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Phenology and growth of fire salamander larvae in streams
and stagnant waters of the Vienna Woods

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Abstract

Females of *Salamandra salamandra* use different aquatic habitats for larval deposition, which can be divided in stagnant and flowing waters. These different water bodies were examined at “Maurer Wald“, „Neuwaldegg“, „Lainzer Tiergarten“ and „Moosgraben“ of the Vienna Woods. The aim of the study was to examine and compare the size of fire salamander larvae from these different waters (stagnant and flowing waters as well as the individual stagnant and flowing waters) from 2020 and 2018 and to explain possible differences for the size between the larvae.

Fire salamander larvae were caught from these aquatic habitats and photographed to compare their length. Variable investigated was the total length (body length + tail length). Due to the extremely fluctuating weather conditions, especially this year but also in 2018, larvae were deposited at least until mid-June. In 2020, the newly deposited individuals of the dried up ponds had roughly the same total length than the first deposited ones at the last possible data collection after the ponds dried out. These fire salamander larvae which were deposited after the ponds refilled also grew faster than the first deposited ones of the ponds as well than the larvae of the streams. In 2018, there was no big difference between larvae from stagnant and flowing waters, except for the two ponds “Jupiter” and “Schlammtümpel” at “Maurer Wald”. Individuals from these two water bodies were significant larger than those from the other aquatic habitats. During late spring more small larvae were caught in the streams compared to the ponds.

Fire salamander larvae from some ponds with better conditions of growth were significantly larger than those from other water bodies. Individuals from stagnant and flowing waters did not differ except the growth after the ponds were refilled. I sum up that the differences in total length between the areas and different water bodies are consequences of environmental conditions concerning temperature and food availability.

Key words: amphibians, *Salamandra salamandra*, fire salamander larvae, Vienna Woods, stagnant and flowing waters, length differences

Introduction

In the course of evolution, amphibians developed their different life cycles, ranging from a completely aquatic to a completely terrestrial life-history (Duellman & Trueb, 1986). Amphibians that occur in the temperate zone are mostly semi-aquatic or have at least two different phases of life, namely the larvae living in the water and the terrestrial adults (Semlitsch, 1998).

The fire salamander (*Salamandra salamandra*) – unmistakable by its colour – belongs to the order of the Urodela and is mainly distributed across Western and Central Europe and the Balkans (Westheide & Rieger, 2010). Fire salamanders, which prefer deciduous forests (Alcobendas et al., 1996), are terrestrial, nocturnal animals that normally hide in their shelters under dead wood, stones or tree stumps during the day, but are often active when it rains (Duellman & Trueb, 1986, Westheide & Rieger, 2010). If the night temperature is higher than 4° C, they also show increasing activity (Zahn, 2007). In general, the temperature has a decisive impact on the duration of activity in amphibians (Morrison & Hero, 2003).

Amphibians such as fire salamanders strongly depend on accessible water bodies for reproduction and terrestrial habitat, offering foraging and hiding opportunities (Wilbur, 1980, Schmidt et al., 2005, Sparreboom, 2014). Fire salamanders have a complex life cycle with an aquatic larval phase and adult animals living on land, where only courtship and mating takes place. The mating period in Central Europe extends from March to September (Westheide & Rieger, 2010). The male places his spermatophore on the ground, which the female picks it up with her cloaca (Westheide & Rieger, 2010). The fertilization happens in the oviduct, where the offspring develops to an advanced stage until the yolk of the egg is consumed (Kopp & Baur, 2000). Body condition of females and environmental factors such as temperature and food availability may play an important role for size of eggs (Alcobendas et al., 2004). The amount of energy existing for reproduction influences the egg size as well (Morrison & Hero, 2003). Variability in egg size, clutch size and size at birth occurs within and between populations (Rebelo & Leclair, 2003). With increasing number of fertilizations, females reduce their total investment in eggs (Kopp & Baur, 2000). They produce smaller broods of larger individuals (Rebelo & Leclair, 2003).

About 80 well-developed aquatic fire salamander larvae – in a size range of 27 to 35 mm (Thiesmeier, 2004) – are then released in the following spring period from March to mid-May

(Steinfartz et al., 2006), by the adult pregnant females. The larval deposition mostly takes place during rainy nights (Thiesmeier 2004; Weitere et al. 2004) in different habitats, with the main distinction being made between stagnant and flowing waters (Greven, 1976, Weitere et al., 2004). Because fire salamanders are quite mobile (Schulte et al., 2007), females have often the choice between these two different habitats for larval deposition. For depositing larvae in streams females prefer quieter pond-like sections (Manenti et al., 2009b, Reinhardt, 2014) with clearly reduced flow speed instead of fast-flowing ones because they are stressed by turbulences (Baumgartner et al., 1999). Additionally, there is a strong downstream drift due to high flow speeds (Thiesmeier & Schuhmacher, 1990). After the ovoviviparous birth process, the larvae stay in the aquatic habitat up to a year but normally they change to a terrestrial environment after about four months (Kopp & Baur, 2000).

The streams and stagnant waters, which are used by the salamanders as breeding waters, can differ greatly from one another. The standing waters in forests have higher risk of drying out, especially at high temperatures. The ponds are created by melting ice and rain, which only temporarily carry water. In contrast the year-round flowing waters, which are mostly shallow streams, are not so endangered of drying out (Reinhardt et al., 2013, Caspers et al., 2015). For example, an unpredictably short period without precipitation can lead to mass mortalities (Weitere et al., 2004). Streams also have higher oxygen contents (Warburg, 2010, Reinhardt et al., 2013, Reinhardt, 2014) and food availabilities than ponds (Warburg et al., 1979, Thiesmeier & Grossenbacher, 2004). High densities of fire salamander larvae can lead to food overexploitation and increasing competition (Reinhardt, 2014). Furthermore, larvae in flowing waters have more opportunities to spread than those ones in standing waters – their water availability can vary seasonally depending on climatic conditions (Caspers et al., 2015) – which are usually associated with higher water temperatures (Kopp & Baur, 2000, Weitere et al., 2004, Reinhardt, 2014). The temperature is very important because it influenced growth rate and activity in all animals, especially in ectotherms (Beachy, 1995, Van der Have & De Jong, 1996, Grant et al., 2014).

Big disruptions of the stream systems can occur when heavy rain creates strong flush floods and catastrophic drift which increases the mortality in stream fauna (Anderson and Lehmkuhl 1963). The individual ponds but also the different streams diversify in terms of size, structure and vegetation. Ponds and streams can have many structurally different places, so they can vary greatly. Other factors which can influence the water bodies are exposure to the sun (Czypionka et al., 2018) or shadiness. These factors as well as the population density

(Reinhardt, 2014) and the occurrence of predators (Matsunami et al., 2015) affect fire salamander larvae size and growth.

Environmental conditions constantly change, (Clobert et al., 2009, Kokko & Lopez-Sepulcre, 2006) especially the spatially and temporally ponds, (Hendrix et al., 2017) but also the more stable streams. Therefore, the larvae constantly have to adapt well to the different conditions (Alcobendas, 2004, Zahn, 2007, Schulte, 2008). All these factors and differences, mentioned above between flowing and stagnant waters can have drastic consequences (e.g. mass dying or decreased growth) especially on the larvae in ponds (Weitere et al., 2004; Reinhardt et al., 2013). But also the flowing and stagnant waters among themselves influence the development of the fire salamander larvae and limit the time available until metamorphosis (Warburg et al., 1979, Vences et al., 2002, Alcobendas et al., 2004, Weitere et al., 2004).

Schulte (2008) carried out a study on fire salamander larvae in Kottenforst in Germany, comparing the larvae from streams and ponds. He showed that individuals in ponds had a significantly higher body mass and a longer tail length at birth than those ones of streams. Larger larvae at birth tended to have a shorter duration of development (Alcobendas et al., 2004). A higher body mass of new born larvae, which were deposited in ponds, is a maternal investment to develop faster in an unpredictable habitat and saves the offspring one week of eating (Weitere et al., 2004, Schulte, 2008). Furthermore, Schulte substantiated that longer tail fins in ponds would be helpful for a quick escape from predators, while shorter tail fins in streams are important so that animals are not carried away by the water flow.

The fact that the larvae at birth in standing waters are larger than those in flowing waters was also supported by two further studies, namely Rebelo and Leclair (2003) and Weitere et al. (2004). Rebelo and Leclair assume that the size of the larvae at birth depends on the size of the females and is not adaptable. This means that older and larger females would also have a larger offspring (Caspers et al., 2015). Furthermore, larvae born in ponds grow faster because of the higher water temperature and the short duration of the pond (Kopp & Baur, 2000).

In Vienna, Mayerhofer (2013) showed that newly deposited larvae from ponds at “Maurer Wald” were slightly larger than those ones from the two streams “Eckbach” and “Moosgraben”. That the larvae in ponds had a longer tail length average than in streams was of the occurrence of the larger females.

Keckeis (2013) compared the body shapes of fire salamanders from different types of water in Vienna and showed that larvae from temporary stagnant waters were longer, had a longer tail length and a narrower skull than those from flowing waters. A general behaviour that Crump (1983), Reinhardt (2014), Manenti et al. (2015) and Reinhardt et al. (2015) also pointed out is cannibalism. This behaviour may occur towards smaller species, for example if food is scarce. Reques and Tejedo (1996) proved this by showing significantly more aggressive behaviour of fire salamander larvae at high population densities.

