Understanding niche conformance in fire salamander larvae: Insights from reciprocal transplant experiments

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Abstract

Amphibians are in particular vulnerable to (climatic) changes in their habitat as they are highly dependent on precipitation and temperature. The larval stage can be considered the most critical life stage in the ontogeny of most amphibians as predation is very high, and larvae are restricted to their natal aquatic habitat. The same applies for larvae of the fire salamander (*Salamandra salamandra*) that can occur in temporary ponds or in first-order streams. To investigate if larvae can conform to changing habitat conditions, we have performed two different reciprocal transplant experiments in which larvae of streams and ponds were reciprocally transferred in a two by two design. In the first experiment, individuals were individually housed in semi-natural enclosures, restricting larvae from predation and social contact to others. In the second experiment, the reciprocal transplant was conducted under completely natural conditions (i.e., individuals were released into the transfer habitat and during subsequent capture events recognized based on their tail fin pattern). Unexpectedly, we did not find larvae in matching conditions to perform better, i.e. to grow faster or to have a higher survival. Instead, in both experimental setups we found

larvae transferred into ponds to grow faster than larvae transferred into stream independent of habitat of origin. Likewise, under completely natural conditions, we found that larvae transferred into ponds have higher growth in gill size. Considering the different impact that extreme weather events will have on the different habitat types in the future (i.e. flooding of streams with extreme precipitation and desiccation of ponds through droughts), it is worth supporting both habitat types through conservation measures. Additionally, transferring larvae from one habitat type to the other when facing extreme weather can help preserving the species as they are able to conform to a certain degree to the changing habitat conditions.

Introduction

The world is changing rapidly. Climate change, habitat loss, as well as pathogens, are the main drivers for the biodiversity decrease, which becomes predominantly noticeable in amphibian species (Bickford et al., 2018; Bungard et al., 2021; Hof et al., 2011; Wake and Vredenburg, 2008). Amphibians are particularly vulnerable to climate change due to their strong dependence on temperature and precipitation as they are ectotherm and have a permeable skin (Bickford et al., 2018; Huey et al., 2012). Temperature has a major impact on physiological functions and performance of amphibians and can thus be considered a key environmental parameter (Rome et al., 1992).

One way to cope with negative environmental changes is, if possible, choosing a different micro habitat to escape detrimental thermal environmental conditions (Rome et al., 1992). In cases where choosing a different habitat is not an option, individuals have to conform to a given environment. In such situations, amphibians often respond towards environmental change with developmental plasticity, for instance by changing the timing of metamorphosis (Sinai et al., 2022). However, this can have fitness consequences (Kopp and Baur, 2000). Independent of whether individuals choose their microhabitat or conform to a given habitat (i.e. coping with a new or changing environment), can thus be considered a fundamental ability to survive in the future.

In the European fire salamander (*Salamandra salamandra*), adults are terrestrial while the larvae are completely aquatic, until metamorphosis (Thiesmeier, 2004). Female fire salamanders typically deposit their larvae in first order streams, although in some areas, larvae are also deposited in temporary ponds (Reinhardt et al., 2013; Steinfartz et al., 2007; Weitere et al., 2004). Ponds and streams are ecologically different and streams are expected to be the superior

habitat, with higher food sources, less predators, higher oxygen levels and lower temperature variation (Reinhardt et al., 2013; Thiesmeier and Mutz, 1997; Weitere et al., 2004). Indeed, this also leads to a higher apparent survival in stream larvae (Oswald et al., 2023). Furthermore, temporary ponds are negatively affected by increasing temperatures and extreme weather events like draughts, whereas first order streams are affected by heavy rainfalls as the water can cause lethal larval drift. All of these changes are occurring more often due to climate change (IPCC, 2021; Kohli et al., 2019). Fire salamander larvae are deposited by the mother into a specific, spatially delimited habitat (Thiesmeier, 2004). While females can choose the habitat in which they deposit their larvae, larvae need to conform to the given habitat, e.g. with a change in their phenotype to improve the match of the individual's phenotype to the given environment (Müller et al., 2020; Trappes et al., 2021). However, if and how amphibians cope with changing environments is not fully understood, yet. Here we want to address this question by investigating if and how fire salamander larvae can conform to their larval habitat. The potentially less suitable habitats, the ponds, often dry out and shortly before desiccation, i.e. when the water body has a low water volume, larvae are restricted in movement and food availability and face a higher density of conspecifics and a higher detectability by predators (Kohli et al., 2019). Moreover, as known from yellow-bellied toads, drying out of a pond can cause a reduced body size at metamorphosis leading to negative fitness consequences (Prokić et al., 2021). In addition, the food availability in ponds is limited and the energetic value in ponds is more than three times lower than in streams (Bletz et al., 2016; Weitere et al., 2004). The larvae from the respective habitat do not only show differences in their feeding behaviour according to the available food resources (Ptatscheck et al., 2025), they also differ in their feeding related morphology (Ptatscheck et al., in prep). Whether these differences are due to genetic adaptation or phenotypic plasticity is currently unknown.

