two species (Guillaume, 2006).

Alternative developmental strategies also occur in newts. The most widespread pattern implies the metamorphosis of aquatic gilled larvae into juveniles that mature on land (Wells, 2007). However, in some populations, larvae skip metamorphosis and retain gills at the adult stage; a process known as paedomorphosis (Whiteman, 1994). In the palmate newt (*Lissotriton helveticus*),

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this occurs with the highest incidence on the Larzac plateau in southern France (Gabrion et al., 1977; Denoël, 2007).

Although found in the springs and streams of peripheral areas of Southern Larzac (Geniez and Cheylan, 2012), cases of reproduction of fire salamanders have not yet been described on the plateau itself and, to our knowledge, coexistence patterns with paedomorphic newts have not been reported in the literature. In this context, the aim of this study was to determine the occurrence of fire salamander larvae on the Larzac plateau, to present the characteristics of a pond-breeding population in cohabitation with both newt morphs, and to propose hypotheses on this unusual pattern.

MATERIAL AND METHODS

A total of 277 ponds were surveyed for the presence of amphibians, with a special focus on palmate newts as part of a long-term survey on the Southern Larzac plateau (2001-2013) in the Hérault and Gard departments (Languedoc-Roussillon region). This encompassed all the ponds, potentially adequate for amphibians which were found using varied sources: literature searches, topographical maps, ortho-image analyses and local contacts. Running waters are extremely rare on the plateau and consist in small springs that water directly some ponds, and springs of larger streams on the limits of the plateau, i.e. almost not running in the plateau itself. These habitats were all investigated during the present survey. The region is a limestone area with traditional agriculture, particularly at its southern limits (Durand-Tullou, 1959). The Blandas plateau was also included in this study, since it is globally part of Larzac.

Most sampling occurred in spring months during the peak of the newt breeding season (670 censuses, i.e., an average ± SE of 2.4 ± 0.1 visits per pond), but also in summer and autumn in some years. The present study focused on the pond where fire salamander larvae were found (see results). At this pond, the sampling of amphibians was done during day-time on 7 June 2011, 27 March 2013, and 13 July 2013.

Sampling in the study pond was done as exhaustively as possible by dip-netting, i.e., stopping netting when no more adult newts or salamander larvae where found after several trials in all the micro-habitats of the pond. The same technique was used in the other Larzac ponds, but seining was also used for the deepest ones (see Denoël and Ficetola, 2014). Given the high capture effort in each habitat and the rather high fecundity of fire salamanders, it is very unlikely that breeding events were missed in ponds. Although the study was aimed first at studying palmate newts, larvae of fire salamanders would not have been overlooked as a special focus was done in all ponds for the larvae of palmate newts, which are much different from those of fire salamanders. However, the abundances determined are likely underestimated as some individuals, particularly in the larval cohorts can hide more easily than adults in ponds. In the population inhabited by fire salamander larvae, the census included both adult newt morphs and fire salamander larvae. Paedomorphic palmate newts were distinguished from metamorphic ones by the presence of gill slits and external gills. Adulthood was assessed by the presence of a developed cloaca (Denoël et al., 2001). Snout-vent length (from the tip of the snout to the end of cloaca) was measured in the field. Because of the very low number of paedomorphs, values were pooled across sexes, so focusing only at the level of species and phenotypes. Since the mesh size of the dip net was 4 mm, it is likely that the smallest palmate newt larvae were not caught. Consequently, the results on larvae are indicative of the size of individuals from the largest cohort only.

The non-parametric Mann-Whitney test was used because of the non-normality of data even after transformation. Some individuals were likely the same in the analyses done at different dates so the data sets are not fully independent. For this reason, comparisons were done only within each sampling date. All tests were computed in Statistica 10 (http://www.statsoft.com).

Some habitat variables were recorded in the field: maximum water depth, pond size, presence of aquatic vegetation, oxygen concentration, conductivity, pH and turbidity. Forest cover was obtained from analysis of ortho-images and elevations above sea level from a digital terrain model (Institut Geographic National, France) in ArcGIS 10.2 (http://www.esri.com).

RESULTS

Fire salamander larvae (*Salamandra salamandra terrestris*) were found in only one out of the 277 sampled ponds (0.36% occurrence; Fig. 1). This population is located on the Plateau de Courcol at one of the southern margins of Larzac at an elevation of 711 m a.s.l. This area is part of the Forêt Domaniale Notre-Dame de Parlatges and of the Saint-Pierre de la Fage municipality (Hérault department). The pond is on the plateau but close to the rupture of slopes making the transition with the foothills and lowlands (Fig. 1). It is a man-made pond built in concrete for game management. A small ditch drives rain water to the pond. On average, the pond's surface area covered 19 m^2, the maximum depth was 55 cm, conductivity 212 μS/cm, and oxygen concentration 6.2 mg/l. The pH of the pond in June 2011 was 8.1. No vegetation was present in the pond, except on the border, and a layer of green algae covered parts of the sediment layer in July 2013. The water was muddy in 2011 and transparent in 2013. Forests covered 51% of the 20-m radius and 77% of the 100-m radius around the focal pond. Only the south-eastern side of the pond was directly bordered by tree plantations, mainly comprising Austrian pines (*Pinus nigra*).