In the Vienna Woods – study area in both years (2018 and 2020) – *Salamandra salamandra* is a characteristic species for living in beech and oak dominated forests and depositing larvae in stagnant or flowing waters. Zutz (2012) compared the genetic parameters of these two populations of *Salamandra salamandra* in the Vienna Woods that differ in their habitat structure and climatic conditions. She showed that although there was a rather large degree of genetic subdivision between these two populations, the genetic diversity hardly differed between the sites. Even though salamanders are very common throughout Europe there are only a few investigations of biology and ecology of this species occurring in Austria.

The aim of this study was to:

- examine the size of fire salamander larvae in various waters in Vienna from the beginning of spring until all larvae metamorphosed or the water bodies dried up
- compare the size of fire salamander larvae from stagnant and flowing waters as well as the individual stagnant and flowing waters from 2018 and 2020
- explain possible differences for the size between the larvae of the different waters

Materials and Methods

Species

The fire salamander (*Salamandra salamandra*) (Fig. 1) counts as the largest salamander species in Europe by reaching a total length of up to 20 cm and an age of up to 20 years in central Europe (Thiesmeier, 2004). In Europe the taxon consists of various subspecies, but in Austria only the nominate form *S. s. salamandra* occurs (Cabela et al., 2001). As already mentioned, it inhabits broadleaf or mixed forests (beech, oak and hornbeam trees predominant) (Burgstaller, 2019) with stagnant or flowing waters, which are utilized for larvae deposition (Greven, 1976, Weitere et al., 2014).



Figure 1: An adult fire salamander found at “Moosgraben”, one of the sampling sites.

First, the fire salamander larvae are inconspicuously brown and on average 25 to 35 millimetres (Schulte, 2008). They have outer tufts of gills and from the beginning four legs. Furthermore, the head is noticeably wider than the body. Salamander larvae count as generalist predators because they feed everything that fits in their mouth. This includes both invertebrates like for example chironomids, oligochaetes, plecopterans and small crustaceans (Weitere et al., 2004) and small vertebrates. Although fire salamander larvae can coexist with other caudate species (Thiesmeier & Dalbeck, 2011), in environments such as small streams and underground waters they are often the top predators (Davic & Welsh, 2004) that determine the composition of aquatic communities (Blaustein et al., 1996, Reinhardt et al., 2013). Towards other larvae of caudate species, fire salamander larvae are more robust because they reduce the abundance through competition for invertebrates and predation of small newt larvae (Segev and Blaustein, 2007). Fire salamander larvae rely on visual, chemical, electric and mechanical stimuli to detect prey (Himstedt et al., 1982). Their most common strategy is the sit-and-wait behaviour. Fire salamander larvae often remain on the substrate or hide under stones or vegetation and from these places they can attack organisms moving close to them (Manenti et al., 2013). At the same time this strategy reduces the risk of being captured by other possible predators of the larvae for example large dragonfly larvae, fish and also birds (especially crows) but is only advantageous in the presence of detectable and active invertebrates (Hawlena et al., 2011). For example Baumgartner et al. (1999) and

Bänziger (2017) demonstrated that the density of fire salamander larvae was reduced by the presence of some fish species. In contrast, active predators have a greater range of motion that enhances the probability of detecting prey (Hodar et al., 2006, Winandy & Denoël, 2013) but at the same time it increases the risk of being discovered by a predator. After metamorphosis, the salamanders are completely terrestrial and as adults (usually: after 3-5 years) only visit the water again to deposit their offspring (Thiesmeier, 2004, Burgstaller, 2019).

Study area

The study was carried out in the Vienna Woods (Austria), which is largely fully designated as a UNESCO Biosphere Park. In this area I investigated different water bodies where a distinction is made between stagnant and flowing waters. These also showed some varieties in their habitat structure. The areas located in the west and northwest of Vienna are “Maurer Wald“, „Neuwaldegg“ („Schwarzenbergpark“ & „Eckbach“), „Lainzer Tiergarten“ („Auerochsengehege“ & „Lainzer Bach“) and „Moosgraben“ (Fig. 2). Sampling at the stream always proceeded upstream to maintain water clarity and only took place on dry days, to avoid discharge and water turbulence from rain.

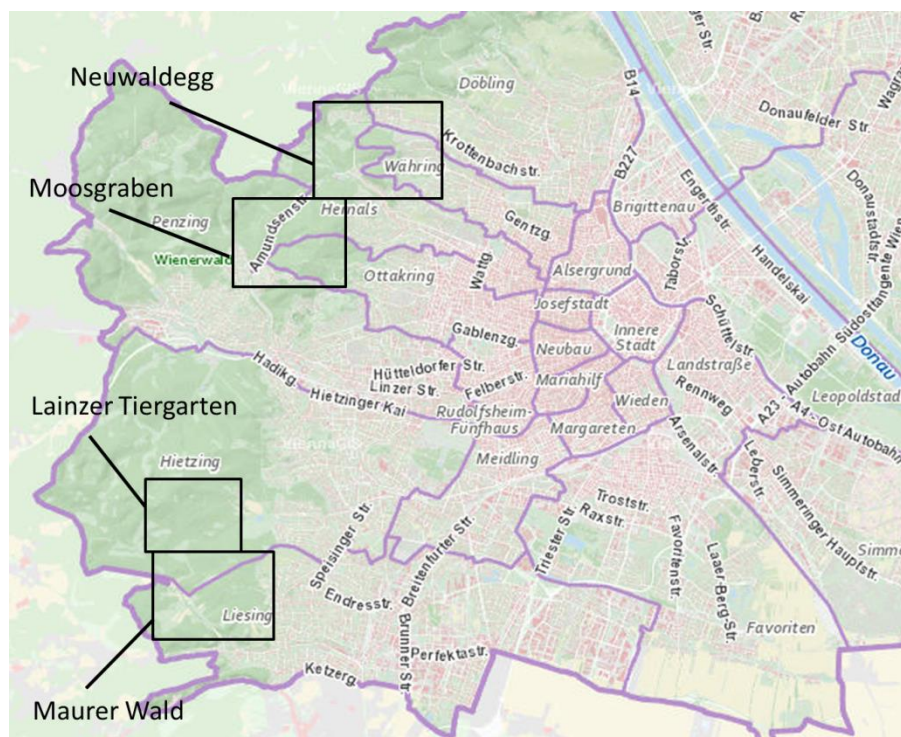


Figure 2: Study areas in the Vienna Woods. Sample sites are outlined in black.

During and after data sampling different variables in and around the water bodies were recorded. These biotic and abiotic factors could influence the size and also the abundance of

fire salamander larvae. Abiotic factors included water temperature (Habor CP011A), water bodies' size and depth, characteristics of the water body (branches, leaves/leaf litter, stones, etc.), turbidity and flow speed (not measured but observed). Biotic factors included food availability (mosquitoes larvae, etc.), abundance, presence of predators (dragonfly larvae, crows) and occurrence of adult fire salamanders.

The “Maurer Wald” ($48^{\circ} 8' 57''$ N, $16^{\circ} 14' 40''$ E) – 260 to 385 m above sea level – on the south-western outskirts of Vienna is dominated by oaks, hornbeams and pines. In this area I surveyed six different ponds, but investigated only three this year, because the other three (“Großer Tümpel beim Wilden Berg”, “Saturn” and “Pappeltümpel”) were not filled with water. Three of these six are located near the “Wilden Berg” ($48^{\circ} 9' 11''$ N, $16^{\circ} 14' 36''$ E), which is approximately 370 m high. These ponds were called: “Kleiner Tümpel beim Wilden Berg“, “Großer Tümpel beim Wilden Berg“ and “Schlammtümpel“. Two ponds are located next to the wall of “Lainzer Tiergarten”, on which the solar system is shown to scale in the ratio 1 to 1 billion (1 mm = 1000 km). One of these was called "Jupiter" ($48^{\circ} 9' 17''$ N, $16^{\circ} 14' 33''$ E) and the other one “Saturn” ($48^{\circ} 9' 7''$ N, $16^{\circ} 14' 10''$ E), because on the wall opposite these ponds the planets were depicted. The sixth pond was called "Pappeltümpel" ($48^{\circ} 9' 5''$ N, $16^{\circ} 14' 38''$ E) because it was only about 50m from the “Pappelteich”(Fig. 3).

