RESEARCH PAPER

There is no place like home: Larval habitat type and size affect risk-taking behaviour in fire salamander larvae (*Salamandra salamandra*)

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Abstract

Individual life histories are strongly influenced by early environmental conditions and experiences. They shape morphology as well as behaviour and can promote adaptive divergence and phenotypic plasticity with regard to different habitat types. The fire salamander (*Salamandra salamandra*) in the Kottenforst forest in Bonn, Germany, exhibits two genetically distinct ecotypes occurring in two larval habitats, either ponds or streams. In this study, we investigated whether both ecotypes differ in risk-taking behaviour, measured as the behavioural response during a shelter-emergence test and a shelter-seeking test, and whether larval habitat type and size impact these behaviours. Our results revealed an influence of size as well as habitat type. Larger larvae of both habitats appear to be more risk-prone, as they spent more time outside the starting shelter in the shelter-emergence test. Irrespective of size, pond larvae sought shelter more often in the shelter-seeking test and are thus considered to be less risk-prone. These results indicate that larvae conform to a given niche by adjusting their behaviour. Future studies are needed to disentangle the role of genetic adaptation or phenotypic plasticity and to investigate long-term consequences of the larval habitat for the adult phenotype. Thereby, efforts should be made to create a concise set of multiple tests assessing behavioural patterns.

KEYWORDS

boldness, habitat type, niche conformance, *Salamandra salamandra*, size-dependent behaviour

1 | INTRODUCTION

Different environments have different selective pressures, thus promoting adaptive variation within one species (e.g. Monaghan, 2008; van Valen, 1965). Thereby, the interplay between genetic factors and environmental phenotypic plasticity is a key force of local adaptation and drives intraspecific individual variation (Ghalambor, McKay, Carroll, & Reznick, 2007; Lande, 2009). In particular, early

experiences shape individual life histories and phenotypes and can have long-term consequences for future performance (Krause, Krüger, & Schielzeth, 2017; Monaghan, 2008; Salvanes, Moberg, & Braithwaite, 2007). This may be beneficial in predictable habitats, but can lead to maladaptive effects under unexpectedly changing conditions (reviewed in Monaghan, 2008). Among several factors such as population structure (Brent, 2010; Vignoli et al., 2018), the environment (Braithwaite & Salvanes, 2005; Francis, Diorio, Plotsky, &

Meaney, 2002), as well as predation (Alcalay, Tsurim, & Ovadia, 2018; Bell, Dingemanse, Hankison, Langenhof, & Rollins, 2011), early nutritional conditions have severe implications for the individual performance in later life stages (Krause, Honarmand, Wetzel, & Naguib, 2009; Metcalfe & Monaghan, 2001). For example, early nutrition was found to influence adult pheasant morphology (Ohlsson & Smith, 2001). In fire salamanders, the early nutrition influences the colour pattern after metamorphosis (Caspers et al., 2020) and risk-taking behaviour in laboratory-raised fire salamanders (Ibáñez, Caspers, López, Martín, & Krause, 2014; Krause & Caspers, 2016) under laboratory conditions.

Fire salamanders have a biphasic life cycle with aquatic larvae and terrestrial adults. Females choose the habitat for their offspring (niche choice) and usually deposit their larvae into small first-order streams (Thiesmeier, 2004). However, in our study area, the Kottenforst forest, a deciduous forest in Bonn, Germany, fire salamander larvae can also be found in small ponds and genetic analyses revealed the existence of two genetic clusters corresponding to the larval habitat (Hendrix, Schmidt, Schaub, Krause, & Steinfartz, 2017; Steinfartz, Weitere, & Tautz, 2007). Furthermore, common garden experiments showed that pond and stream females differ in their larval deposition behaviour, probably as an adaptation to the specific challenges of each larval habitat (Caspers, Steinfartz, & Krause, 2015). In contrast to first-order streams, ponds have a higher risk of drying out during the period of larval development, the temperature variation is higher, there is no water current, the food abundance is lower and the predation risk by newts or cannibalistic larvae is higher (Reinhardt, 2014). As a consequence, pond breeding females deposit their larvae in a more bet hedging like strategy, that is pond breeding females use more deposition events compared to stream females and each time they deposit only a small number of larvae (Caspers et al., 2015). In addition, during the course of larval deposition, larvae from pond breeding females are deposited at a larger size towards the end of the deposition period (Caspers et al., 2015). This might be an adaptation to the increased predation risk in ponds or as metamorphosis is size dependent, and it might enable larvae to metamorphose even if the food source is limited.

