SALAMANDRA

German Journal of Herpetology

The ravages of time – Life-long consequences of early larval nutritional conditions on the terrestrial life of fire salamanders (*Salamandra salamandra*)

E. Tobias Krause[1,2], Sebastian Steinfartz[2,3] & Barbara A. Caspers[4]

[1] Friedrich-Loeffler-Institut, Institute of Animal Welfare and Animal Husbandry, Celle, Germany

[2] Department of Animal Behaviour, Bielefeld University, Bielefeld, Germany

[3] Institute of Biology, Molecular Evolution and Systematics of Animals, University of Leipzig, Leipzig, Germany

[4] Department of Behavioural Ecology, Bielefeld University, Bielefeld, Germany

Corresponding author: E. Tobias Krause, e-mail: tobias.krause@fli.de

Abstract. Besides immediate effects, early nutritional conditions also have an impact on the entire life history of individuals. We tracked a cohort of captive fire salamanders that experienced only during their early larval phase, either rich or poor nutritional conditions, and thereafter intermediate standard conditions for almost 10 years. We measured on a regular basis, their morphometric variables, noted behavioural and colouration developments, and monitored their survival. While deficits in body mass and colouration from initially poorly raised individuals vanished in adults, differences in size in comparison to initially richly raised larvae remained throughout life. Behaviour at adulthood did not differ any further from that during early conditions, nevertheless it tended to be consistent in certain exploratory traits over several years. After almost ten years, the overall survival rate was about 50%, but so far, no effect of early living conditions on subsequent survival became apparent. Taken together, our long-term study on the effects of early nutritional conditions on fire salamanders revealed interesting insights into the life trajectory of these animals. Immediate effects from early nutritional conditions were found in almost all aspects of behaviour and physiology. The majority of effects are compensated within the lifetimes of individuals, apparently without detectable costs.

Key words. Amphibia, Caudata, Salamandridae, early nutritional conditions, early developmental stress, survival, life history, predictive adaptive response, silver spoon effect, early programming, compensatory growth, repeatability, exploration.

Introduction

Fire salamanders (*Salamandra salamandra*) possess, as most amphibians, a biphasic life cycle (Greven 1998, Thiesmeier 2004, Caspers et al. 2014) with an early aquatic larval phase and a distinct subsequent terrestrial adult phase. Salamander larvae are deposited into water bodies where they typically metamorphose within a couple of months (Alconbendas et al. 2004, Krause et al. 2011, Weitere et al. 2004) and become terrestrial for the rest of their life, which last on average 7–8 years in the wild (Thiesmeier 2004) and up to a maximum of 20 years. As for other vertebrates (e.g., Lindström 1999, Monaghan 2008), the early development has a key impact on the later developmental trajectory and life history in fire salamanders. Fire salamander larvae may be deposited and can develop in different aquatic habitats, which will affect their behavioural development. The developmental trajectories, are for example different for larvae found in caves (Manenti et al. 2013a) or ponds (Weitere et al. 2004) in com-

parison to larvae found in streams. Small-scale ecological differences are apparent between these different aquatic larval habitats (Manenti et al. 2011, Reinhardt et al. 2013). Despite the different habitats, salamander females can choose their spots of larval deposition, and social interactions in these habitats can affect subsequent larval development. Interactions with conspecifics depend on larval density and affect development or even survival (Reques & Tejedo 1996, Eitam et al. 2005, Melotto et al. 2019). Furthermore, interactions with heterospecifics can occur, which may be either competitors in the respective habitats' food web, prey or predators (Manenti et al. 2013b, Reinhardt et al. 2013, Reinhardt et al. 2017). Some of these biotic factors indirectly affect food availability. However, food availability is also affected by other biotic and abiotic factors. Food availability has a major effect on the early development on fire salamander larvae (Krause et al. 2011), as they crucially rely on sufficient energy to grow, develop and survive (Lindström 1999, Monaghan 2008, Hector et al. 2012). Availability of nutrients is a key resource for the

development of individuals, and their shortage thus often leads to a reduction of growth rates and may even impact phenotypic expression, such as behavioural patterns (e.g., Lindström 1999, Monaghan 2008, Krause et al. 2011, Hector et al. 2012).

Obtaining a sufficient amount of nutrition is often associated with certain predation risks and individuals in poor condition are assumed to take higher risks in particular (Moran et al. 2021). In case of the fire salamander, predation risk is most pronounced during the aquatic phase (Thiesmeier 2004). Thus, if fast early development is possible it can help the individuals to metamorphose earlier and escape the potential risky aquatic environment. Rich nutritional conditions during the larval phase result in faster growth and, as a consequence, in earlier metamorphosis (Wilbur & Collins 1973, Denoel & Poncin 2001, Eitam et al. 2005, Warburg 2009, Krause et al. 2011). In line with this, larval risk-taking behaviour can be driven by nutritional availability (Krause et al. 2011) and habitat (Oswald et al. 2020), but these effects seem to disappear later in their terrestrial life (Krause & Caspers 2016). The yellow coloration, which only appears during metamorphosis, seems to be an effective warning signal and it is also influenced by food availability during the larval stage (Caspers et al. 2020). Whether lifelong differences in yellow coloration is a result of food availability during the early life stages remain throughout life has remained unknown until yet. Once metamorphosed, the risk of predation is highest shortly after metamorphosis (Caspers et al. 2020, Thiesmeier 2004), whereas adults have only few predators. Thus, the benefits of an aposematic coloration might be highest shortly after metamorphosis (Caspers et al. 2020).