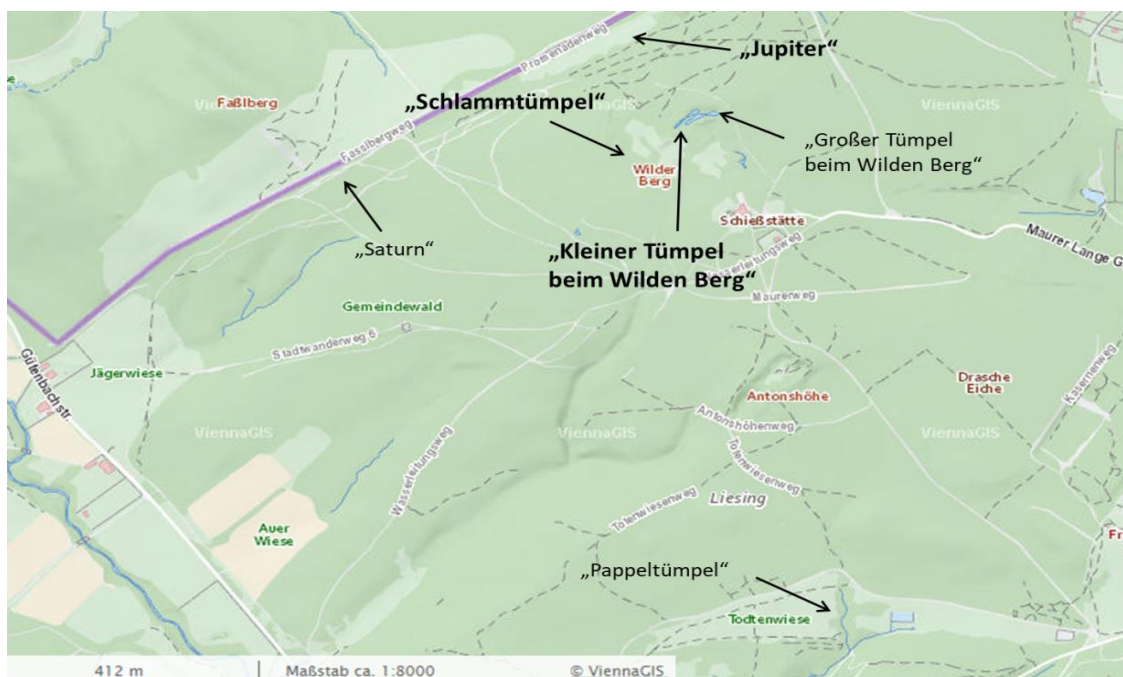


Figure 3: City map of Vienna of the ponds (marked with black arrows and named) in “Maurer Wald”. The filled ponds where data was collected this year are marked in extra bold type.

"Jupiter" was characterized by a muddy underground, numerous larger branches and leaf litter. This pond was at the beginning 9 x 4 m, around 20 cm deep but it dried out faster from week to week. The temperature in this standing water varied from 4,3 to 16,2 °C.

In addition to fire salamander larvae were alpine newt (*Ichthyosaura alpestris*), water striders (Gerridae), mosquitoes larvae, yellow-bellied toad (*Bombina variegata*) and their larvae, common frog (*Rana temporaria*) and agile frog (*Rana dalmatina*) as well as their spawn and tadpoles. Furthermore crustaceans, plankton and terrestrial insects were found in them (Fig. 4 A + B). These animals were seen at all ponds of "Mauer Wald".

The two ponds "Kleiner Tümpel beim Wilden Berg" and "Schlammtümpel" differed in terms of the water composition, size, depth and temperature. "Kleiner Tümpel beim Wilden Berg" had much clearer water compared to "Schlammtümpel", an area of approximately 3 x 3 m, around 20 cm depth and the temperature varied between 1,8 (air temperature +/- 0 °C) and 7,6 °C. The underground of this pond was also completely covered by leaf litter (Fig. 4 C + D). In contrast "Schlammtümpel" had a very muddy ground and a total diameter of 6 m, but was not continuously filled with water – it consisted of several puddles. The lowest point was approximately around 10 cm and the temperature varied from 4,3 to 18,1 °C. At the end of the data collection several grass snakes were found. At "Jupiter" and "Schlammtümpel" also crows were seen. Additionally, "Schlammtümpel" was the only pond, which was exposed directly to sunlight (Fig. 4 E + F).

"Großer Tümpel beim Wilden Berg" was in 2018 the largest pond with a size of approximately 30 x 4 m and 18 cm deep (Fig. 4 G). Due to the fact that "Großer Tümpel beim Wilden Berg" and "Kleiner Tümpel beim Wilden Berg" were very close to each other, they hardly differed in terms of the water composition and the animals into them. Furthermore lots of Cladocera were in this pond.

Just like these two, "Saturn" was very similar regarding the characteristics of the water body. This pond was 3 x 2 m, 20 cm deep and mainly characterized by the numerous occurrences of alpine newts.

"Pappeltümpel" (3 x 7m, 30 cm deep) was very similar to "Saturn" only that it contained more branches (Fig. 4 H).

On April 6th 2020 – about four weeks after the first field trip – "Kleiner Tümpel beim Wilden Berg" was completely dried out. "Schlammtümpel" showed only a very low water level (Fig. 4 F) in which the fire salamander larvae - buried in the mud – could still be found. Two weeks later "Schlammtümpel" was a little more filled because it had been raining a bit before. Eight weeks after the first trip "Jupiter" (Fig. 4 A) and "Schlammtümpel" dried out. So all ponds at

this date were completely dried out but after some rainfalls at the beginning of June, both ponds were filled again.

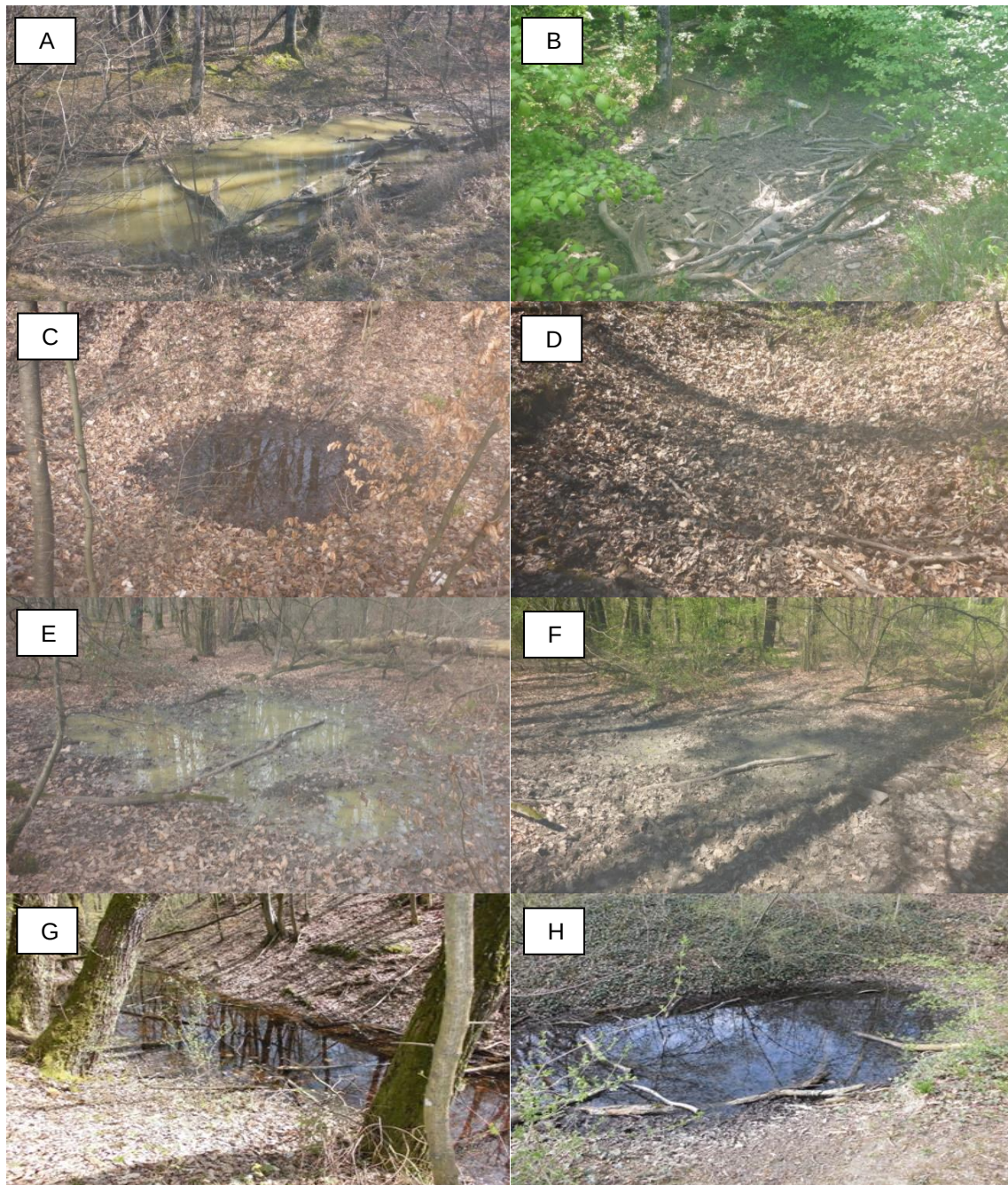


Figure 4: Ponds at „Maurer Wald“. A: “Jupiter” – at the beginning, B: “Jupiter” – after eight weeks, C: “Kleiner Tümpel beim Wilden Berg” – at the beginning, D: “Kleiner Tümpel beim Wilden Berg” – after four weeks (completely dried out), E: “Schlammtümpel” – at the beginning, F: “Schlammtümpel” – after four weeks (nearly dried out), G: “Großer Tümpel beim Wilden Berg” (2018), H: “Pappeltümpel” (2018).

At Neuwaldegg (280 m a.s.l.), which is located in the 17th district of Vienna (Hernals), I examined both, “Schwarzenbergpark” (48° 14' 49" N, 16° 16' 29" E), which contained numerous ponds and also “Eckbach” (48° 14' 47" N, 16° 16' 9" E). “Schwarzenbergpark” is a deciduous forest dominated by beech trees, which is both a park and recreation area (Fig. 5).