Despite the genetic differences and the diverging larval deposition behaviour, the degree of differentiation between individuals of both habitat types is currently unknown and there might be further morphological or behavioural differences (e.g. predator avoidance and foraging strategies) due to the different ecological conditions. The antipredator behaviour can be measured in various ways such as risk-taking (Krause, Steinfartz, & Caspers, 2011) or flight and freezing responses (Urszán, Török, Hettyey, Garamszegi, & Herczeg, 2015). It has been shown to be influenced by predation risk as well as nutritional status. For example, both factors shaped the trade-off between predator avoidance and foraging in perches (Magnhagen & Borcherding, 2008) and had an impact on risk-taking behaviour in several amphibian species (e.g. Anholt, Werner, & Skelly, 2000; Babbitt, 2001; Krause et al., 2011; Nicieza, 2000; Urszán et al., 2015).

Many studies regarding risk-taking behaviour are based on manipulative, laboratory experiments. The two fire salamander ecotypes in the Kottenforst forest provide an excellent possibility to investigate niche conformance and the impact of differing early environmental factors on larval behaviour under semi-natural conditions. In this study, we aimed to examine two different aspects of risk-taking behaviour of the two fire salamander ecotypes during a shelter-emergence test and a shelter-seeking test. We also assessed, whether the laboratory experiments on risk-taking behaviour in fire salamander larvae raised under two different nutritional treatments (high and low quantity nutrition) as performed by Krause et al. (2011) are repeatable under semi-natural conditions and whether size and the larval habitat influences risk-taking behaviour in the two tests. We assumed larger larvae, irrespective of their larval habitat, to be more willing to emerge from the shelter, therefore being more risk-prone than smaller larvae. We further assumed that due to the higher predation risk in ponds (Reinhardt, 2014), pond larvae should in general seek shelter more frequently than stream larvae.

2 | METHODS

2.1 | Study site and study system

The European fire salamander (*Salamandra salamandra*) is an amphibian with a conspicuous black-yellow colouration that occupies a wide geographical range among central, west and south Europe (Thiesmeier, 2004). It is larviparous, that is it deposits fully developed larvae into small water bodies, usually first-order streams, but also small ephemeral ponds (Steinfartz et al., 2007; Weitere, Tautz, Neumann, & Steinfartz, 2004). Due to ecological differences, fire salamander larvae of ponds and streams experience different conditions in their natal habitat in terms of predation pressure, food abundance and abiotic factors such as oxygen level, water current or temperature (Reinhardt, 2014).

During May 2018 and late March to early April 2019, we collected in total 210 fire salamander larvae in the Kottenforst forest in Bonn, Germany (50°39′38.9″N, 7°04′16.7″E) from four ponds and two streams, which were not connected and therefore independent. In 2018 between May 24 and May 29, we collected 24 to 29 larvae per location (pond 1 = 24, pond 2 = 24, stream 1 = 26 and stream 2 = 29). In 2019, we sampled in total 107 larvae, 55 larvae from two different ponds (pond 3 = 27 and pond 4 = 28) and 52 larvae from the same two streams as in 2018 (stream 1 = 27 and stream 2 = 25; for details see Table S1). In 2019, ponds and streams were sampled at five different days to reduce the probability of sampling related individuals. As female salamanders deposit their larvae in multiple batches (Caspers et al., 2014) with first larvae being larger than the later deposited larvae (Caspers et al., 2015) and in several water bodies (Thiesmeier, 2004), there are genetically different larvae from different mothers at each breeding site. In both years, we further avoided the sampling of siblings by collecting at different locations along the streams (e.g. before and after small cascades or obstacles) within a wide area of approximately 50 m. Similarly, we collected larvae from different areas within each pond. The sex of the sampled

larvae remains unknown until they reach sexual maturity at the age of 3–6 years (Seifert, 1991; Thiesmeier, 2004).