Several scenarios have been suggested for vertebrates to cope with nutritional shortages early in life. Individuals may flexibly adjust to such conditions via early adaptive programming (van Buskirk & Relyea 1998, Monaghan 2008, Bateson et al. 2014), which may be beneficial if the adult environment can be expected to be similar to that inhabited early in life. In this scenario, the early environment may work as a predictor for the adult environment. However, in biphasically developing animals, such as amphibians, which includes a major habitat shift, this strategy seems to be less adaptive and therefore less likely. In this case, two other developmental scenarios might be more likely. It might be that individuals that experience good initial nutritional conditions remain in better subsequent condition than those that grew up under early poor nutritional conditions regardless of the adult environmental conditions (e.g., Lindström 1999, Monaghan 2008, Krause et al. 2017). This is called the "silver spoon" effect (Grafen 1988). Alternatively, it is possible that poor initial nutritional conditions affect the subsequent development negatively, but as soon as the conditions improve later in life, deficits can be compensated by so-called compensatory growth (Metcalfe & Monaghan 2001). However, compensatory growth in one trait often causes costs to other traits (Fisher et al. 2006, Krause & Naguib 2011,2015, Sadeh et al. 2011, Hector et al. 2012). Disentangling which developmental effects, i.e., silver spoon, compensatory growth, or mixed effects from both, appear in fire salamanders requires long-term studies. Therefore, we conducted a survey over almost 10 years with fire salamander larvae experiencing either poor or rich nutritional conditions during the first three months of life (Krause et al. 2011). Afterwards all larvae received an intermediate diet (Krause & Caspers 2016). Based on earlier findings in these individuals raised under two different early nutritional conditions (Krause et al. 2011, Krause & Caspers 2016), we expected to obtain mixed findings between compensatory growth and the silver spoon effect. We expected to find that certain, relatively flexible morphometric traits, such as body mass, to have experienced compensatory growth. The yellow coloration of these salamanders shortly after metamorphosis is affected by early nutrition (Caspers et al. 2020), but we expected this effect to be compensated over time. In the case of the silver spoon effect, we expected longevity to be affected by early nutritional conditions, with individuals raised under rich nutritional conditions living longer than those raised under poor nutritional conditions. Other morphometric traits like size were expected to remain more inflexible in life and thus to be subject to the silver spoon effects.

Methods

The fire salamanders that we examined in the present study were born in the laboratory and raised under two different initial nutritional conditions that covered only the first three months of their lives, i.e., the aquatic larval phase (described in detail in Krause et al. 2011, Krause & Caspers 2016). After three months, when all animals had metamorphosed, all individuals from both early nutritional conditions received the same standard diet for the rest of the study period (see Krause & Caspers 2016). During the larval phase, twelve pairs of siblings (n=24 individuals) from twelve mothers were subjected to either poor conditions or rich early nutritional conditions. The early poor and early rich diets differed in the amounts of food provided (details see Krause et al. 2011). Briefly, the poorly fed larvae received food twice a week, while richly fed larvae received it six times per week. The amount of food (*Chironimus* larvae) given to each larva was the same at each feeding. Initially, three live, similarly sized *Chironimus* larvae were provided at each feeding session. This number increased by one every other week. From the time the animals became terrestrial they were fed on an intermediate standard diet of house crickets (*Acheta domestica*) (see Krause & Caspers 2016). All individuals received the same number of same-sized crickets, i.e., six house crickets per week per individual. The size of the crickets increased with age, starting with micro-size. We did not measure the effective food intake of the provided food. Housing of the salamanders until the age of 2.5 years has been specified in Krause & Caspers (2016); from then on, the sibling pairs were each kept together in a large terrarium of 150 × 50 cm, with two aquatic sections along the two long sides (150 × 6 cm).

We tracked their life history and thus their development until an age of almost 10 years. Some data from the first years of life have already been published elsewhere, with data on early larval behavioural and morphological developments having been presented in KRAUSE et al. (2011). These differences remained notable until about an age of two years, a point in time when certain growth and behavioural shortfalls became compensated (KRAUSE & CASPERS 2016). Within the first 100 days after metamorphosis, the number and expanse of yellow markings were greater in individuals raised under rich initial conditions (CASPERS et al. 2020).

We here report the systematically tracked life trajectories until adulthood of the animals and further to the age of almost 10 years, i.e., until the time-point where the cohort's mortality reached 50%. We report here the i) biometric measurements (body mass, total length as snout–tail tip length, and residual condition index as estimated by the residuals of the regression of log(body mass+1) on log(total length+1) (DENOEL et al. 2002, PLAIASU et al. 2010), as well as the ii) development of coloration (i.e., yellow/black ratio on the body surface) from the age of 6 months to the age of 108 months. We collected the data in a standardised scheme, i.e., from 6–12 months in 3-month intervals, thereafter until 5 years in 6-month intervals, thereafter in annual intervals. With this sampling regime, we collected data at the age of 6, 9, 12, 18, 24, 30, 36, 42, 48, 54, 60, 72, 84, 96, and 108 months. Furthermore, iii) we conducted a behavioural exploration test at the age of 5 years, and iv) tracked survival.