Figure 5: City map of Vienna of the ponds (marked with black arrows and named) in “Schwarzenbergpark” at “Neuwaldegg”. The ponds, which were filled in 2020, and also the “Eckbach” where data was collected this year are marked in extra bold type.

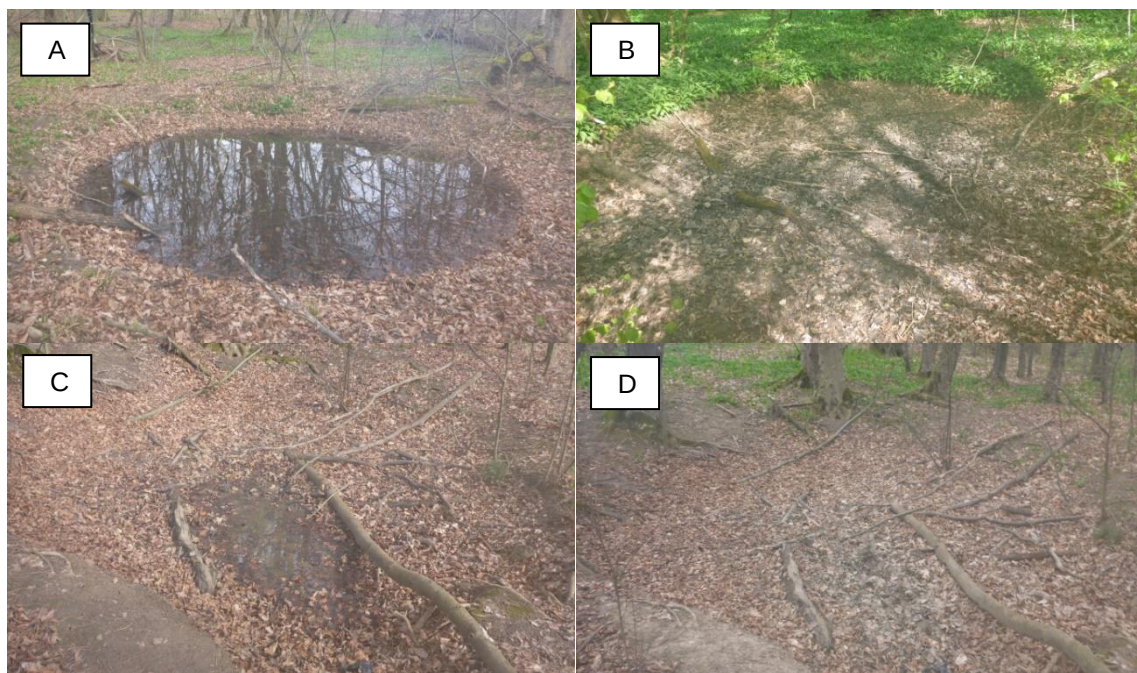
In this area I surveyed five different ponds, but data collection was only possible at “Stechmückentümpel” and “Großer Bärlauchtümpel” this year. In contrast to 2018, all others except “Stechmückentümpel” had dried out (“Großer Bärlauchtümpel” (Fig. 6 E, F + G) & “Kleiner Bärlauchtümpel”), or no larvae were deposited in them before they also dried out (“Bombentrichter” & “Matschtümpel” (Fig. 6 C + D)). “Stechmückentümpel” (48° 14' 44.9" N, 16° 16' 30" E), which was named because of the numerous mosquitoes and larvae there, had a diameter of 5 m and a depth of just over 50 cm at the beginning of the data collection. After four weeks this pond was only 2 x 2 m and 10 cm deep. The temperature varied from 4,1 to 14,3 °C. It was characterized by clear water, lots of leaves and larger branches. Other animals that were found in this pond were: dragonfly larvae, common frog (*Rana temporaria*) and agile frog (*Rana dalmatina*) as well as their spawn and tadpoles (Fig. 6 A + B). The initial sun exposure and subsequent, almost complete shading of the ponds differed only a little from those in the “Maurer Wald” – with the exception of “Schlammtümpel”.

“Matschtümpel” (48° 14' 45.9" N 16° 16' 18.5" E) was completely dried out after two weeks so there were no larvae deposited. In 2018 this pond had a diameter of 5 m and was 25 cm deep. Due to the composition, especially the mud ground, “Matschtümpel” was very similar to "Schlammtümpel" at "Maurer Wald". In this pond and in all the other ponds with the expectation of “Bombentrichter” mosquitoes larvae, common frog (*Rana temporaria*) and agile frog (*Rana dalmatina*) as well as their spawn and tadpoles were found.

“Bombentrichter“ (48° 14' 36.1" N 16° 16' 42.8" E) which was therefore very similar to “Matschtümpel” had a diameter of 4 m and was 12 cm deep (Fig. 6 H).

The two ponds (“Großer Bärlauchtümpel” and “Kleiner Bärlauchtümpel”) that are close together (48° 14' 55.6" N 16° 16' 21.4 "E) were very similar and surrounded by wild garlic. Both were 40 cm deep but “Großer Bärlauchtümpel” had a diameter of 6 m and “Kleiner Bärlauchtümpel” about 5 m (Fig. 6 E – G).

„Stechmückentümpel“ dried out after eight weeks (Fig. 6 B), but there were still no larvae from the third day of exploration. Like the two ponds at “Maurer Wald”, “Stechmückentümpel” and “Großer Bärlauchtümpel” were refilled due to the rain at the beginning of June for one data collection until they dried out again.



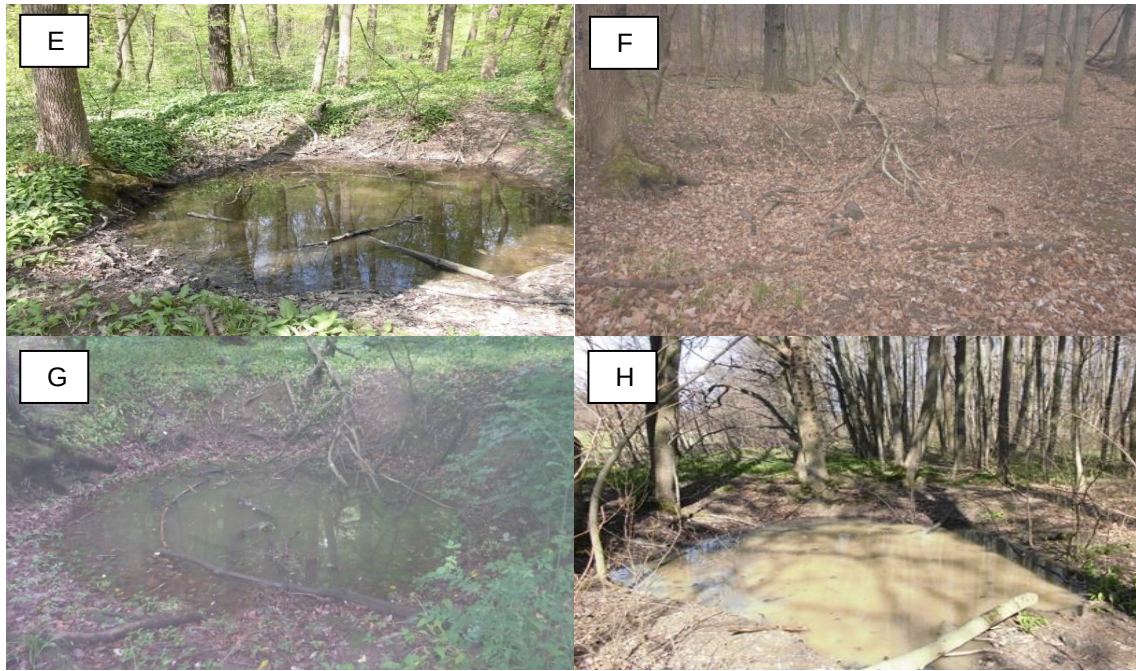


Figure 6: Ponds at „Schwarzenbergpark“. A: “Stechmückentümpel” – at the beginning, B: “Stechmückentümpel” – after four weeks, C: “Matschtümpel” – at the beginning, D: “Matschtümpel” – after two weeks (completely dried out), E: “Großer Bärlauchtümpel” – in 2018, F: “Großer Bärlauchtümpel” – in 2020 at the beginning of the data collection, G: “Großer Bärlauchtümpel” on June 22 (only data collection in 2020), H: “Matschtümpel” (2018).

The data collection at “Eckbach” started in Vienna over a distance of about 300 m to the boundary of Lower Austria. I investigated six sections in more detail, which mainly differed in flow speed, river width and depth. This stream contained of many stones and falling leaves. The temperature of “Eckbach” varied between 3,7 and 13,8 °C. A section of this flowing water is encased by precipitous slopes containing holes, which adult salamanders could use as shelter, and consists of longer riffles but less pools. In general, the flow speed was very high in this stream. The flow conditions and the water levels of the sections changed after heavy rains and storms. Animals in “Eckbach” were: dragonfly larvae, the spawn and tadpoles from common frogs (*Rana temporaria*) and agile frogs (*Rana dalmatina*), a great number of Gammaridae and a lot of other insect larvae like Plecoptera larvae (Fig. 7).





Figure 7: Different sections from “Eckbach” in terms of water compensations, flow speed and river depth.