2.2 | Behavioural tests

All captured larvae were kept in a bucket (10 L) containing approximately 2 L water from their original habitat (one bucket per sample site). This experiment was part of a reciprocal transfer experiment, in which the larvae were placed into an individual enclosure either in its own habitat or in one of the other habitats. The behaviour tests were done before the larvae were transferred into its individual enclosure and thus did not spent any day in captivity before testing, except for the time in the bucket.

Before the transfer, we took each of the 210 larvae, one after the other, out of the buckets and put it into a Petri dish (9 cm diameter), filled with 25 ml of water from the respective bucket, that is from the original habitat. First, the snout–tail length (±0.05 mm) of each larva was measured using millimetre paper. Afterwards, following a time period of approximately one minute for recovery, we conducted one of the two independent tests (shelter-emergence in 2018 or shelter-seeking in 2019). In both tests, one half of the Petri dish was covered with a black lid, while the other half of the Petri dish was left uncovered. The two tests differed in the starting position of the larvae. In the shelter-emergence test (2018), larvae started with, at minimum, their head under the shelter (Figure 1a). During the experiment, we measured the time each larva spent under the shelter. In the shelter-seeking test (2019), larvae started in the uncovered area (Figure 1b). Thereby, we measured the time each larva spent in the uncovered area. This test was named shelter-seeking test, as larvae that moved under the shelter were supposed to actively seek the shelter. During the 2-min test period, we measured the time the individual spent in or outside the shelter, respectively. The Larvae were considered in or outside the shelter, when it had at least its whole head in the respective compartment. After the 120 s of the experiment, we put the larvae into their individual enclosure and assigned it to one of the four locations for the long-term reciprocal transfer experiment.

2.3 | Statistical analyses

The size (snout–tail length in cm) of pond- and stream-bred salamander larvae was compared using an unpaired two sample t test for the data from the shelter-emergence test and using a non-parametric Mann–Whitney U test for the shelter-seeking data, since the length data of the larvae taking part in the shelter-seeking experiments did not fulfil all assumptions for the t test (no homogeneity of variances). The comparison of the shelter-emergence behaviour (measured as the time spent under the shelter) and the shelter-seeking behaviour (measured as the time outside the shelter) between larvae of both habitat types was performed with a non-parametric Wilcoxon test for independent variables. Due to the non-normal distribution of the data, the relationships between the shelter-emergence behaviour and size as well as between the shelter-seeking behaviour and size were analysed with a Spearman rank correlation test. Furthermore, we performed a two-part linear model. In the first step, we used a binomial generalised linear model (GLM) to test, whether the overall probability of leaving or entering the shelter differs between the two ecotypes (dependent variable: change between compartments; independent variables: larval habitat type, snout–tail length; random factor: sample site). Second, we ran a linear model with those individuals that moved between the open compartment and the shelter to investigate, if there are any differences between the ecotypes in the time spent in either of the two compartments (dependent variable: time spent in or outside the shelter; independent variables: larval habitat type, snout–tail length; random factor: sample site). All statistical tests were performed using R version 3.6.1 (R Core Team, 2019). Linear models were run with the package lme4 (Bates, Mächler, Bolker, & Walker, 2015) and lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017), and plots were created with the package ggplot2 (Wickham, 2016) in R (Table 1).