The sexes of the individuals were not taken into account in our study and analysis for several reasons. First, it was not possible to sex subadults, i.e., in their first 3–6 years. Thus, for all individuals that died during this time or before, no information about their sexual identity was available, and a genetic sexing method had not been available at the time. For the other individuals, sex was subjectively assessed by inspecting the cloacal swelling, but this method, in contrast to all other parameters in our study, could be quite imprecise, especially as we were not aware whether the early nutritional treatment affected or delayed sexual maturation. Sexing on the basis of morphometric measurements is not reliable either, as size differences between the sexes, if apparent, are within the variation of the opposite sex (THIESMEIER 2004). Substantial mass differences appear only in gravid females. Nevertheless, we expected the sexes of our individuals to be almost equally distributed, as larvae were initially selected and allocated to the two nutritional treatment groups at random.

Biometric measurements and coloration analysis

Body mass was taken to the nearest of 0.001 g (Sartorius BL150S) and total length was measured on laminated graph paper to the nearest 0.5 mm. We calculated a condition index from body mass and total length (body mass [g]/total length [mm]). At each measuring session, digital pictures were taken from each individual from about an orthogonal position above using a Canon PowerShot S5 IS (at Months 6, 9, 12); a Kodak Easy Share C533 (at 12 months), and thereafter a Panasonic DMC-FZ50. The background and the limbs were removed from these pictures with Adobe Photoshop CS5 as recommended by SANCHEZ et al. (2018), as fire salamanders tend to hold their limbs in different positions. The resulting pictures were analysed for the relative proportion of black and yellow colouration using Python 2.7 and a respective script published by SANCHEZ et al. (2018) freely available at https://github.com/eu-sanisa/Measure_salamander_colors.py.

Behavioural tests

When our salamanders had reached an age of five years (60 months), we conducted an open-arena test as described in KRAUSE & CASPERS (2016) with all individuals still alive, 17 in total. The arena consisted of 8 × 6 squares (each 10 × 10 cm) and each individual was introduced individually in the centre. Within 20 minutes we measured the latency until the individual moved to another square for the first time, the number of squares visited, and the number of switches between squares. The data were analysed for possible early-treatment effects and compared with the data taken at an age of 27 months from KRAUSE & CASPERS (2016) to test for potential long-term correlations.

Survival

We recorded for how long each individual survived. For dead animals, we calculated their lifespans to the exact day, and for the surviving animals, we made a cut-off date as per the 1st of October 2019, on which day the oldest of the 12 surviving fire salamanders had reached an age of 3471 days. The exact causes of death could not be identified.

Statistical methods

Biometric measurements, i.e., total length, body mass, and residual body condition index were analysed using linear mixed models (LME) with early nutritional treatment (2-level factor: rich and poor), age in months, and their respective interaction as factors. As random factors, we considered individual ID nested within MotherID. We used the approach of analysing the entire lifetime for each trait in a single model instead of using age-class specific effects as previous papers have considered already important developmental stages up to the age of two years (KRAUSE et al. 2011, KRAUSE & CASPERS 2016). Here we were explicitly interested in the respective lifetime effects. Relative proportions of black/yellow were analysed in a LME as described above only that the residual body condition index and the resulting two-way interaction were addi-

tionally taken into account. All models were checked for normal distribution of residuals. Behavioural parameters (i.e., number of visited squares and number of switches between squares) in the open arena were log- (log(x+1)) transformed to obtain normally distributed residuals, and each was analysed in a LME with early nutritional treatment as the factor and mother ID as the random factor. To estimate the across-time consistency of the behavioural traits, they were correlated to the behaviour recorded in the same test almost three years earlier (at age 27 months as reported by Krause & Caspers 2016), using the log (x+1) values of Pearson correlations. The LMEs and correlations were calculated in R 3.3.1 (R Core Team2016) using nlme (Pinheiro et al. 2017), and p- and F-values were produced by the respective package in Wald test. Survival was analysed using a Gehan-Wilcox Test, and the Kaplan-Meier procedure in Dell Statistica 13 was applied for plotting (Dell Inc. 2015).

The raw data for developmental, behavioural, survival and coloration data are deposited online (Krause et al. 2021a; Tables S1–3) as are the modified photos used for our colour analysis (Krause et al. 2021b).

Results
Total length, body mass, residual body condition index

The total length throughout the lifetime, from six to 108 months of age, was significantly affected by the nutritional treatment the individuals had experienced during the first three months of their lives as well as by age, whereas the interaction between age and initial nutritional treatment had no effect (Table 1a, Fig. 1a). Body mass was affected by age, while the early nutritional treatment had no effect (Table 1b, Fig. 1b). The residual body condition index was affected by the initial nutritional conditions and tended also to be influenced by age (Table 1c, Fig. 1c).