Fire salamander larvae were present at each of the three visits (n = 19, 5 and 9, respectively, for each sampling session; Fig. 2), always in presence of adult palmate newts (n = 8, 62 and 64, respectively) and their larvae

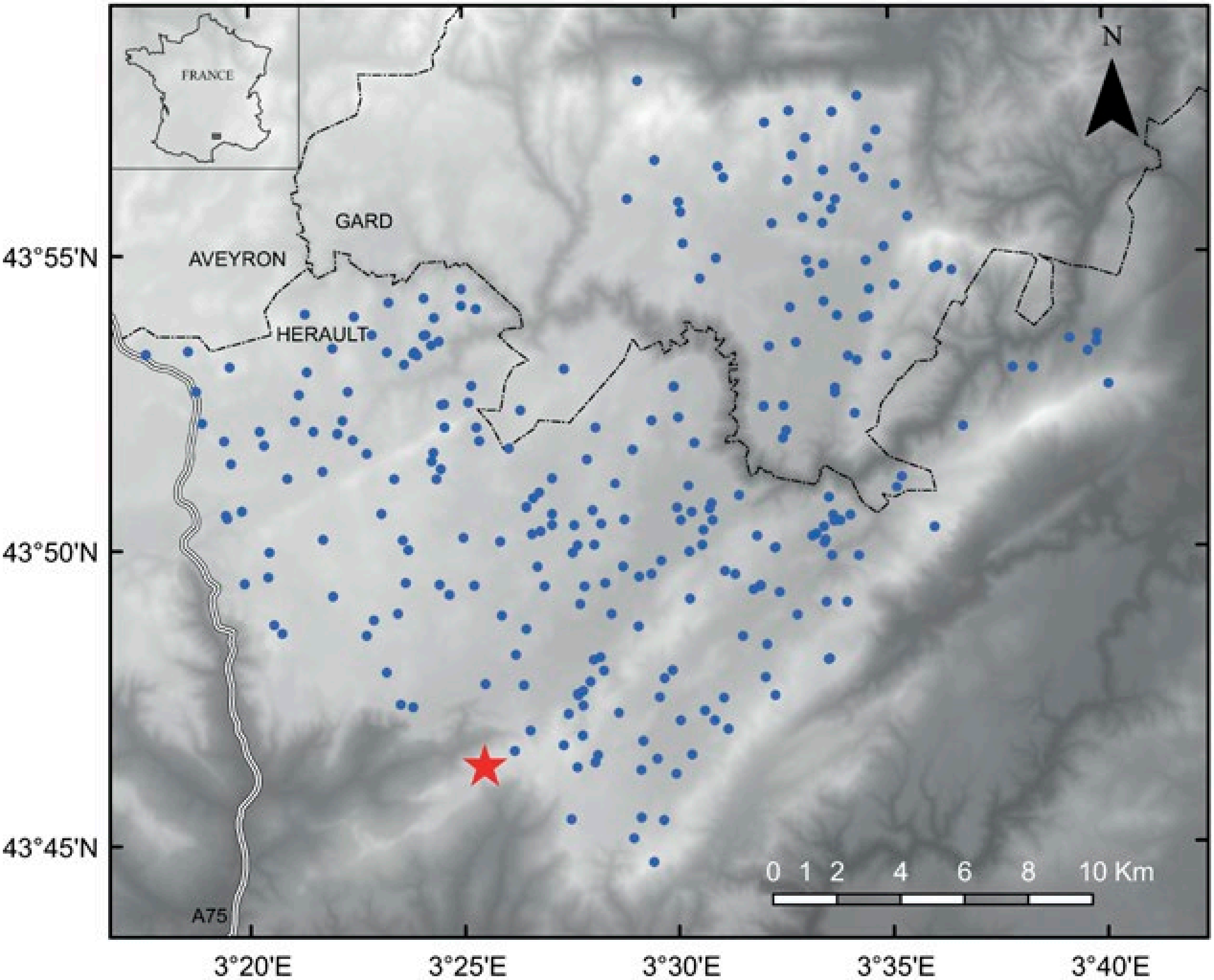

Fig. 1. Localization of the studied pond with fire salamander larvae (large star) and the other inventoried ponds without fire salamanders (full circles: some appear superposed) on the Southern Larzac Plateau, France. The background of the map represents the relief (the lowest elevations are darker). The continuous and interrupted traits represent, respectively, the A75 highway and the boundaries between administrative departments (Hérault, Gard and Aveyron). See text for discussions on external records in valleys and foothills outside the study area.