3 | RESULTS

The larval size varied between a mean of 3.64 cm (stream) and 3.76 cm (pond) for the larvae of the shelter-emergence experiments and between a median of 2.95 cm (pond) and 3.20 cm (stream) for
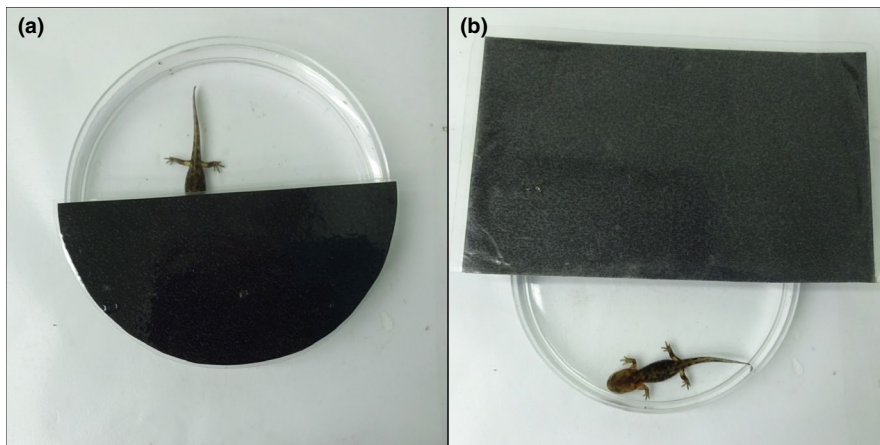
FIGURE 1 (a) Set-up of the shelter-emergence test. Larvae were placed with, at minimum, their head under the black lid. (b) Set-up of the shelter-seeking test. Larvae started in the light environment. Each test took 120 s [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Descriptive statistics of the salamander larvae from the shelter-emergence and shelter-seeking tests grouped by their larval habitat type (pond or stream)

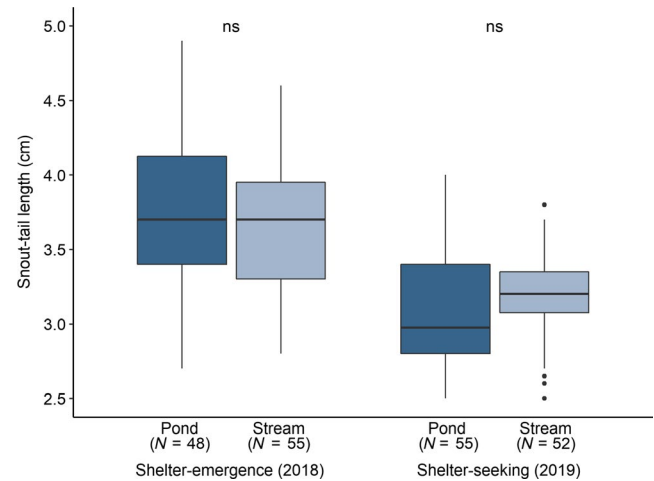|	Shelter-emergence (2018)		Shelter-seeking (2019)	
	Pond	Stream	Pond	Stream
N	48	55	55	52
Minimum size (cm)	2.70	2.80	2.20	2.40
Maximum size (cm)	4.90	4.60	4.00	3.80
Mean size (cm)	3.77	3.64	3.09	3.16
Median size (cm)	3.70	3.70	2.95	3.20
Minimum time in shelter (s)	1.00	4.93	NA	NA
Maximum time in shelter (s)	120.00	120.00	NA	NA
Mean time in shelter (s)	104.61	99.12	NA	NA
Median time in shelter (s)	120.00	120.00	NA	NA
Minimum time outside shelter (s)	NA	NA	6.69	1.09
Maximum time outside shelter (s)	NA	NA	120.00	120.00
Mean time outside shelter (s)	NA	NA	68.39	94.54
Median time outside shelter (s)	NA	NA	61.25	120.00

Note: The table shows sample size (N) per habitat type for both tests, size information measured as the snout–tail length in centimetres and behavioural variables measured as either the time spent in the shelter during the shelter-emergence test, or the time spent outside the shelter during the shelter-seeking test in seconds.

Abbreviation: NA, not available.

the larvae of the shelter-seeking experiments. There were no significant size differences between larvae of both habitat types (Figure 2; shelter-emergence: t test, N_{pond} = 48, N_{stream} = 55, t = 1.3, p = .20; shelter-seeking: Mann–Whitney U test, N_{pond} = 55, N_{stream} = 52, W = 1,179, p = .12). Size differences between the two study years are probably resulting from different sampling periods. In 2018, the field season started about two months later (May) than in 2019 (March). Therefore, individuals from 2018 have likely been older and thus larger at the time of measurements, which explains the overall larger body size in this year.