Population genetic analyses in our study population showed two genetic clusters that correspond to the habitat the larvae were found in (Steinfartz et al. 2007, Hendrix et al. 2018). Larvae found in streams almost exclusively belong to the stream genotype and larvae found in ponds to the pond genotype (Steinfartz et al., 2007). These findings indicate that females either choose males of their own genotype and deposit their larvae exclusively in the larval habitat that matches their own genotype (stream or pond), or that natural selection favours those larvae where genotype and larval habitat match. Common garden experiments with females from this population further revealed that females of the two genetic clusters differed

in their larval deposition behaviour (Caspers et al., 2015). Females using ponds for larval deposition, for instance, deposited larvae over a longer period of time in comparison to females using streams. These findings suggest that females already show adaptations to their larval deposition habitat. In addition, in a reciprocal transplant experiment, in which larvae from streams and ponds were transferred, Sabino-Pinto et al. (2019) found a divergent response in conformance to a new habitat of pond and stream originated larvae from the Kottenforst population. They found differences in body condition, gill length and growth rate, e.g. larvae transferred into ponds had bigger gills than larvae transferred into streams. However, this study was conducted under semi-natural conditions and only over the period of 14 days. A longer time period might have led to deviating results. We repeated this study and advanced it by conducting a reciprocal transplant experiment under both, seminatural conditions and completely natural conditions. For the first time, all naturally occurring and potentially influencing factors were present and might have affected the larvae after the transfer, including larval drift, predation pressure, food restrictions and intraspecific competition. We hypothesize that under semi-natural conditions (i) larvae in ponds will grow faster in line with the results of Sabino-Pinto et al. (2019), however, we expect under completely natural conditions (ii) larvae under the matched conditions to perform better than larvae under mismatched conditions.

From our results, we will be able to identify conservation measures, for example which habitat should be supported through conservation actions towards better larval survival in the future and which other measures can be used to increase suitability of the habitat for larvae. This is essential as water bodies will be exposed to extreme weather events more often in the future (IPCC, 2021).

Methods

Semi-natural conditions

Prior to testing our hypotheses under completely natural conditions, we performed a study under semi natural conditions with enclosures. Between March 20th and April 8th, 2019, we performed a reciprocal transplant experiment (RTE) between larvae from two ponds and two streams in the Kottenforst near Bonn (Germany, figure 1). We captured 48 pond larvae (P1-P n=24, P2-P n=24) and 49 stream larvae (S1-P n=24, S2-P n=25).

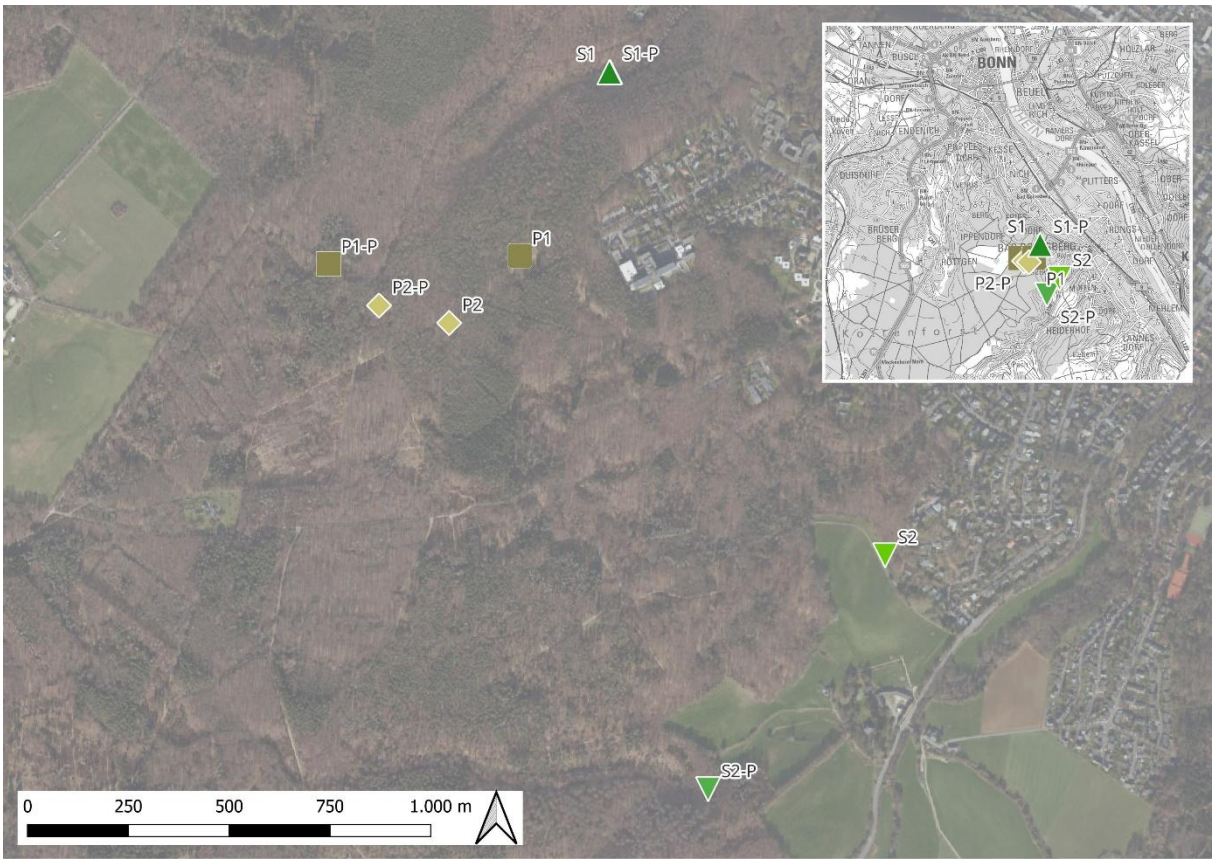

Figure 1 The map shows the location of the pond (P1,P2) and stream (S1,S2) locations from the reciprocal transplant experiment. The "-P" indicates the locations from the semi-natural study from the year 2019. The brown squares represent the pond locations while the stream locations are represented by the green triangles. The inlet shows the position of the locations in the Kottenforst in relation to the city of Bonn, Germany.