At “Lainzer Tiergarten“ (300 m a.s.l.) – a nature reserve in the 13th district of Vienna (Hietzing), – I examined the “Auerochsengehege“ ($48^{\circ} 10' 56''$ N, $16^{\circ} 14' 51''$ E), which contained many ponds and also the “Lainzer Bach“ ($48^{\circ} 9' 58''$ N, $16^{\circ} 15' 20''$ E). The “Lainzer Tiergarten” is both, a hunting enclosure and a recreation area, where rare animal species can be found. This area is dominated by beech and oak trees (Fig. 8).

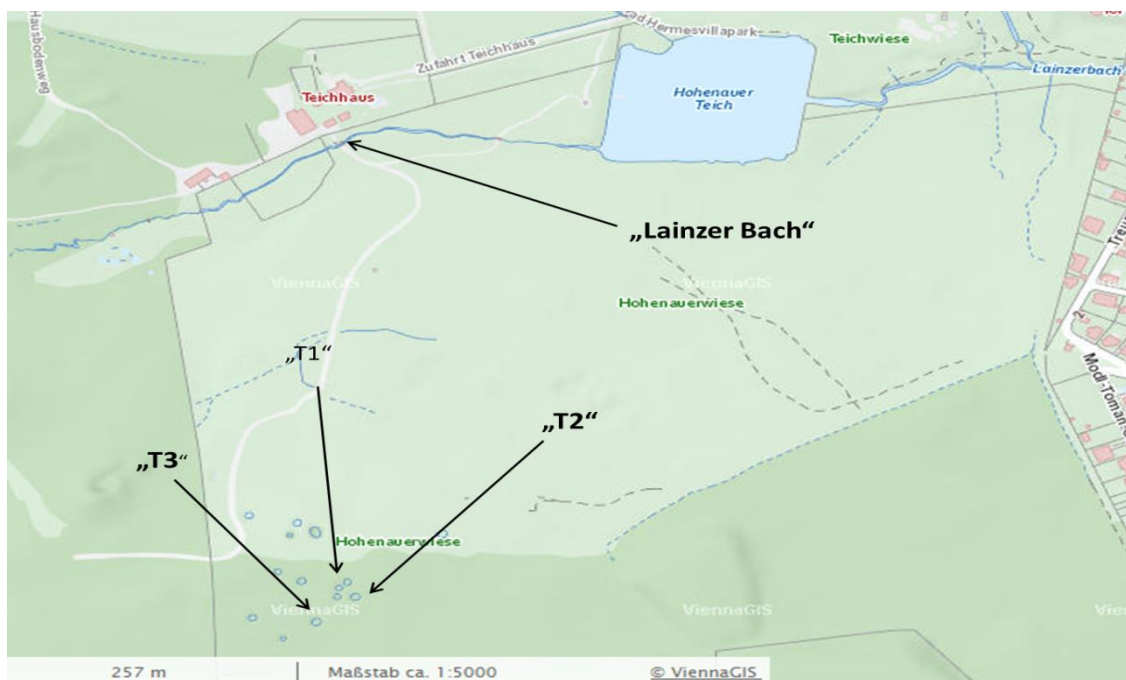
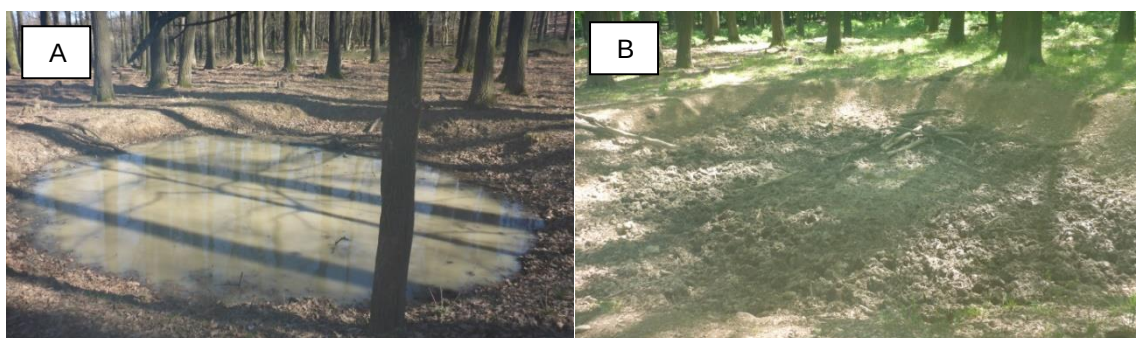


Figure 8: City map of Vienna of the ponds (marked with black arrows and named) in “Auerchsengehege” at “Lainzer Tiergarten”. The two ponds, where data was collected this year and also the “Lainzer Bach” are marked in extra bold type.

In the “Auerchsengehege” I surveyed three different ponds but a data collection was only possible at two of these, because “T1” was not filled this year. “T2” had a diameter of over 8 m and a depth of just 25 cm at the beginning of the data collection. The temperature varied from 2,8 °C (air temperature +/- 0 °C) to 16,7 °C. This pond was characterized by clear water, lots of leaves and some branches. In addition to fire salamander larvae there were mosquito larvae, water striders (Gerridae), Dytiscidae, common frog (*Rana temporaria*) and agile frog (*Rana dalmatina*) as well as their spawn and tadpoles. On one day, two ducks were seen in this standing water (Fig. 9 A + B).

The other pond at “Auerchsengehege” – which was called “T3” – was much smaller, less deep, very muddy and had more branches in it. “T3” was very similar to “Schlammtümpel” at “Maurer Wald” – had also a total diameter of 6 m, but was not continuously filled with water. The lowest point was approximately around 10 cm and the temperature varied from 2,4 to 19,8 °C. In “T3” alpine newt (*Ichthyosaura alpestris*), dragonfly larvae as well as the spawn and tadpoles from common frogs (*Rana temporaria*) and agile frogs (*Rana dalmatina*) were found. Furthermore, a small grass snake was seen one time. The initial sun exposure and subsequent, almost complete shading of “T2” and “T3” were very similar to the other ponds at “Maurer Wald” (Fig. 9 C + D). After four weeks “T3” was completely dried out, but due to the rain it refilled. “T2” was filled with water, a bit longer (less from week to week), since it changed with a few raining days at the beginning of June.



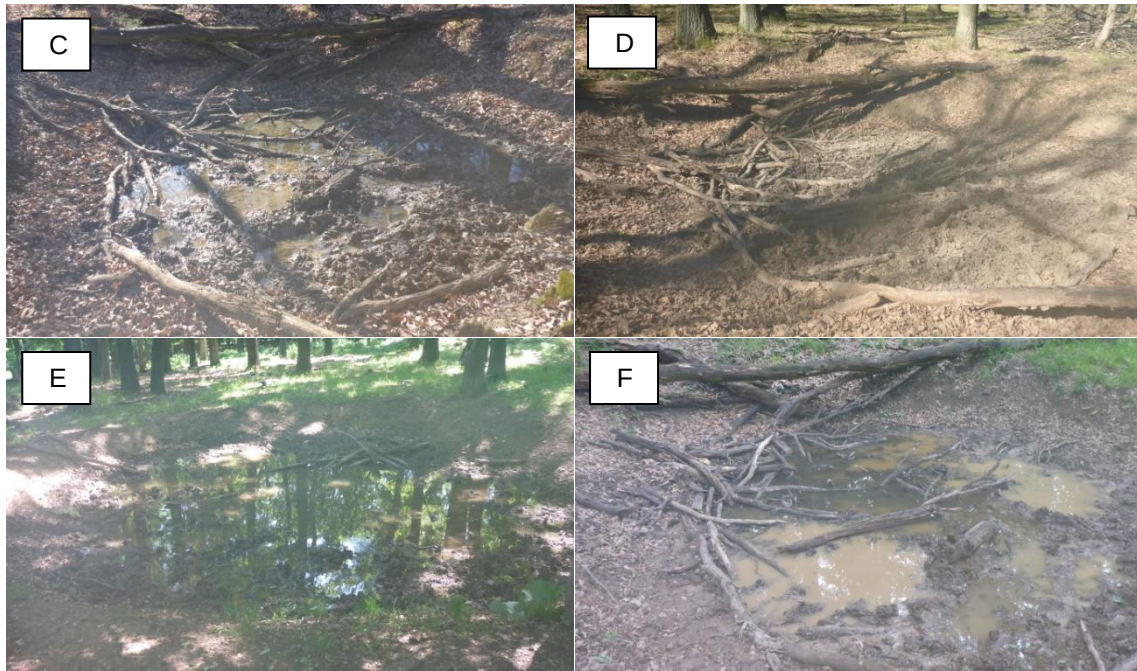


Figure 9: Ponds in the “Auerochsengehege” at “Lainzer Tiergarten. A: “T2” – at the beginning, B: “T2” – after eight weeks, C: “T3” – at the beginning, D: “T3” – after four weeks (completely dried out), E + F: “T2” and “T3” refilled due to the rain.

“Lainzer Bach” rises in “Katzengraben” in the southeast of “Lainzer Tiergarten” and flows through the “Hohenauer Teich”. I examined also six different sections over a length of about 300 m at the upper course of “Lainzer Bach”. This stream contained of a few stones, falling leaves and a great deal of branches. In contrast to the “Eckbach”, the “Lainzer Bach” did not flow continuously - it contained many isolated sections (pools) with only very slow or no flow rates and are therefore very similar to stagnant waters. These habitat structures are important prerequisites so that many fire salamander larvae were deposited and occurred in a very high frequency. The temperature of “Lainzer Bach” varied between 3,9 and 12,9 °C. Animals in this stream were: water striders (Gerridae), Dytiscidae, Gammaridae and a lot of other insect larvae like Plecoptera larvae (Fig. 10).