3.1 | Shelter-emergence test

Pond- and stream-bred larvae did not differ in their shelter-emergence behaviour (Figure 3a; Mann–Whitney U test, N_{pond} = 48, N_{stream} = 55, W = 1,439, p = .38) and spent a similar amount of time in the shelter. The median time spent in the shelter was 120 s for
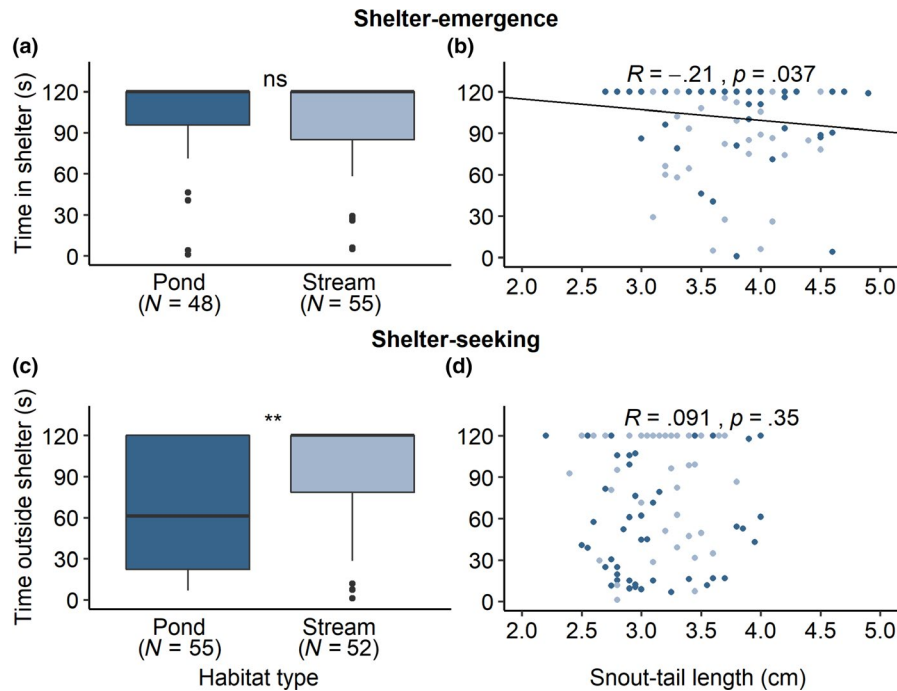

FIGURE 2 Snout–tail length of larvae from pond and stream habitats that took part in either the shelter-emergence or shelter-seeking experiments. The box plots are representing the median (black horizontal line within the box), the upper quartile and lower quartile (upper/lower edge of the box) and the maximum (end of upper whisker) and minimum values (end of lower whisker) lying within 1.5 times the interquartile range. Data points that are >1.5 times the interquartile range (upper quartile–lower quartile) are defined as outliers. The annotations above each pair of box plots represent possible differences in the length between fire salamander larvae from the two habitat types based on p-values; ns = non-significant [Colour figure can be viewed at wileyonlinelibrary.com]

both groups. However, there was a negative correlation between shelter-emergence behaviour and size (Figure 3b; N_{pond} = 48, N_{stream} = 55, R = −.21, p = .04), as larger larvae spent less time under the cover. The two-part model revealed an influence of size but not of habitat type on the probability of emerging from the shelter (GLM; habitat: p = .31; size: p = .01). Among those individuals that emerged from the shelter, there was no influence of size nor habitat type on the time spent in the shelter (LM; habitat: p = .66; size: p = .49).

3.2 | Shelter-seeking test

There was a significant difference of the shelter-seeking behaviour between both habitat types. Pond larvae spent significantly less time outside the shelter (median of 61.25 s) and sought shelter more often than stream larvae (median of 120 s) did (Figure 3c; Mann–Whitney U test, N_{pond} = 55, N_{stream} = 52, W = 939.5, p < .01). In contrast to the shelter-emergence behaviour, the shelter-seeking behaviour did not correlate with size (Figure 3d; N_{pond} = 55, N_{stream} = 52, R = .09, p = .35). The two-part model showed that the probability of shelter-seeking was affected by the habitat type but not by size (GLM; habitat: p < .01; size: p = .99). After excluding the individuals that did not seek shelter at all, neither habitat type nor size had an influence on the time spent in the shelter (LM; habitat: p = .21; size: p = .75).