Relative yellow coloration

The relative proportion of yellow to black on the body surface throughout life time was affected by age and the residual body condition index whereas the initial nutritional treatment had no effect. The proportion of yellow relative to black decreased within the first postmetamorphic year of life and thereafter increased slightly until the age of three years from when it remained relatively stable. The body condition index is positively linked to the proportional content of yellow (Table 1d, Fig. 2).

Behaviour at 5 years and consistency over the last 3 years

The number of visited squares in the open arena at the age of five years (60 months) was not significantly different

Table 1. Detailed statistical results of the linear mixed-effect models (LME) for a) total length, b) body mass, c) residual body condition index, and d) relative yellow content in the colour pattern of fire salamanders, *Salamandra salamandra*.

Measurements and factors	F-value	df	p-value
a) Total length			
nutritional treatment	12.43	1,8	0.0078
age	323.84	1,254	<0.0001
nutritional treatment × age	0.29	1,254	0.59
b) Body mass			
nutritional treatment	2.22	1,8	0.17
age	227.28	1,254	<0.0001
nutritional treatment × age	0.25	1,254	0.62
c) Residual body condition index			
nutritional treatment	12.67	1,8	0.007
age	3.77	1,254	0.053
nutritional treatment × age	0.29	1,254	0.59
d) Relative Body Surface Yellow Colouration			
nutritional treatment	2.30	1,8	0.17
age	54.80	1,251	<0.0001
residual body condition index	48.37	1,251	<0.0001
nutritional treatment × age	0.33	1,251	0.57
nutritional treatment × residual body condition index	0.93	1,251	0.34
age × residual body condition index	2.72	1,251	0.10

between individuals that had been raised as larvae under rich or poor nutritional conditions (LME : early nutritional treatment $F_{1,5}$ = 0.38, p = 0.56). The same was the case for the number of switches between squares at the age of five years in that they did not significantly differ between initially richly and poorly fed fire salamanders, respectively (LME: early nutritional treatment. $F_{1,5}$ = 1.48, p = 0.28). Activity, as indicated by the number of switches between squares, was not significantly correlated between the two points of time, i.e., at 60 months vs. the age of 27 months, (Pearson correlation r_p = 0.40, t_{15} = 1.67, p = 0.11). However, the number of visited squares tended to be positively correlated across the three-year period (Pearson correlation r_p = 0.43, t_{15} = 1.87, p = 0.08; Fig. 3)

Survival

Half of the study cohort had perished after about nine and a half years. However, the early nutritional conditions had no significant influence on the survival of individuals (Gehans Wilcoxon Test, WW = -6.00, test statistic = -0.17, p = 0.87; Fig. 4)
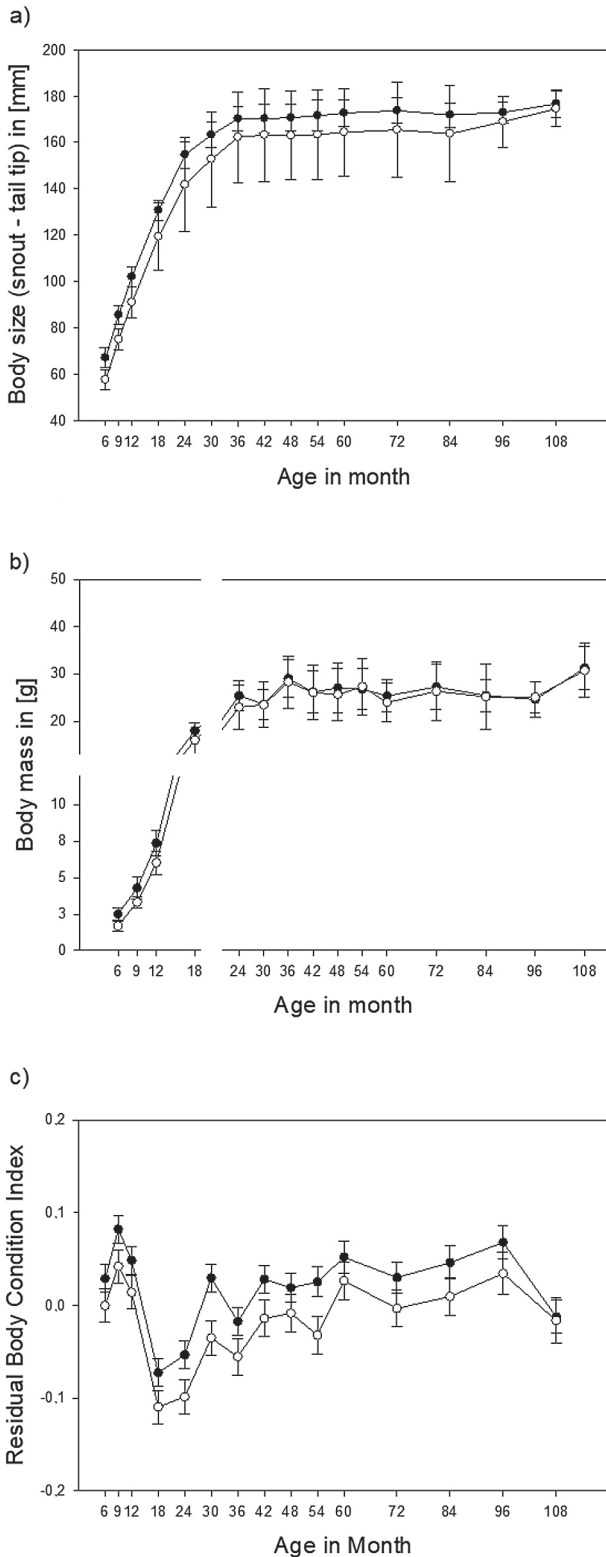
a)

b)

c)

Figure 1. Long-term representation of a) total length, b) body mass, and c) residual body condition index of fire salamanders, *Salamandra salamandra* from initially poor nutritional conditions (open circles) and from initially rich nutritional conditions (filled circles). Shown are means with SE.