Eight weeks after the first field trip, “Lainzer Bach” was completely dried out. At the beginning of June one data collection was possible until this stream dried out again.

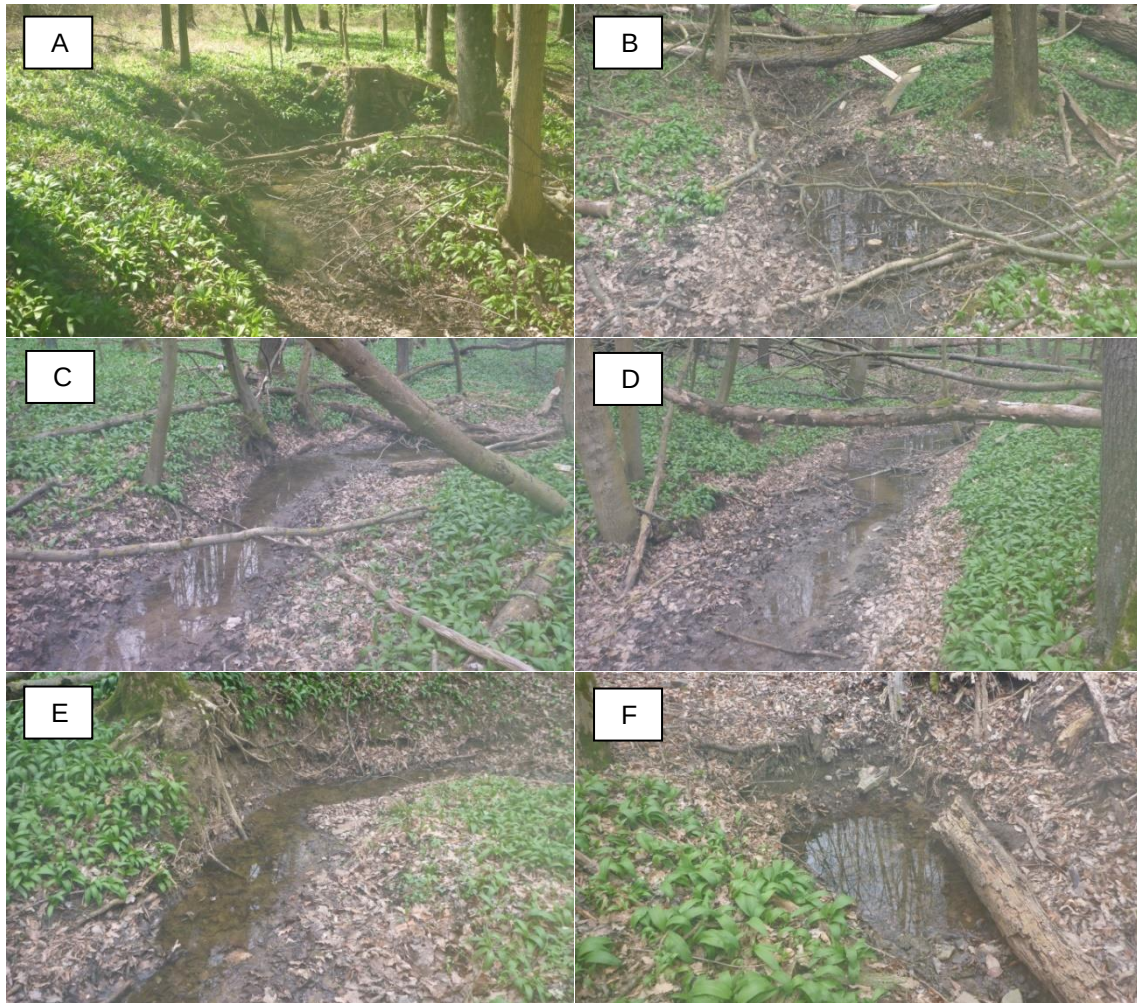


Figure 10: Different sections at “Lainzer Bach” in terms of water compensations, flow speed and river depth. There is generally a very slow or no stream of velocity at all six sections. A, C, D + E: slow flow rates; B + F: very quiet sections – no flow rates (similar to ponds).

“Moosgraben” (48° 13' 25" N, 16° 15' 28" E) is a reservation of natural forest since 2005, which means that the natural development of the ecosystem is supported, because among other things, the removal of dead wood is not allowed. As well as “Eckbach” and “Lainzer Bach”, I examined six different sections from 400 to 500 m upstream. The temperature varied between 3,9 and 13,7 °C. The stream was divided into a stony gently sloping section with a higher flow rate and also some pools with lots of leaves and branches which were therefore very similar to ponds. As “Moosgraben” is located westwards of “Wilhelminenberg”, it rains very often there, and leads to generally more humid and colder weather conditions. This is a reason why adult fire salamanders were often encountered there. At “Moosgraben” I found the same animals as at “Eckbach”, but with a greater frequency. Almost every time I was there the same pair of ducks was also seen in this area. At the end of my data acquisition, smaller grass snakes were spotted again and again (Fig. 11).

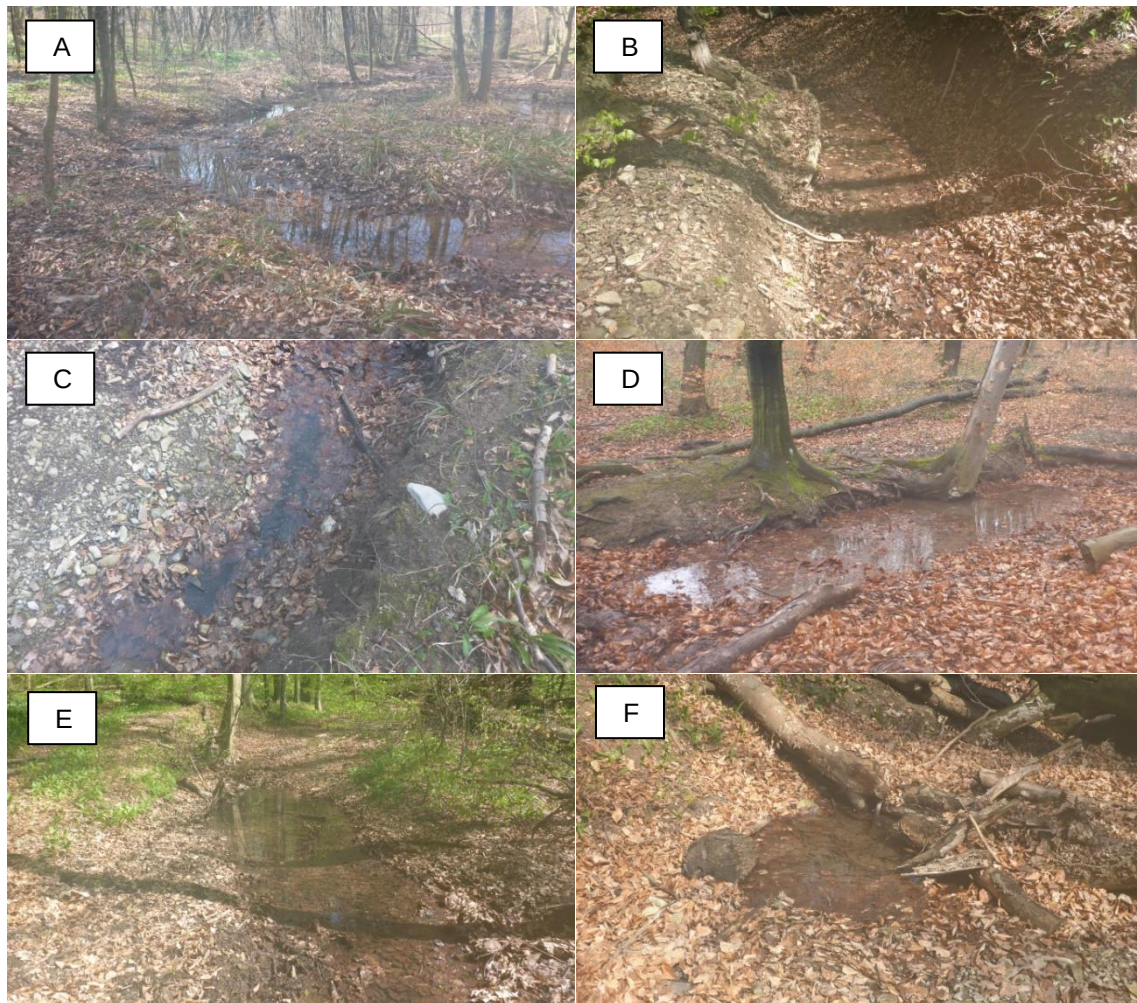


Figure 11: Different sections at “Moosgraben” in terms of water compensations, flow speed and river depth. A – C: stony, higher flow speeds, D - F: leafy, quieter sections (similar to ponds, especially F).

Table 1: Overview of the main ponds in terms of characteristics, potential prey and predators.

Water bodies' size and depth was from the first data collection, where the water bodies were most filled. Additionally, in all water bodies were: crustaceans, plankton and plunged terrestrial insects which also represent a very important prey spectrum for the larvae. Furthermore common frogs (*Rana temporaria*) and agile frogs (*Rana dalmatina*) which were seen at all water bodies. Their tadpoles are also counted as potential prey.