We measured the total length (i.e., from snout to tail fin tip) of each individual before placing it into an individual enclosure (8.5x 8.5 x 17 cm). The enclosures were equipped with two small areas of mesh that allowed prey items to enter. However, they excluded other external factors such as predation or competition. The individuals were then randomly and in equal amounts distributed to the other locations, while one group always stayed at their original habitat. In this way, we created four treatment groups: 1. Pond originated – transferred to ponds (P/P), 2. Pond originated – transferred to streams (P/St), 3. Stream originated – transferred into streams (St/St), and 4. Stream originated – transferred into ponds (St/P). This in turn leads then to matched and mismatched conditions regarding the habitat type: The habitat of origin matches the habitat of transfer (P/P and St/St) or the habitat of origin mismatches the habitat of transfer (P/St and St/P).

We checked the transferred larvae every second day for their well-being. After the initial measurement on the day of capture (day 0), we also measured the total length after ten days

(day 10) and after 30 days (day 30). Each larva spent on average 47.05±7.91 days in the individual enclosure depending on the day of capture.

Natural conditions

To test if larvae under matched conditions perform better than larvae under mismatched conditions, in the setting under completely natural conditions, we performed another reciprocal transplant experiment over the duration of two years without the use of individual enclosures. By conducting the experiment over two consecutive years, we covered different, year specific environmental conditions that may affect the larvae in different ways over the years and thus give a more accurate picture of the larval performance. In 2023, we captured and transferred larvae on the 4th of April and in 2024 on the 9th of April. In 2023, we captured 130 pond larvae (P1 n=78, P2 n=52) and 91 stream larvae (S1 n=49, S2 n=42) and in 2024, we captured 122 pond larvae (P1 n=76, P2 n=46) and 112 stream larvae (S1 n=67, S2 n=45). After capturing, measuring and photographing each individual, we were able to release them into the randomly assigned transfer locations without enclosure. Individual identification was possible without enclosures by using the Amphibian and Reptile Wildbook (ARW). The ARW is a free and open-source software that allows reliable individual identification of fire salamander larvae based on the tail fin pattern (Schulte et al., 2024a). After the day of capture and transfer, we returned to the transfer locations every week until mid-May, captured the larvae following a standardized protocol (Oswald et al., 2023) and after measuring and photographing them again we were able to identify recaptures based on the photographs. This time, we did not only take pictures from the side of each larva for individual identification, we also took a picture from the top to be able to measure the gill length. Additionally, in both years, we measured water temperature and dissolved oxygen levels at the bank of each water body with every visit at each location. The temperature and oxygen data from 2023 were already reported in Schulte et al. (2025).

Statistical analysis

Semi-natural conditions

We used a linear model (LM) to investigate if there is a significant difference in the daily growth rate in total length (dependent variable) from larvae in the different treatment groups (P/P, P/St, St/St, St/P) with regard to the initial body size (fixed factor). In eight cases, we could

only measure the larvae after ten days as they died before the 30 days measurement. We measured the larvae in mm (±0.1 mm). In cases with a "negative" daily growth rate due to a measurement error, we set the growth rate to 0 (N=8).

Natural conditions

First, we compared the water temperature and the dissolved oxygen level between the two habitat types for both years by performing a linear model per dependent variable (water temperature; dissolved oxygen level) with habitat type (pond/stream) and year (2023/2024) as explanatory factors. To investigate if the recapture rate of the larvae at the different pond and stream locations was evenly distributed, we performed a Chi^2 test per year. We compared the observed with the expected values while using standardized values; i.e, accounting for the overall recapture rate. We analysed if the period over which we were able to recapture the larvae differed between the two habitat types by performing a Mann-Whitney-U test and between the treatment groups by performing a Kruskal-Wallis test. To test if the larvae from ponds and streams differ in their size in the beginning of the experiment and between the years, we performed a linear model with initial body size as the dependent variable and original habitat and year as dependent variable. We excluded one larva from 2023 from the data due to a measurement error in the field.

To test for potential differences in gill size, we compared the initial gill size of larvae from ponds and streams and between the years using again a linear model. Next, we tested for a correlation of the initial body size (total length) and initial gill size using Pearson correlation as the data was not normally distributed. We used a linear mixed effect model (LMM) to investigate if there is a significant difference in the daily growth rate (dependent variable) from larvae in the different treatment groups (P/P, P/St, St/St, St/P) (fixed factor) with regard to the year (random factor). We then used *eemeans* as posthoc test.

Likewise, we performed another LMM to test if there is a significant difference in the daily gill size change (dependent variable) from larvae in the different treatment groups (P/P, P/St, St/St, St/P) taking initial gill size into consideration (fixed factor) and year as a random factor. As larvae reduce the gill size once they are approaching metamorphosis, we took the change in gill size (positive or negative) into account and not only the growth. All statistical analyses were carried out using R (version 4.4.2 2024-10-31). We set the significance level to α=0.05.