Shelter-emergence

FIGURE 3 Results of the shelter-emergence (a and b) and shelter-seeking experiments (c and d) of pond (dark blue) and stream larvae (light blue). Each test took 120 s. (a) Time (in seconds) spent in the shelter for larvae from pond and stream habitats. (b) Correlation between the time in shelter and the snout–tail length of the larvae. Each point represents one single individual. (c) Time (in seconds) spent outside the shelter for larvae of pond and stream habitats. (d) Correlation between the time outside the shelter and the snout–tail length of the larvae. Each point represents one single individual. The box plots (a and c) are representing the median (black horizontal line within the box), the upper quartile and lower quartile (upper/lower edge of the box) and the maximum (end of upper whisker) and minimum values (end of lower whisker) lying within 1.5 times the interquartile range. Data points that are >1.5 times the interquartile range (upper quartile–lower quartile) are defined as outliers. The annotations above each pair of box plots represent possible differences in the time spent inside or outside the shelter between fire salamander larvae from the two habitat types based on p-values; ns = non-significant, ** = $p < .01$ [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Different environmental conditions during early development can lead to differences in morphology, physiology as well as behaviour. In this study, we tested whether the larval habitat influences risk-taking behaviour (measured as shelter-emergence and shelter-seeking behaviour) in fire salamander larvae. Within a series of two experiments, accounting for different aspects of risk-taking behaviour, we found that both size and larval habitat type had an impact on the larval behaviour. While shelter-emergence behaviour was affected by size rather than by origin (the larval habitat type), shelter-seeking behaviour was influenced by origin, but not by size. Thus, as expected, our data revealed an impact of size and origin on risk-taking behaviour in fire salamander larvae.

While previous literature comprehensively reports the effect of the early environment on adult morphology and physiology (e.g. Alcobendas, Buckley, & Tejedo, 2004; Gutiérrez et al., 2014; Searcy, Peters, & Nowicki, 2004), less studies have focussed on behavioural traits (but see Fox & Millam, 2004; Hollemans, Vries, Lammers, & Clouard, 2018). However, a previous study of Krause et al. (2011) included behavioural data and found that the nutritional condition during larval development led to differences in risk-taking behaviour in fire salamander larvae. The experiment was conducted in the laboratory with 2-month-old fire salamander larvae raised under

different nutritional conditions (poor versus rich nutritional conditions). Thereby, salamander larvae were released in a half-covered Petri dish, through an opening in the uncovered part and the time that each larva spent in the covered area was measured. Larvae raised under rich nutritional conditions were found to take a higher risk, that is spent less time under the cover than those raised under poor nutritional conditions (Krause et al., 2011). As larvae from the rich nutritional conditions were also larger, our study is in line with the study by Krause showing an effect of size on risk-taking behaviour.

According to Reinhardt (2014), we assumed that there are better conditions and a higher food abundance in streams, which should favour size as well as behavioural differences between larvae of both habitat types, as found for larvae under poor and rich nutritional conditions (Krause et al., 2011). However, we did not find size differences in larvae of the two habitat types, that is stream and pond larvae did not differ significantly in size. Probably as a consequence, we did not find any influence of the early larval environment (pond or stream) on shelter-emergence behaviour. However, size was correlated with shelter-emergence behaviour irrespective of the original habitat type, which might have masked potential differences between the two habitats.

Assuming that the time spent in the shelter is a suitable proxy for predator avoidance, while the time spent outside the shelter

represents risk-prone behaviour, the underlying drivers remain unclear. Larger larvae might be in overall better condition and less vulnerable to predation (Eklöv & Werner, 2000; Jara & Perotti, 2010), which makes them more risk-prone. On the other hand, a small body size indicates bad nutritional conditions, which might drive the need for extensive foraging and risk-prone behaviour to get access to food (Day, Kyriazakis, & Lawrence, 1995). This conflict has been termed as the growth/predation trade-off and describes the balance between foraging for growth purposes and avoiding predation via decreased foraging (McPeek, 2004; Sih, 1980).

In contrast to the shelter-emergence experiment, there was no correlation between size and behaviour in the shelter-seeking test. However, as expected we found a difference in the shelter-seeking behaviour according to the two different ecotypes, pond and stream, indicating that experiences and given circumstances in the two habitats matter more than individual body condition in this specific test. Our finding might either be linked to different experiences and/or to different environmental conditions during early development.