Name of the water body	Characteristics	Potential prey	Potential predators
“Jupiter”	muddy underground, branches 9 x 4 m, 20 cm deep	mosquitoes larvae	crows, alpine newt
„Schlammtümpel“	muddy underground, 6 x 6 m (several puddles), 10 cm deep, influenced by insolation	mosquitoes larvae	larger dragonfly larvae, grass snakes, crows
“Großer Tümpel beim Wilden Berg“	clear water, leaves 30 x 4 m, 18 cm deep	Cladocera	crows
„Saturn“	clear water, 3 x 2 m, 20 cm deep		alpine newt
„Stechmückentümpel“	clear water, leaves, branches 5 x 5 m, 50 cm deep	mosquitoes larvae, small dragonfly larvae	larger dragonfly larvae
“Großer Bärlauchtümpel”	Clear water, leaves, branches, 6 x 6 m, 40 cm deep	mosquitoes larvae	larger dragonfly larvae
„Eckbach“	longer riffles less pools – high flow speed	Gammaridae, Plecoptera larvae, small dragonfly larvae	larger dragonfly larvae
„T2“	clear water, leaves, branches, 8 x 8 m, 25 cm deep	mosquitoes larvae	ducks
„T3“	muddy underground, branches 6 x 6 m (several puddles), 10 cm deep	small dragonfly larvae	larger dragonfly larvae, grass snakes
„Lainzer Bach“	many pools with very slow or no flow rates	<i>Gammaridae</i> , Plecoptera larvae	
„Moosgraben“	stony gently sloping section with higher flow rate and some pools	Gammaridae, Plecoptera larvae, small dragonfly larvae	larger dragonfly larvae, ducks, grass snakes, crows

Data collection

Data were collected between March 4th and August 10th 2020. Each of the six examination sites was visited every 10 to 14 days – usually from 10 a.m. – and the respective ponds and streams were examined for fire salamander larvae. In total, each water body were visited 12 times. The larvae were caught using a small dip net and/or kitchen strainer either on sight in clear water or blindly in ponds with a muddy underground (Fig. 12 A). The search was ended at a number of 30 (if possible) caught fire salamander larvae per pond or stream. After that the larvae were kept in a plastic box – which was filled with water from the ponds and streams – and then placed in a photo box to document their body length (Fig. 12 B). In this photo box which is equipped with millimetre paper and filled with water, five larvae were photographed at once using a camera (Panasonic Lumix DMC-FT5 digital camera). After the photos were taken, all fire salamander larvae were released at the site of capture.

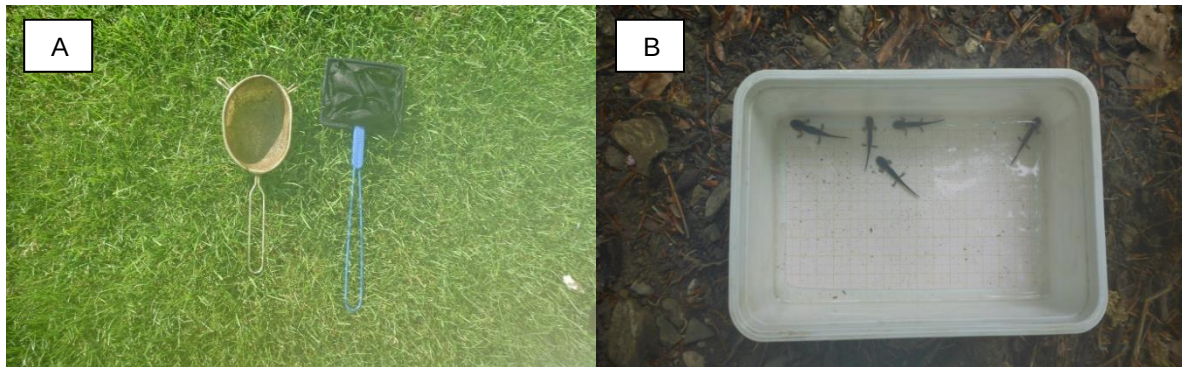


Figure 12: A: kitchen strainer, dip net, B: 5 fire salamander larvae in a millimetre paper equipped photo box.

The data collection in 2018 - which is compared to this year's - took place between March 29th and June 14th. At that time, fire salamander larvae were searched at four different locations, namely at: “Maurer Wald”, “Moosgraben”, “Schwarzenbergpark” and “Eckbach”. Each of the four examination locations were examined every two weeks ($\pm$ one day). In total, the standing waters were visited 6- and the flowing waters 5- times. The procedure was the same as this year.

One big difference between these two years was the weather because due to the strongly changing weather pattern in 2020 with less precipitation in winter – at the same time quite warm with a short period of freezing, less rain at the beginning of the spring and many rainy days in early June, the stagnant waters dried out much faster and then refilled. In 2018 the weather was much milder and the ponds dried up later in the year.

Data analysis

To measure the length of the fire salamander larvae, I used the program ImageJ (version 1.52u), with which I measured the body length (from apex of snout to beginning of hind limbs) and the tail length (from the beginning of hind limbs to the tip of the tail) of the larvae. The sum of body length and tail length was defined as the total length (Mayerhofer, 2013). For the measurements with ImageJ a scale of 20 mm was defined as a reference to the millimetre paper (Fig. 13).

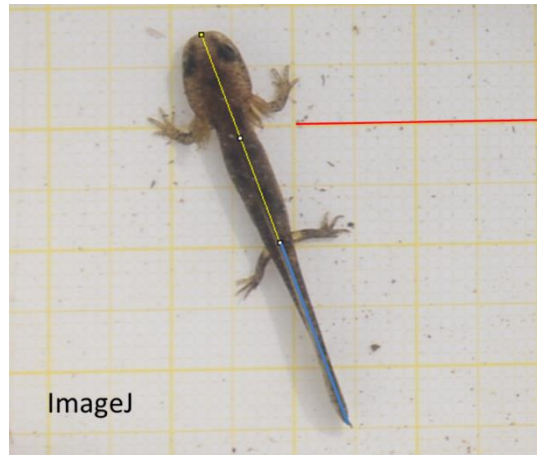


Figure 13: Measuring a fire salamander larva in a plastic box (photo box) on millimetre paper using ImageJ. Red line: reference line of 20 mm, yellow line: body length (from the apex of the snout to the beginning of the hind limbs), blue line: tail length (from the beginning of the hind limbs to the tip of the tail). The sum of body length and tail length was defined as the total length (Mayerhofer, 2013).

The body-, tail- and total length of each larva and also the calculated mean value of these sizes were entered in an Excel chart, only the total length was used for evaluation and creation of the graphics. Although a piece of the tail was missing in some larvae, it still makes more sense to use the total length, because in many larvae the tail length was greater than the body length and also tails are important storages for fat and perhaps offer energy during metamorphosis (McCracken & Stebbings, 2012). The graphs were created with Microsoft Excel.

Statistical analyses were done using IBM SPSS Statistics 27. I used Shapiro-Wilk test to test the normal distribution and Kruskal-Wallis H-test to find out if the fire salamander larvae between the water bodies differ in their total length. Afterwards I used Kruskal-Wallis post hoc tests to analyse which areas differed. According to the study "Kruskal-Wallis in SPSS" (Marshall, 2020), these pairwise comparisons are the Dunn-Bonferroni-tests. The alpha level was set of 0.05 for all tests with Bonferroni as p-value adjustment.

Results

2020

In total a number of 1514 fire salamander larvae were caught, measured and analysed in the four different study areas (“Maurer Wald” n = 453, “Lainzer Tiergarten” n = 514, “Neuwaldegg” n = 207, “Moosgraben” n = 340). At “Lainzer Tiergarten” 375 larvae were caught of the ponds from “Auerochsengehege” and 139 larvae of “Lainzer Bach”. At “Neuwaldegg” 94 of the 207 fire salamander larvae were from the ponds at “Schwarzenbergpark” and 113 larvae from “Eckbach”.

Due to the strongly changing weather pattern this year so that all previously dried ponds were refilled, it turned out that fire salamander larvae were deposited at least until June 16th (Tab. 2).

Between the first and second time of visiting the ponds at the respective locations it was freezing and a great number of larvae died. Particularly affected were “Kleiner Tümpel beim Wilden Berg”, “Stechmückentümpel” and “T3”. At the end of the data collection, some larvae were found that were just before to metamorphose (loss of the gill tufts, yellow black color).

Table 2: Overview of the water levels of the water bodies in 2020. Each month was divided into two halves (1: Day 1 – 15, 2: Day 16 – 31). ●... Water body filled, ◐... Water body less full, ○*... Water body almost dried out (fire salamander larvae in small puddles), ○... Water body dried out.