Results

Semi-natural conditions

We found no size difference between larvae from ponds and streams in the beginning of the experiment as reported in (Oswald et al., 2020). For the daily growth rate, we found that larvae that were transferred from ponds into streams (P/St) as well as larvae that remained in streams (St/St) grew significantly less ($p<0.001$ for both treatment groups) than larvae that were transferred into ponds or remained in ponds (figure 2, table 1).

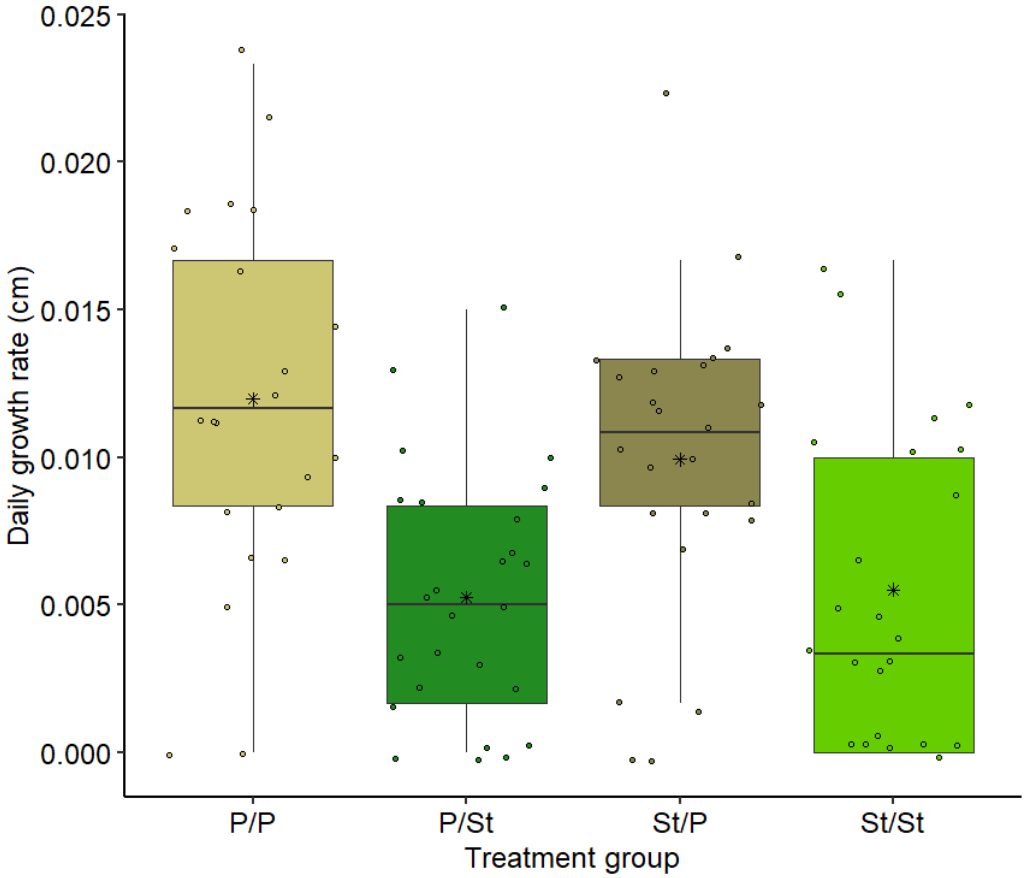

Figure 2 Daily growth rate (cm) of larvae in the different treatment groups (P/P, P/St, St/P, St/St) under semi-natural conditions (year 2019). The larvae that were transferred into streams are shown in green while the larvae that were transferred into ponds are shown in brown. Each point illustrates one measurement, while the horizontal line represents the median and the asterisks the mean. The lower and upper quartile are represented by the boxes and the whiskers show the minimum and maximum values within 1.5 times the interquartile range.

Table 1 Overview of the calculated linear model (LM) with the dependent variable and fixed effect for 2019. For each fixed effect the estimate, standard error (Std error) and the p value is shown. The significant effects are shown in bold.

Model type	Dependent variable	Fixed effect	Estimate	Std error	p value
LM	Daily growth rate	Treatment group P/St	-1.055	0.237	**<0.001**
		Treatment group St/St	-0.9814	0.2445	**<0.001**

Natural conditions

When comparing the abiotic factors that we measured at the different habitat types, we found that water temperature was significantly higher (p=0.038) and that the level of dissolved oxygen was significantly lower in ponds (p<0.001), while we did not find an effect of year (p=0.109 and p=0.248, respectively; figure 3).