Discussion

We studied the life trajectory of the fire salamander, a long-lived vertebrate, over a period of almost 10 years in captivity. Our previous studies had highlighted that the first months of life, i.e. the period of aquatic development, is crucially affected by the nutritional conditions, and, even more interesting, we here show that these early conditions have lifelong consequences. Certain phenotypic traits are affected throughout subsequent life, such as total length and the residual body condition of the salamanders. In contrast, other initial deficits such as body mass, yellow
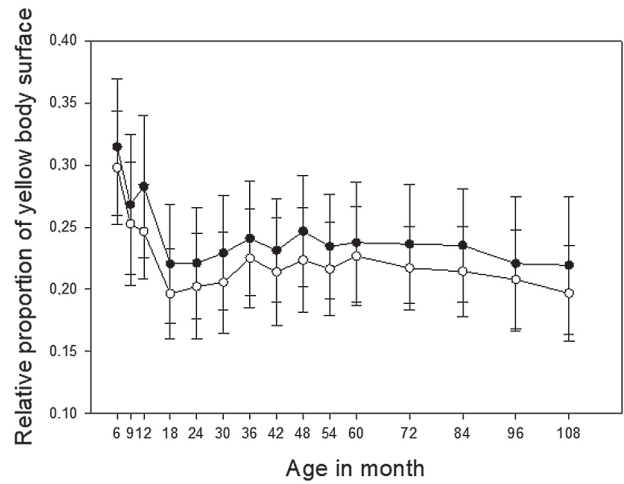
Figure 2. Relative proportion of yellow in the colour pattern over the study period. Mean values (± SE) of fire salamanders, *Salamandra salamandra*, from initially poor nutritional conditions (open circles) and from initially rich nutritional conditions (filled circles) are shown.
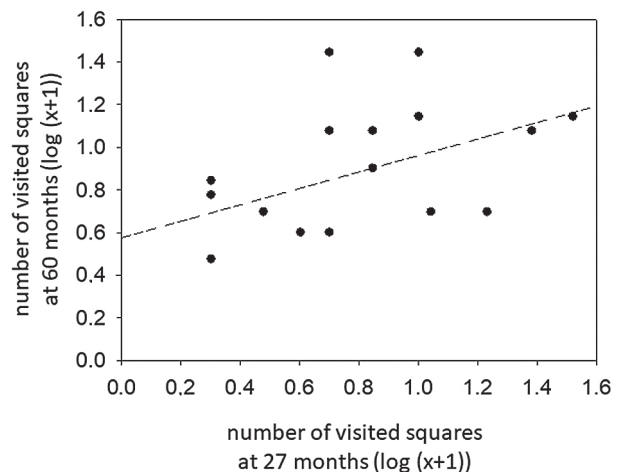
Figure 3. Correlation between the number of visited squares at the age of 27 and 60 months of age of fire salamanders, *Salamandra salamandra*. Two data point overlap.

321

content in the colour pattern, or explorative behaviour can be compensated during subsequent development. However, neither lasting impacts from early conditions nor the potential costs for trait-specific compensation led to an accelerated mortality in the individuals that initially experienced poor nutritional conditions during our study period.

Different early-life conditions led to differences in the body mass of the salamanders, with animals raised in rich nutritional conditions being heavier (Denoel & Poncin 2001, Warburg 2009, Krause et al. 2011, Krause & Caspers 2016). However, these differences were compensated later in life and had already disappeared when reaching an age of about one and a half years, presumably as a result of compensatory growth (Krause & Caspers 2016). This compensation seems to have continued over the entire study period. Similar compensatory growth processes are known to occur also in other vertebrates (Metcalfe & Monaghan 2001, Krause & Naguib 2011, Hector & Nakagawa 2012) including amphibians (e.g., Sadeh et al. 2011, Hector et al. 2012). Usually, compensation trajectories come at certain costs (Metcalfe & Monaghan 2001, Fisher et al. 2006, Krause & Naguib 2011), but in our fire salamanders, in contrast to our initial expectations, we could not so far detect any cost, at least not in the measured traits. Compensation also seems to be trait-specific: body mass might be compensated relatively easy, as it is a relatively flexible trait throughout life, whereas no compensation might be possible for less flexible traits such as, for example, measurements that rely more on the fixed structure of the animals. Here it seems that the silver spoon effect kicks in. By the age of about three years, individuals will have completed most of their size development. At this point of time, fire salamanders from initially poor nutritional conditions were still of a smaller size than those from initially rich nutritional conditions. That these ear-

ly conditions affect skeleton-related parameters throughout life is also known from other vertebrate species (e.g., Krause et al. 2017). Important to notice here is that the perceived increase in size (Fig. 1a) of individuals from initially poor nutritional conditions at the age of 96 and 108 months is most likely a result of mortality, i.e., the small individuals have died and have left only the larger ones in the sample.