Reinhardt (2014) found significant differences in the ecological parameters of ponds and streams and in concordance we also observed higher temperatures in ponds than in streams (personal observation). As amphibians are ectothermic, that is their body temperature depends on the external temperature climatic factors such as temperature have an impact on their activity (e.g. Heatwole, 1961; Martof, 1953) and might promote differential behaviour in ponds and streams depending on current thermal conditions. Higher temperatures in ponds could increase overall activity and thus the probability of individuals seeking shelter. However, temperature is rather unlikely to explain the outcome of our experiments, since the water temperature during the experiment was similar for all tested individuals. Another explanation might be differences in predation pressure, which can be assumed higher in ponds due to cannibalism and predation by newts. Predation pressure might have selected for individuals with a pronounced shelter-seeking behaviour to avoid predation and cannibalism. A third explanation for our finding that pond larvae moved more likely towards the shelter than stream larvae might be different experiences with water current that might affect movement behaviour of fire salamander larvae. Stream larvae have a risk of drifting downstream (Reinhardt, 2014). Thus, selection might favour stream larvae that move less to avoid drifting, in contrast to pond larvae that are not faced with the risk of drifting. In a pilot study, we found indeed that stream larvae were less active in an activity test (Hahn, Caspers pers. observations). Thus, the experience with different water current might explain, why stream larvae are less active, but it cannot explain why pond larvae spent more time underneath the shelter. Further experiments testing general activity patterns, for example in a novel environment test could provide useful insights into the impact of the water current on movement behaviour.

Considering both experiments, pond larvae seem to have a preference for being in the shelter. They showed a lower probability of leaving the shelter (though this difference was non-significant) and

sought shelter significantly more often than stream larvae. This might be due to the different environmental conditions in the two habitat types, as discussed above.

One drawback of our study is that the two experiments have been conducted in two different years. Thus, we cannot exclude that our findings, that is size influencing shelter-emergence behaviour and habitat type influencing shelter-seeking behaviour, could result from random effects of the specific year.

Nevertheless, we are convinced that our results might hint to the possibility that the behavioural differences could result from adaptation (niche conformance) to the specific larval habitat. As fire salamander females choose the larval habitat (niche choice) and there is genetic differentiation between salamanders of both habitat types (Caspers et al., 2015; Steinfartz et al., 2007), stream and pond larvae might also have genetic prerequisites in accordance with their larval habitat. However, in this current study, we did not include genetic data and thus can only speculate about potential genetic differences. Further studies are needed to disentangle genetic from environmental effects. The behavioural differences might also result from phenotypic plasticity, which promotes the short-term adaptation to given circumstances. A future experiment could shed light on the underlying mechanisms and disentangle the impact of genetic adaptation versus phenotypic plasticity on the behaviour of the two fire salamander ecotypes.

5 | CONCLUSION

Though it is known that fire salamanders, which preferably deposit their larvae into small first-order streams (Thiesmeier, 2004), also use other water bodies such as small ponds (Weitere et al., 2004) or even underground springs and caves (reviewed in Manenti, Lunghi, & Ficetola, 2017), little is known about the specific adaptations to those habitats (but see Caspers et al., 2015; Manenti, Denoël, & Ficetola, 2013; Manenti & Ficetola, 2013; Weitere et al., 2004). Some studies investigated the ecological conditions of the unusual habitats (Manenti, Ficetola, Bianchi, & Bernardi, 2009; Reinhardt, 2014), but except for a few studies on growth (Limongi, Ficetola, Romeo, & Manenti, 2015), metamorphosis traits (Weitere et al., 2004) or larval deposition behaviour (Caspers et al., 2015), possible adaptive differences have been widely neglected. Using a combination of two different experiments testing different aspects of risk-taking behaviour, that is shelter-emergence and shelter-seeking, we showed that size as well as the larval habitat influences risk-taking behaviour in fire salamander larvae, providing new insights how ecologically different habitats can promote behavioural differences.

DATA AVAILABILITY STATEMENT

The raw data and the R script are available at the online repositories GitHub and Open Science Framework (https://doi.org/10.17605/OSF.IO/QRY9P)

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