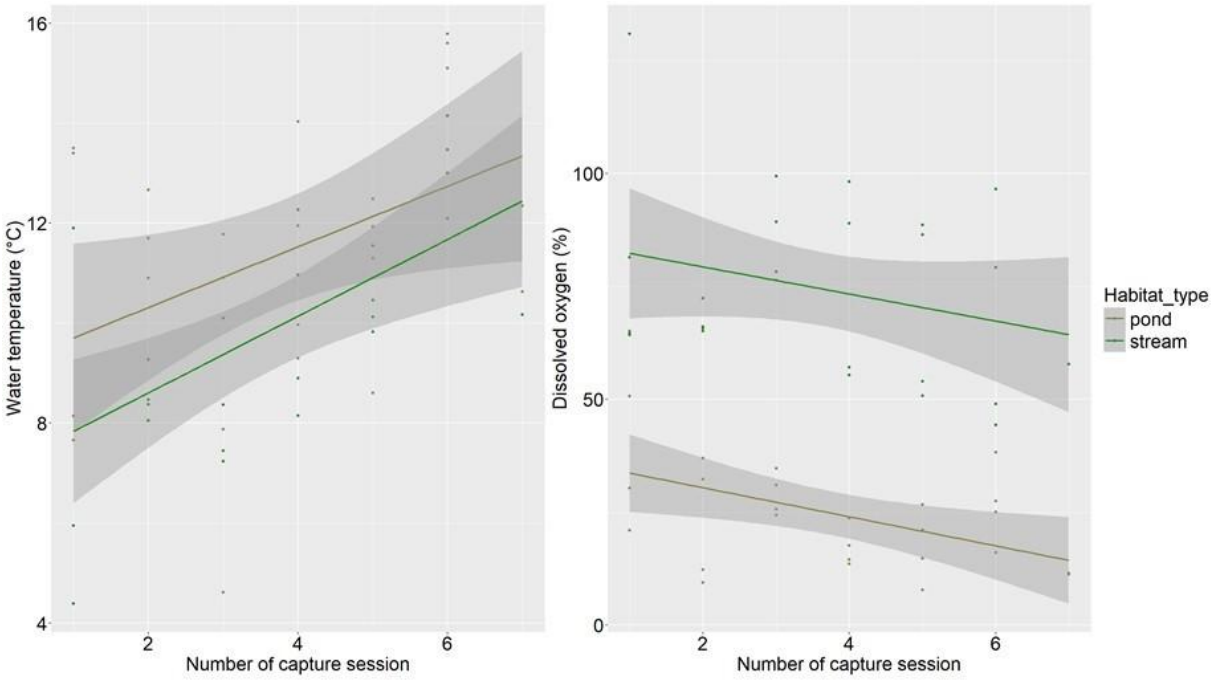

Figure 3 Water temperature (°C., left) and dissolved oxygen (%, right) during the capture sessions over the weeks per habitat type (pond/stream) for the years 2023 and 2024.

In 2023, we recaptured 43 larvae out of the transferred 221 individuals leading to a total recapture rate of 19.46% (table 1). The highest recapture rate was achieved at one stream (S1), whereas, in one pond location (P2) no larvae could be recaptured (table 2). In 2024, we recaptured in total 48 larvae from the transferred 234 larvae leading to an overall recapture

rate of 20.51%. The highest recapture rate was achieved in one pond (P1) while the lowest rate was found at the other pond (P2).

Table 2 Number of captures and recaptures are given for all larvae as well as per location and per year. The percentages are added in brackets.

	Total number of larvae captured/ recaptured	Number of larvae captured/ recaptured at S1	Number of larvae captured/ recaptured at S2	Number of larvae captured/ recaptured at P1	Number of larvae captured/ recaptured at P2
2023	221/43 (19.46%)	57/20 (35.09%)	54/8 (14.81%)	54/15 (27.78%)	56/0 (0%)
2024	234/48 (20.51%)	67/11 (16.42%)	45/8 (17.78%)	76/23 (30.26%)	46/6 (13.04%)

In 2023, we found a significant difference between the recapture rate at the transfer locations and the expected probabilities (2023 X-squared=21.613, $p<0.001$), but we did not find a difference in 2024 (X-squared = 5.485, p-value = 0.14).

The larvae were recaptured over a period from seven (N=12) to 72 and 73 days, respectively (N=4). The latter included two larvae from the St/St treatment and two larvae from the P/St treatment group. Larvae that were transferred into streams and ponds did not significantly differ in the period over which we were able to recapture them (Mann-Whitney-U test, W = 1247.5, p-value = 0.0562), however, we found a strong tendency for larvae transferred into ponds to be captured over a longer period of time. Likewise, we found no difference in the time periods over which individuals from the different treatment groups (P/P, P/St, St/St, St/P) were recaptured, but we found a trend that larvae transferred into ponds were captured over a longer period of time (Kruskal-Wallis chi-squared = 6.7181, p-value = 0.081).

In contrast to our study under seminatural conditions, we found that larvae from streams were smaller than larvae from ponds ($p=0.007$) in both years and larvae captured in 2023 were smaller than larvae captured in 2024 ($p=0.014$). Likewise, the gill size in the beginning of the experiment was smaller in stream larvae ($p<0.001$), but this time we found no effect of year ($p=0.506$). As expected, we found a strong positive correlation between the initial body size and the initial gill size ($p<0.001$), with larger larvae having larger gills.

For the daily growth rate, we found a significant effect of the transfer treatment with larvae transferred from ponds into streams (P/St) to grow significantly less (p=0.001) and a trend for larvae that remained in streams (St/St) to grow less (p=0.054) (figure 4, table 3).