Fire salamanders are known to be relatively long-lived with a reported average lifespan in the wild of 7–8 years, up to a maximum of 20 years (Thiesmeier 2004). Thus, the time frame of our study covers the most important life trajectories and life history. After about 9.5 years, half of our initial cohort was still alive. In contrast to findings from long-term studies of other vertebrate species (e.g., Lemon 1991, Birkhead et al. 1999, Ricklefs & Wikelski 2002, Krause et al. 2017), we unexpectedly found that early nutritional conditions had no effects on longevity. We initially expected that individuals from initially poor nutritional conditions die younger, due to direct effects of early conditions and indirectly due to the additional costs of compensation (Birkhead et al. 1999, Metcalfe & Monaghan 2001). In other amphibian species it has been shown that size at metamorphosis is positively linked to survival and that compensatory growth might be costly (Szekely et al. 2020). However, at least within the first ten years of life, we could not detect such an effect. Maybe these effects appear even later in life, are not present in salamanders at all, or do not surface in our captive setting where they the salamanders may be buffered against such an effect due to their relatively slow development (Krause & Caspers 2016). Nevertheless, it would be interesting in the future to study such direct and indirect effects of plastic developmental growth trajectories under natural conditions.

We also tracked the relative yellow content in the dorsal colour pattern of individual salamanders for up to almost 10 years. As yet, little is known about the ontogeny of colour markings in the fire salamander (e.g., Thiesmeier 2004), only that there might be sex-dependent differences at adulthood (Balogova & Uhrin 2015, Preissler et al. 2019). Yellow pigment may be costly to produce, as fire salamander larvae raised under poor nutritional conditions end up with a lower amount of yellow shortly after metamorphosis (Caspers et al. 2020). This difference was present for up to 100 days after metamorphosis (Caspers et al. 2020). At this age, young terrestrial fire salamanders are still commonly a target of predation and it seems that the yellow markings act as a warning signal to potential predators (Caspers et al. 2020). The effects of the early nutritional conditions on the yellow content in the colour pattern will already have vanished at an age of six months, i.e., at the first point of auditing in in the present study. Interestingly, the proportion of yellow vs. black decreased further with increasing age and varied slightly until reaching a relatively stable level at about three years of age; this was the same point of time when size and mass reached stable values. As the risk of predation decreases with becoming larger, the overall benefit from additional larger
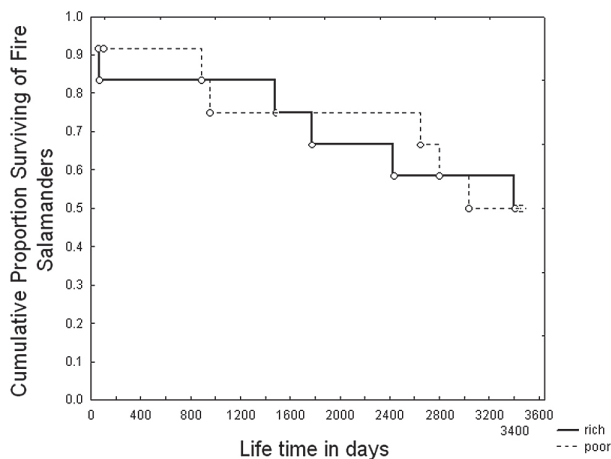

Figure 4. Survival data of fire salamanders, *Salamandra salamandra*, from the two different initial nutritional conditions. Solid lines and corresponding circles indicate individuals from initially rich conditions, while dashed lines indicate initially poor ones. Each circle indicates the point of time of a completed life history, i.e., when a salamander died.

proportions of yellow might not be adaptive with respect to the predation risk, and permit individuals in initially poorer condition can catch up. Outgrowing the capabilities of predators by becoming larger is probably a more efficient strategy against predation than conspicuous coloration in young terrestrial fire salamanders. The proportion of yellow in the colour pattern does not seem to be directly linked to the level of toxicity (Preissler et al. 2019), but rather to body condition. However, whether the onset or extent of toxicity is linked to early life conditions is subject to future studies.

The behavioural differences in risk-taking and exploration behaviour that were caused by the early nutritional conditions in larvae (Krause et al. 2011) have disappeared at an age of about two years (Krause & Caspers 2016), and our present results support that this behavioural adjustment remains similar at the age of five years of life. Such flexible behavioural adjustments in risk-taking in response to environmental conditions have been reported also from other fire salamander populations (Manenti et al. 2013). While we found no correlation in activity (number of switches between squares) between the behaviour at two and five years of age, we found a tendency for a positive link between the exploration behaviour (number of visited squares) over the three-year period. Such a long-term correlation is remarkable and may indicate a stable behavioural phenotype of the individuals (Wuerz & Krüger 2015).

Taken together, we found two different effects acting simultaneously in response to early nutritional conditions in fire salamanders. Compensation appears to be flexible, affecting traits such as body mass and colour pattern, while other traits, like size, appear to be more fixed and are affected by the silver spoon effects throughout life. Behavioural traits appear to maintain a certain level of consistency over the years. Interestingly, survival appears unaffected by early nutritional conditions even after almost ten years.