(even more than 60, March 2013). Paedomorphic newts were found only at the two 2013 sampling sessions: four in March and three in July. Some parsley frogs (*Pelodytes punctatus*) but no marbled newts (*Triturus marmoratus*) were found in the pond.

The mean ± SE snout-vent length of fire salamander larvae was 26.6 ± 3.2 mm in March 2013 (n = 5) and 29 ± 0.6 mm in July 2013 (n = 9), whereas for paedomorphs it was 36.3 ± 1.6 mm (n = 4) and 36.3 ± 1.5 mm (n = 3) and for metamorphs it was 41.7 ± 0.6 mm (n = 47) and 42.5 ± 0.7 mm (n = 40) for the two dates, respectively. In March 2013, the snout-vent length of the largest cohort of palmate newt larvae was 20.4 ± 0.2 mm (n = 15). The size of fire salamander larvae was significantly smaller than that of metamorphs (Mann-Whitney U test: $Z = -3.632$, $P < 0.001$ and $Z = -2.404$, $P < 0.05$ in March and July 2013, respectively) and paedomorphs in July ($Z = -4.634$, $P < 0.001$), but not in March ($Z = -1.152$, $P = 0.08$), although the small sample size needs to be taken into account for the interpretation of the P-value. The size of fire salamander larvae was larger than that of larval palmate newts in July 2013 ($Z = 4.067$, $P < 0.001$).

DISCUSSION

The occupancy of an alternative reproductive habitat (i.e., a pond) led to an unusual coexistence between

Fig. 2. Fire salamander larva (Plateau de Courcol, Larzac, France).

aquatic larvae of a terrestrial species, the fire salamander, and an alternative paedomorphic phenotype of a newt species. Such situations are valuable for understanding the success of strategies in presence of potential competitors or predators (Rheinhardt et al. 2013; Werner et al., 2013). In the case studied herein, the low prevalence of both alternative strategies (i.e., pond use by the fire salamander and paedomorphosis) may suggest that the habitat is not optimal, either because of the lack of adequate environmental features for both alternatives or because the cohabitation reduced individual payoffs as a consequence of competition or predation pressures (Segev and Blaustein, 2007; Wissinger et al., 2010). Long-term or experimental studies including foraging and comparative analyses are needed to test these hypotheses.

The preliminary results presented here suggest that habitat characteristics are not fully optimal for paedomorphosis, which may explain its low rate (maximum 6%) in the population. A multivariate analysis of the ecological correlates of paedomorphosis in Larzac ponds showed the importance of deep water for the occurrence and abundance of paedomorphic palmate newts (Denoël and Ficetola, 2014). The advantage of deep ponds for paedomorphs is in that they are less likely to dry up and they can provide habitat heterogeneity favourable to the persistence of the dimorphism (Denoël, 2003; 2005; 2006). Here the shallow depth and the size of the studied pond (55 cm, 19 m²) make it a homogeneous habitat that might occasionally dry up in summer.

Fire salamanders are among the top foragers in pond environments that drive the composition of aquatic communities (Blaustein et al., 1996; Reinhardt et al., 2013). Although their larvae can coexist with other amphibian species, they are often the only reported amphibian in the habitats where they are found (Thiesmeier and Dalbeck, 2011). Fire salamander larvae reduce the abundance of newt larvae through both competition for invertebrates and predation of small newt larvae (Segev and Blaustein, 2007) and avoidance–attraction mechanisms (Guillaume, 2006). In the studied Larzac pond, fire salamander larvae accounted for a small part of the amphibian community in both 2013 sampling sessions but not in June 2011. It is therefore too premature to conclude on the direction of possible competitive or predatory interactions. However, it can be expected that larval and paedomorphic newts may share some feeding similarities with fire salamander larvae given that they also rely on the aquatic suction mechanisms of aquatic invertebrates (Reilly, 1996; Denoël and Joly, 2001; Denoël, 2004; Denoël et al., 2004; Reinhardt et al., 2013).