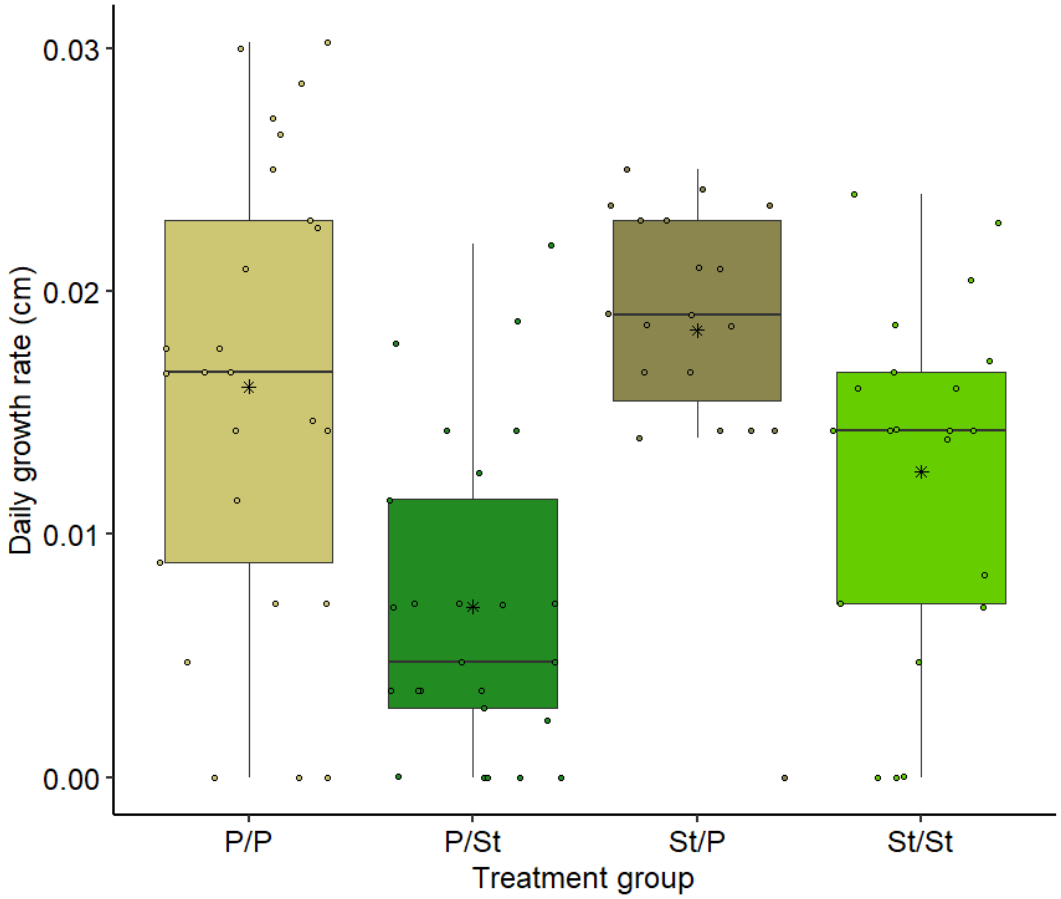

Figure 4 Daily growth rate (cm) of larvae in the different treatment groups (P/P, P/St, St/P, St/St) for the larvae under completely natural conditions (years 2023 and 2024). The larvae that were transferred into streams are shown in green while the larvae that were transferred into ponds are shown in brown. Each point illustrates one measurement, while the horizontal line represents the median and the asterisks the mean. The lower and upper quartile are represented by the boxes and the whiskers show the minimum and maximum values within 1.5 times the interquartile range.

Table 3 Overview of the calculated linear models (LM) and linear mixed effect models (LMM) with the dependent variable and fixed effect for the years 2023 and 2024 combined. For each fixed effect the estimate, standard error (Std error) and the p value is shown. The significant effects are shown in bold.

Model type	Dependent variable	Fixed effect	Estimate	Std error	p value
LM	Water temperature	Habitat stream	-1.5439	0.7215	**0.038**
LM	Dissolved oxygen	Habitat stream	1.5377	0.1759	**<0.001**
LM	Initial body size	Original habitat stream	-0.5659	0.2039	**0.007**
		Year	0.5084	0.2031	**0.014**
LM	Initial gill size	Original habitat stream	-1.51644	0.14303	**<0.001**
		Year	0.09534	0.14279	0.506
LMM	Daily growth rate	Treatment group P/St	-0.8234	0.2365	**0.001**
		Treatment group St/St	-0.4677	0.2392	0.054
LMM	Daily change in gill size	Initial gill size	-5.2649	1.0274	**<0.001**

Larvae that originated from streams and were transferred into ponds (St/P) had a significantly higher change in gill size than all the other groups (post hoc test with pairwise comparison: P/P: p=<0.001, P/St: p<0.001, St/St: p<0.001). Larvae that originated from ponds and were transferred into ponds (P/P) differed significantly from larvae originated from ponds and transferred into streams (P/St, p<0.001), but did not differ from larvae from streams that remained in streams (St/St, p=0.826). The latter (St/St) also differed significantly from larvae that originated from ponds and were transferred into streams (P/St, p=0.011). Additionally, the initial gill size had a significant effect on the growth of the gills (p<0.001, table 3).