Acknowledgements

References

Alcobendas, M., D. Buckley, & M. Tejedo (2004): Variability in survival, growth and metamorphosis in the larval fire salamander (*Salamandra salamandra*): effects of larval birth size, sibship and environment. – Herpetologica, **60**: 232–245.

Balogova, M. & M. Uhrin (2015): Sex-biased dorsal spot patterns in the fire salamander (*Salamandra salamandra*). – Salamandra, **51**: 12–18.

Bateson, P., P. Gluckman & M. Hanson (2014): The biology of developmental plasticity and the predictive adaptive response hypothesis. – Journal of Physiology, **592**: 2357–2368.

Birkhead, T. R., F. Fletcher & E. J. Pellatt (1999): Nestling diet, secondary sexual traits and fitness in the zebra finch. – Proceedings of the Royal Society London B, **266**: 385–390.

Caspers, B. A., E. T. Krause, R. Hendrix, M. Kopp, O. Rupp, K. Rosentreter & S. Steinfartz (2014): The more the better – polyandry and genetic similarity are positively linked to reproductive success in a natural population of terrestrial salamanders (*Salamandra salamandra*). – Molecular Ecology, **23**: 239–250.

Caspers, B. A., E. T. Krause, I. Hermanski, C. Wiesbrock, F. W. Kastrup & S. Steinfartz (2020): Developmental costs of yellow colouration in fire salamanders and experiments to test the efficiency of yellow as a warning colouration. – Amphibia-Reptilia, **41**: 373–385

Dell Inc. (2015). Dell Statistica (Software-System für Datenanalyse), Version 13. – software.dell.com.

Denoel, M. & P. Poncin (2001): The effect of food on growth and metamorphosis of paedomorphs in *Triturus alpestris apuanus*. – Archiv für Hydrobiologie, **152**: 661–670.

Denoël, M., F. Hervant, R. Schabetsberger & P. Joly (2002): Short-and long-term advantages of an alternative ontogenetic pathway. – Biological Journal of the Linnean Society, **77**: 105–112.

Eitam, A., L. Blaustein & M. Mangel (2005): Density and intercohort priority effects on larval *Salamandra salamandra* in temporary pools. – Oecologia, **146**, 36–42.

Francis, E. T. (1934): The anatomy of the salamander. – Clarendron Press, Oxford, UK.

Fisher, M. O., R. Nager & P. Monaghan (2006): Compensatory growth impairs adult cognitive performance. – PLoS Biology, **4**: 1462–1466.

Grafen, A. (1988): On the uses of data on lifetime reproductive success. – pp. 454–471 in: Clutton-Brock, T. (ed.): Reproductive success. – University of Chicago Press, Chicago, IL.

Greven, H. (1998): Survey of the oviduct of salamandrids with special reference to the viviparous species. – Journal of Experimental Zoology, **282**: 507–525.

Hector, K. L., P. J. Bishop & S. Nakagawa (2012): Consequences of compensatory growth in an amphibian. – Journal of Zoology, **286**: 93–101.

Hector, K. L. & S. Nakagawa. (2012): Quantitative analysis of compensatory and catch-up growth in diverse taxa. – Journal of Animal Ecology, **81**: 583–593.

Krause, E. T. & M. Naguib (2011): Compensatory growth affects exploratory behaviour in zebra finches, *Taeniopygia guttata*. – Animal Behaviour, **81**: 1295–1300.

Krause, E. T., S. Steinfartz & B. A. Caspers (2011): Poor nutritional conditions during the early larval stage reduce risk-taking activities of fire salamander Larvae (*Salamandra salamandra*). – Ethology, **117**: 416–421.

Krause, E. T. & M. Naguib (2015): Zebra finch males compensate in plumage ornaments at sexual maturation for a bad start in life. – Frontiers in Zoology, **12**: S11.

Krause, E. T. & B. A. Caspers (2016): Long-term consequences of early nutritional conditions on the behaviour and growth of fire salamanders. – Amphibia-Reptilia, 37: 69–77.

Krause, E. T., O. Krüger & H. Schielzeth (2017): Long-term effects of early nutrition and environmental matching on developmental and personality traits in zebra finches. – Animal Behaviour, 128: 103–115.

Krause, E.T., S. Steinfartz & B.A. Caspers (2021a): Data from The ravages of time – Life-long consequences of early larval nutritional conditions on the terrestrial life of fire salamanders (Salamandra salamandra). – figshare. Dataset. https://doi.org/10.6084/m9.figshare.14686194.v1.

Krause, E.T., Steinfartz, S,, Caspers, B.A. (2021b): Picture data from The ravages of time – Life-long consequences of early larval nutritional conditions on the terrestrial life of fire salamanders (Salamandra salamandra). – figshare. Media. https://doi.org/10.6084/m9.figshare.14686398.v1

Lemon, W. C. (1991): Fitness consequences of foraging behavior in the zebra finch. – Nature, 352: 153–155.

Lindström, J. (1999): Early development and fitness in birds and mammals. – Trends in Ecology and Evolution, 14: 343–348.