It is unlikely that fire salamanders were more abundant in Larzac in the past few centuries than during the present study (2001-2013). Many Larzac ponds are recent and Larzac used to be less forested (at least since agriculture was established in the area), i.e., factors that are usually not favourable for the fire salamander (Manenti et al., 2009b). Specifically, the Austrian pine plantations around the pond date from the 1930s. The atlas of Languedoc-Roussillon amphibians highlights a gap in the distribution map, corresponding to the Larzac and Blandas plateaux (Geniez and Cheylan, 2012). When fire salamanders were present at nearby localities outside the plateau, they were associated with springs and running waters but, at a broader scale in Languedoc-Roussillon, they were also found in ponds (Geniez and Cheylan, 2012). The only published record of the presence of the species strictly on the plateau was made in an area known as Lac des Rives – a temporary lake – but it refereed to an adult individual (observation of M.F. Lapeyrie in 1995: Geniez and Cheylan, 2012). No larvae were seen in this area when the lake and surrounding ponds were flooded in 2004 (M. Denoël, pers. obs.). In contrast, the fire salamander was reported more frequently in the hills north-east of the Blandas plateau and in the Cevennes (Geniez and Cheylan, 2012). The species is also present in the wooded slopes at the southern limits of Larzac, for instance in Cirque de Labeil and Cirque du Bout du Monde (P. Arnaud, pers. comm.) as well as at varied localities of the bottom of Vis Canyon, such as Mas du Pont, Madières and Grenouillet (G. Hanula, M. Salze, R. Servaye, pers. comm.). West of Southern Larzac, terrestrial fire salamander individuals were also found in the southern foothills of the Plateau de Guilhaumard (a satellite plateau of Larzac) in the upper Orb Valley, close to a running water network (Midi-Pyrénées database: Pottier, 2008; LPO Aveyron database). The near absence of springs and running waters on the Larzac plateau itself has probably limited the presence of this species. Moreover, the studied area and its southern foothills are at the margin of its distribution range, with fire salamanders absent from the lowlands along the Mediterranean in Languedoc-Roussillon (Geniez and Cheylan, 2012; Riberon and Miaud, 2012). More inventories should be done in springs and small streams in the foothills at the edges of Larzac to determine the exact distribution and ecology of the species and to better understand its rarity on the plateau.

As the studied pond was only recently created (in 1995), colonization may be interpreted as recent, which may have been facilitated by the movement capabilities of this species (Schmidt et al., 2007; Schulte et al., 2007) and by the tree plantations around the pond. The closest observations of the fire salamander were made around 0.8 km north-west (Parlatges), 2 km south-west (Champ du Lac) and 2.4 km south-east (Salces) of the study area, all referring to larvae in streams and/or springs and to adults on land (P. Arnaud and G. Hanula, pers. comm.). The linear distance, and particularly the large differences in altitude (up to 400 m), and the steep slopes separating these places from the pond studied herein, suggest that they may have been connected through dispersal of some individuals rather than by regular exchanges. This hypothesis is supported by the fact that reported values of home ranges in the literature (e.g., an average of 1295 m^2; Schulte et al., 2007) are lower than the distances to the nearby locations. The easiest connection pathway may have been from the south-west as several dozens of terrestrial fire salamanders were seen there, with some individuals up to the slope rupture (P. Arnaud, pers. comm.) and because there are no major breaks in elevation from this observation site to the studied pond. This case constitutes the highest number of adult salamanders reported in the area. The number of adult individuals that used the present pond is not known because only few larvae were observed. The larvae could thus result from either a single or very few parturition acts. However, the repeated observations in 2011 and 2013 suggest that this is a local specialization or a breeding opportunism. More research (e.g., microsatellite analyses) to find the closest related populations could help to determine possible differentiations. One more potentially favourable pond, intermediate between the records of fire salamanders under the slope rupture and the studied pond also remains to be sampled.

Finally the rarity of the fire salamander in Southern Larzac (0.36% of water bodies inhabited, all included) makes this site highly vulnerable. The observed accumulations of sediments in the pond may be detrimental for both fire salamander larvae and newts, particularly paedomorphs, because it reduces water availability (Denoël and Ficetola, 2014). Local interventions to remove excess sediments helped in this perspective. No external signs of dermocystid parasites were seen in the fire salamander larvae and palmate newt individuals of this population, although these pathogens were found on newts at other Larzac ponds (González-Hernández et al., 2010). Both introduced fish and crayfish were seen nearby on the plateau, whereas crayfish were also found in streams peripheral to Larzac (M. Denoël, pers. obs.; G. Hanula, pers. comm.). Palmate newt populations from Larzac are declining due to these fish introductions (Crochet et al., 2004; Denoël et al., 2005), whereas fire salamanders from other areas suffered from both fish and crayfish introductions (Martinez-Solano et al., 2003; Cruz et al., 2006; Ficetola et al., 2011). Studies at other edges of the fire salamander distribution range also showed high risks of local extirpations (Spitzen-Van Der Sluijs et al., 2013). Consequently, much attention needs to be paid to the fire salamander populations from Larzac and its foothills.

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