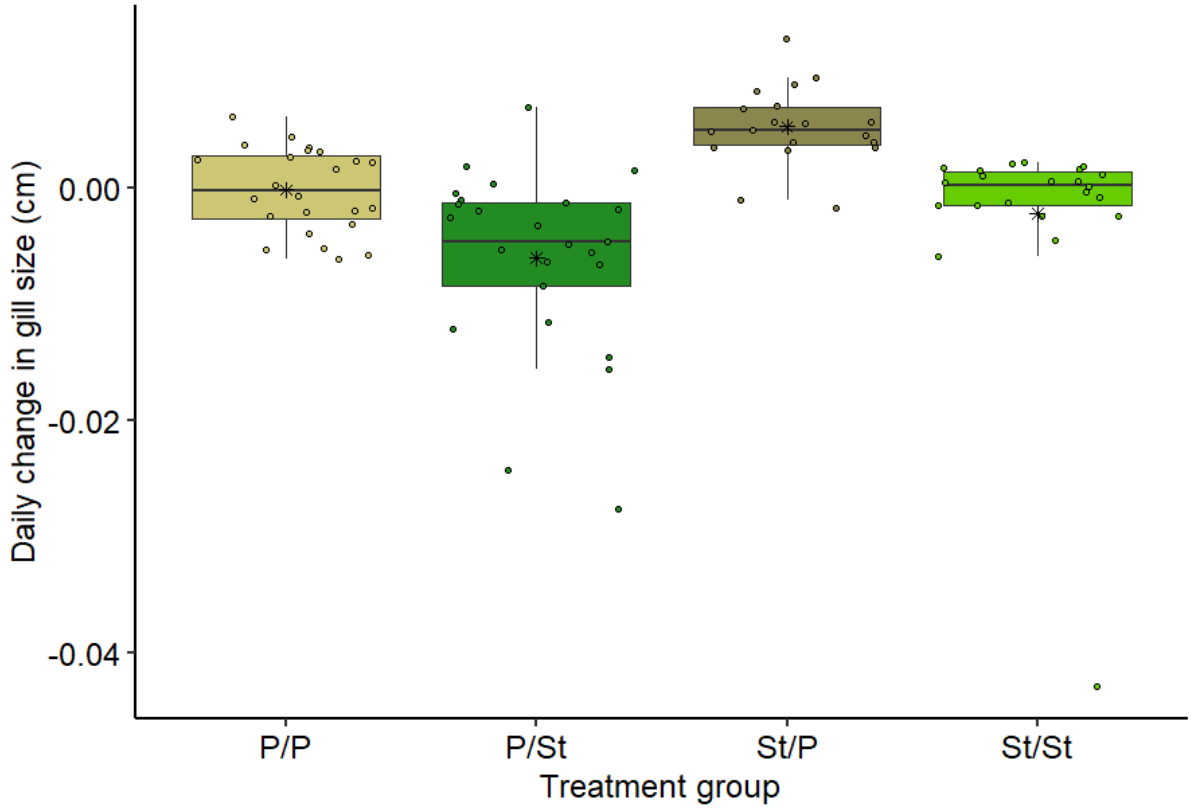

Figure 5 Daily gill size change (cm) of larvae in the different treatment groups (P/P, P/St, St/P, St/St). The larvae that were transferred into streams are shown in green while the larvae that were transferred into ponds are shown in brown. Each point illustrates one measurement, while the horizontal line represents the median and the asterisks the mean. The lower and upper quartile are represented by the boxes and the whiskers show the minimum and maximum values within 1.5 times the interquartile range.

Discussion

The ability to conform to a given habitat is a pivotal ability to cope with environmental change. Amphibians are particularly vulnerable to environmental change. Here, we tested in a set of reciprocal transplant experiments, under seminatural and under completely natural conditions, whether fire salamander larvae are able to conform to a given habitat.

In both experiments, we found larvae that were transferred into ponds to grow faster than larvae that were transferred into streams, which matches our hypothesis (i) that larvae in ponds will grow faster than in streams. We found larvae originated from streams that were transferred into ponds to have a higher growth in gill size under completely natural conditions. Both experiments indicate that fire salamander larvae are able to conform to a changing habitat by showing phenotypic plasticity.

During the enclosure study, mainly biotic factors were altered, as predation and density of conspecifics for instance were excluded while prey items were still able to enter the

enclosures trough the mesh. However, we also found larvae in this study transferred into ponds to be growing faster, just like under completely natural conditions. This indicates that these biotic interactions such as predation do not seem to primarily or exclusively influence the growth rate of the larvae. However, it is important to note that infochemicals (Müller et al., 2020), such as Kairomones released from potential predators, could pass the mesh and thus might have triggered habitat specific growth. In addition, the abiotic factors, i.e. water temperature and dissolved oxygen levels, differed significantly between the two habitat types, ponds and streams, with ponds being warmer and having lower oxygen levels. This might have influenced the differences in growth rates. Based on the lower levels of oxygen and the warmer temperature, ponds have being considered the less favourable habitat as these conditions poorly fit the needs of fire salamander larvae (Reinhardt et al., 2013; Thiesmeier, 2004; Weitere et al., 2004). Nevertheless, our experiments show that fire salamander larvae grow faster under these conditions. Amphibians will face warmer water temperatures in the future (Lee et al., 2023). The larval stage represents a particularly vulnerable life stage as the typically aquatic larvae only have a limited possibility to escape unfavourable habitat conditions in their natal habitat (Rome et al., 1992; Woodward et al., 2010). A systematic review showed that amphibian larvae in general develop faster and undergo metamorphosis at a smaller size when facing warmer temperatures (Sinai et al., 2022), and warmer temperatures can lead to a reduced capacity for physiological plasticity (Ruthsatz et al., 2018). Young larvae of *Rana temporaria* for instance showed a low tolerance of extreme temperatures indicating a high vulnerability towards the consequences of climate change (Ruthsatz et al., 2022). Higher temperatures can also influence the consequences of poor nutritional conditions in fire salamanders such as a longer larval stage, and larvae reared under warm water temperature showed a much lower weight than larvae reared under colder conditions (Weitere, 1997). This can lead to fitness consequences in their later life. However, Lackey and Whiteman (2022) did not find a negative impact of a warmer temperature during the larval stage of *Ambystoma talpoideum* on the survival and the reproductive investment. Similarly, Oswald (2022) took the larvae from our experiment to the lab and followed their development further, finding that that the larvae transferred into ponds have a higher survival than the larvae transferred into streams one year after metamorphosis. This indicates the ability of the fire salamander to compensate for the costs of the unfavourable habitat. Fire salamander larvae showed a decrease in developmental rate