Manenti, R., G. F. Ficetola, A. Marieni & F. De Bernardi (2011): Caves as breeding sites for Salamandra salamandra: habitat selection, larval development and conservation issues. – North-Western Journal of Zoology, 7: 304–309.

Manenti, R., M. Denoël & G. F. Ficetola (2013a): Foraging plasticity favours adaptation to new habitats in fire salamanders. – Animal Behaviour, 86: 375–382.

Manenti, R., M. E. Siesa, & G. F. Ficetola (2013b): Odonata occurrence in caves: active or accidentals? A new case study. – Journal of Cave and Karst Studies, 75: 205–209.

Melotto, A., G. F. Ficetola & R. Manenti (2019): Safe as a cave? Intraspecific aggressiveness rises in predator-devoid and resource-depleted environments. – Behavioral Ecology and Sociobiology, 73: 1–14.

Metcalfe, N. B. & P. Monaghan (2001): Compensation for a bad start: grow now, pay later? – Trends in Ecology and Evolution, 16: 254–260.

Monaghan, P. (2008): Early growth conditions, phenotypic development and environmental change. – Philosophical Transactions of the Royal Society London B, 363: 1635–1645.

Moran, N. P., A. Sánchez-Tójar, H. Schielzeth & K. Reinhold (2021): Poor nutritional condition promotes high-risk behaviours: a systematic review and meta-analysis. – Biological Reviews, 96: 269–288.

Oswald, P., B. A. Tunnat, L. G. Hahn & B. A. Caspers (2020): There is no place like home: Larval habitat type and size affect risk-taking behaviour in fire salamander larvae (Salamandra salamandra). – Ethology, 126: 914–921.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar & R Core Team (2017): nlme: Linear and Nonlinear Mixed Effects Models. – R package version 3.1-131.

Plăiaşu, R., T. Hartel, R. I. Băncilă, D. Cogălniceanu & J. Smets (2010): Comparing three body condition indices in amphibians: a case study of yellow-bellied toad Bombina variegata. – Amphibia-Reptilia, 31: 558–562.

Preissler, K., S. Gippner, T. Lüddecke, E. T. Krause, S. Schulz, M. Vences & S. Steinfartz (2019). More yellow more toxic? Sex rather than alkaloid content is correlated with yellow coloration in the fire salamander. – Journal of Zoology, 308: 293–300.

R Core Team (2016): R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. – https://www.R-project.org/.

Reques, R. & M. Tejedo (1996): Intraspecific aggressive behaviour in fire salamander larvae (Salamandra salamandra): the effects of density and body size. – Herpetological Journal, 6: 15–19.

Reinhardt, T., S. Steinfartz, A. Paetzold & M. Weitere (2013): Linking the evolution of habitat choice to ecosystem functioning: direct and indirect effects of pond-reproducing fire salamanders on aquatic-terrestrial subsidies. – Oecologia, 173: 281–291.

Reinhardt, T., M. Brauns, S. Steinfartz & M. Weitere (2017): Effects of salamander larvae on food webs in highly subsidised ephemeral ponds. – Hydrobiologia, 799: 37–48.

Ricklefs, R. E. & M. Wikelski (2002): The physiology/life-history nexus. – Trends in Ecology and Evolution, 17: 462–468.

Sadeh, A., N. Truskanov, M. Mangel, & L. Blaustein (2011): Compensatory development and costs of plasticity: larval responses to desiccated conspecifics. – PLoS One, 6: e15602.

Sanchez, E., S. Gippner, M. Vences, K. Preissler, I. J. Hermansk, B. A. Caspers, E. T. Krause, S. Steinfartz & F. W. Kastrup (2018): Automatic quantification of color proportions in dorsal black and yellow colored amphibians, tested on the Fire Salamander (Salamandra salamandra). – Herpetology Notes, 11: 73–76.

Székely, D., D. Cogălniceanu, P. Székely, D. Armijos-Ojeda, V. Espinosa-Mogrovejo & M. Denoël (2020): How to recover from a bad start: size at metamorphosis affects growth and survival in a tropical amphibian. – BMC Ecology, 20: 24.

Thiesmeier, B. (2004). Der Feuersalamander. – Laurenti-Verlag, Bielefeld.

Van Buskirk, J. & R. A. Relyea (1998): Selection for phenotypic plasticity in Rana sylvatica tadpoles. – Biological Journal of the Linnean Society, 65: 301–328.

Warburg, M. R. (2009): Age and size at metamorphosis of half-sib larvae of Salamandra infraimmaculata born in the laboratory and raised singly under three different food regimes. – Belgian Journal of Zoology, 139: 156–165.

Wilbur, H. M. & J. P. Collins (1973): Ecological aspects in amphibian metamorphosis. – Science, 182, 1305–1314.

Weitere, M., D. Tautz, D. Neumann & S. Steinfartz (2004): Adaptive divergence vs. environmental plasticity: tracing local genetic adaptation of metamorphosis traits in salamanders. – Molecular Ecology, 13: 1665–1677.

Wuerz, Y. & O. Krüger (2015): Personality over ontogeny in zebra finches: long-term repeatable traits but unstable behavioural syndromes. – Frontiers in Zoology, 12: S9.