with water temperature above 25°C and oxygen levels from 20% (Weitere, 1997), both conditions, which are out of the range of conditions we observed.

In addition to the detrimental effects of high temperatures, low oxygen levels have been shown to increase the risk of being predated in anuran larvae (Moore and Townsend, 1998). Although we predicted that larvae under matching conditions, i.e. larvae from ponds transferred into ponds and larvae from streams transferred into streams, perform better, we found no evidence for this. Instead, we found growth rates to be higher in larvae that were transferred into ponds irrespective of their habitat of origin. However, measuring performance only in growth rate cuts too short on what actually influences the larval development and well-being and further studies should focus on long term consequences of different larval habitat conditions. In general, ponds are already known to be the more stressful habitat for fire salamander larvae (Schulte et al., 2024b), while the long-term consequences especially after metamorphosis remain poorly studied. Stressful environments can lead to a change in foraging activity (McCallum et al., 2020). Considering that the different energetic value of potential food organisms for fire salamander larvae is much higher in streams than in ponds (Weitere et al., 2004), the larvae are likely to be negatively affected by this, as poor nutritional conditions during the larval stage can impact the behaviour as well as the morphology across life stages (Caspers et al., 2020; Krause and Caspers, 2016). Moreover, Weitere (1997) found larvae from ponds to be significantly smaller at metamorphosis than larvae from streams when kept under the same conditions in the lab. The larvae from our enclosure study that were kept under semi-natural conditions in the field however did not differ in their size at metamorphosis (Oswald, 2022), indicating different influencing factors than just the habitat type of origin.

We found a trend for larvae transferred into ponds to be recaptured over a longer period of time than larvae transferred into streams, while at the same time, the larvae that we recaptured after the longest time all belonged to treatment groups that were transferred into streams. In a previous study, we found the apparent survival rate, that was based on recapture rates from a weekly monitoring, to be higher in streams than in ponds (Oswald et al., 2023). In line with these findings, Schafft et al., (2022) describe a high site fidelity of stream larvae and that drift events primarily occur during floods (see also Reinhardt et al., 2018). Thus, the probability of recapturing the larvae over a longer period of time in one of the two habitat types might reflect year specific differences and not a general pattern. For the

recapture rate at the transfer location we found a year effect with a significant difference between the expected and observed probabilities in 2023 but not in 2024. We expect the difference in 2023 to be most likely driven by the fact that we did not recapture any larvae at one pond location. We always capture larvae at the bank of the ponds and streams where they stay in the shallow part of the water body. The difference in the pond without recaptured might have been caused by altered water levels which made the bank of the pond steeper and unideal for larvae to reside.

In conclusion, we found larvae transferred into ponds to be growing faster in terms of body length and gill size. Fire salamander larvae from ponds and streams differ in their morphology, physiology and their behaviour (e.g., Oswald et al., 2020; Sabino-Pinto et al., 2019b; Schulte et al., 2024b; Schulte, 2008; Weitere et al., 2004). They are adapted to the specific abiotic and biotic conditions in their respective habitat type. This study illustrated that when being transferred to ponds, larvae showed an increased growth in body and gill size, reacting to the harsher habitat conditions there such as less oxygen. The studied population of fire salamanders already shows first signs of differentiation and speciation correlating with the larval habitat (Hendrix et al., 2017; Steinfartz et al., 2007). The existence of both strategies in sympatry, i.e. depositing larvae into ponds and into streams, might be the result of different selection pressures in extreme and changing weather conditions now and in the future. In years with heavy precipitation and subsequent flooding, stream larvae are less likely to survive because of the drift (Reinhardt et al., 2018; Schafft et al., 2022). However, years with low precipitation and warm temperatures can lead to droughts and desiccation which will particularly impact pond habitats. Our study shows that larvae show high levels of phenotypic flexibility and can conform to a changing habitat, which has strong impact for conservation purposes. In years with catastrophic climatic conditions, a transfer of larvae can be considered as our results suggest an ability to conform to a certain degree to the changed conditions (e.g., increased growth of gills in pond transferred larvae). Future studies should focus on the long-term fitness consequences, such as reproductive success and the interplay with abiotic and biotic conditions.

Data availability

Data and code can be found https://github.com/LauraSchulte/Transfer.git.

Author Contribution

BAC designed the study; LS, PO, ER, MM, MS performed the RTE in the field; LS, PO and ER analysed the data, LS wrote the first draft of the manuscript. All authors contributed to the final manuscript.

Conflict of Interest

We declare no conflict of interest.

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