Water body	March		April		May		June		July		August	
	1	2	1	2	1	2	1	2	1	2	1	2
“Stechmückentümpel”	●	◐	○	○	○	○	○	●	○	○	○	
“Gr. Bärlauchtümpel”	○	○	○	○	○	○	○	●	○	○	○	
“Eckbach”	●	●	●	●	●	●	●	●	●	●	●	
“Moosgraben”	●	●	●	●	●	●	●	●	●	●	●	
“Jupiter”	●	◐	◐	◐	○	○	○	●	●	●	●	
“Kl. T. b. WB”	●	◐	○	○	○	○	○	○	○	○	○	
“Schlammtümpel”	●	●	○*	◐	○	○	○	●	●	◐	◐	
“T2”	●	●	●	◐	○	○*	●	●	●	◐	◐	
“T3”	●	○*	○	○	○	◐	●	●	●	○	○	
“Lainzer Bach”	●	●	●	◐	○	○	◐	○	○	○	○	

Stagnant waters

The data collection at “Schwarzenbergpark” started on March 4th where larvae were only found at “Stechmückentümpel”. At “Maurer Wald” the first data acquisition was one week later on March 10th but only at “Schlammtümpel” and “Kleiner Tümpel beim Wilden Berg” fire salamander larvae were caught. At “Jupiter” the first larvae were deposited two weeks after the first field trip. The first data collection at “Lainzer Tiergarten” in the “Auerchsengehege” was on March 13th where larvae had already been deposited in both ponds (“T2” and “T3”). At all of these three study areas, 30 fire salamander larvae could only be caught at “Stechmückentümpel”. This pond dried out very quickly so that only two data acquisitions were possible. Since it rained at the beginning of June, “Stechmückentümpel” and “Großer Bärlauchtümpel” were refilled and so it was possible to record data from both of these ponds on June 22nd until they completely dried out again. At “Maurer Wald” all ponds dried up at least until May 4th. “Kleiner Tümpel beim Wilden Berg” dried out earlier, so at this pond only one data collection was possible. Between the first and second field trip it was freezing and all fire salamander larvae of this pond died. Maybe they could have suffocated under the layer of ice. Due to the rain at the beginning of June, “Jupiter” and “Schlammtümpel” were filled again. Fire salamander larvae were found there on June 16th. The ponds at “Lainzer Tiergarten” were also very badly affected due to the weather conditions at the beginning of the data acquisition so that at each pond larvae were caught only two times. The next possible data collections at “T2” were from May 20th (with the exception of April 22nd where four small larvae were deposited in a tiny puddle). “T3” were also refilled due to the rain which enabled larvae to be caught from June 3rd to July 13th until this pond dried out again (Fig. 14).

„Schwarzenbergpark“

At “Stechmückentümpel” on March 4th, most of the fire salamander larvae were between 26 and 34 mm. Two weeks later – on March 17th – almost all of them were between 28 and 36 mm. At the next possible data collection on June 22nd most of the larvae were also between 28 and 36 mm. On the same day – the only possible data collection at “Großer Bärlauchtümpel” – almost all captured fire salamander larvae had a total length between 26 and 34 mm (Fig. 14).

„Maurer Wald“

At “Jupiter” on March 24th, almost all captured individuals had total lengths between 30 and 36 mm. On April 6th, only fourteen fire salamander larvae were caught because it was freezing few days before, all of them were from 28 to 38 mm and the half of them had a total length between 32 and 36 mm. Two weeks later, on April 20th, new larvae were deposited and therefore 30 individuals were caught again. Almost all of them had total lengths of 30 to 36 mm. The next possible data collection when “Jupiter” filled again was on June 16th were more than the half of the larvae was between 30 and 36 mm. Two of the 30 were smaller and six of them were larger with a total length of around 40 mm. On June 29th, approximately two thirds of the captured individuals were larger than the individuals two weeks ago and had a total length of up to 48 mm. Only three of the 30 fire salamander larvae were smaller than 32 mm. Two weeks later, on July 13th, the size distribution was roughly the same as on June 29th, except that one individual had a total length of up to 54 mm. On July 27th, there were also larger larvae in contrast to two weeks before. Most of them were between 40 and 48 mm. At the last data acquisition, on August 10th, were more than the half of the only twelve caught fire salamander larvae between 42 and 46 mm. A few larvae were a bit larger with a total length of up to 52 mm.

The only possible data collection at “Kleiner Tümpel beim Wilden Berg” was on March 10th where two thirds of the animals were between 34 and 38 mm.

At “Schlammtümpel”, at the first data collection, on March 10th, the half of the captured individuals had total lengths between 26 and 32 mm and the other half between 32 and 36 mm. Two weeks later, on March 24th, more than the half of the fire salamander were between 32 and 36. In addition there were a few smaller ones and a few larger ones with total lengths of up to 42 mm. On April 6th, all larvae were between 30 and 40 mm. Two weeks later, on April 20th, two thirds of the 30 individuals had a total length of 32 to 36 mm. As well as at “Jupiter”, the next possible data acquisition was on June 16th. Almost all the fire salamander larvae were between 30 and 36 mm. On June 29th, none of the larvae was smaller than 32 mm. The half of the 30 captured individuals was between 36 and 40 mm and the biggest had a total length of up to 44 mm. On July 13th, the size distribution was roughly the same as two weeks ago but there were also a few smaller larvae. Two weeks later, on July 27th, there were less, smaller and larger larvae. More than the half of the 30 fire salamander larvae was between 38 and 44 mm. At the last data collection, only three individuals were found because the water

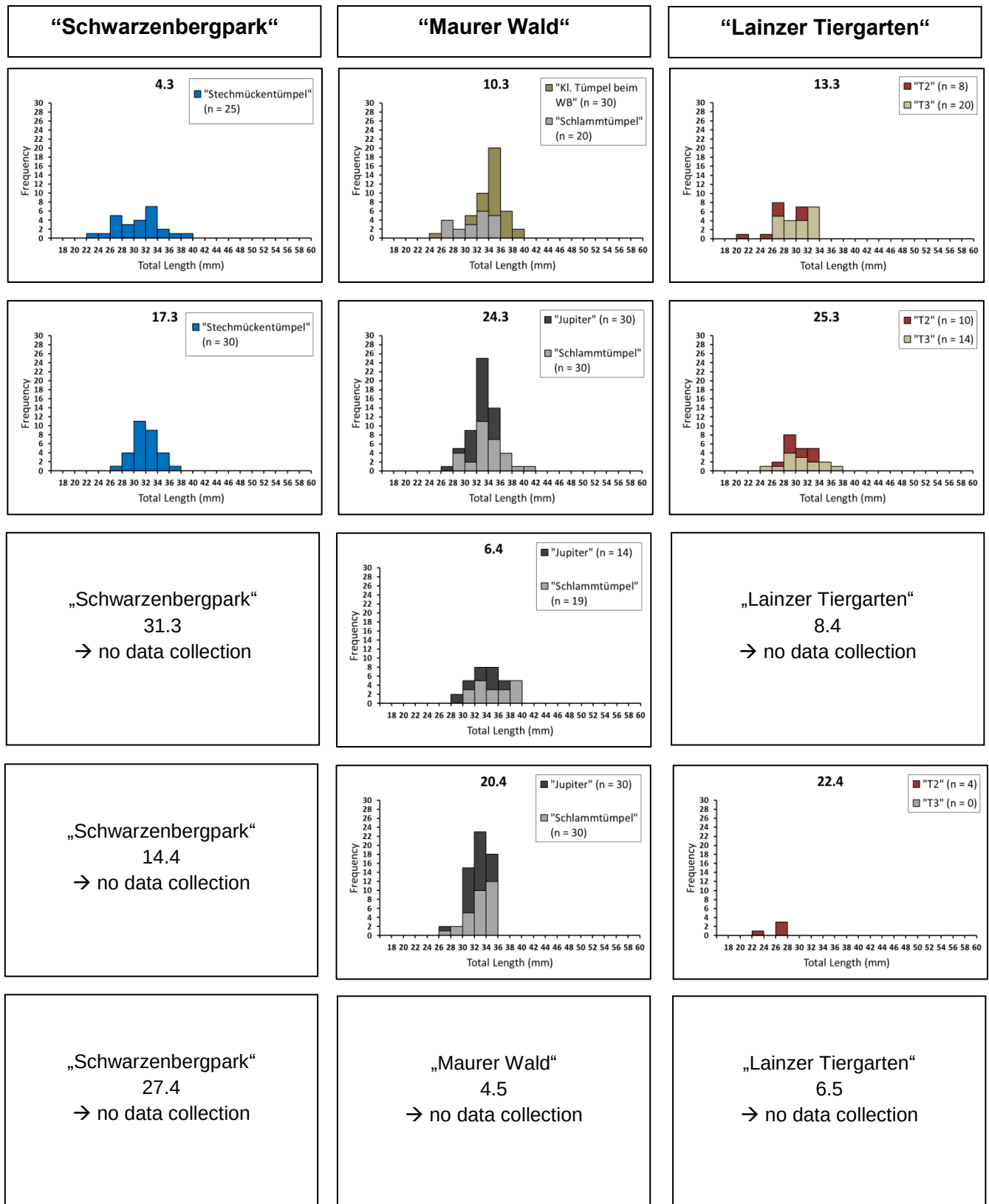
level of “Schlammtümpel” was very low and many larvae had already metamorphosed (Fig. 14). At the end of the data acquisition cannibalism towards the individuals were seen twice at “Jupiter” and “Schlammtümpel”.

„Lainzer Tiergarten“

At the first data collection at “T2”, on March 13th, only eight fire salamander larvae were caught. The smallest one had a total length of 20 to 22 mm and the three largest ones of 30 to 32 mm. Two weeks later, on March 25th, where only ten individuals were found, all of them were between 26 and 34 mm. Between this date and May 20th, there were only one small data collection possible, on April 22nd, where four larvae could be caught. Three of the four captured individuals had a total length between 26 and 28 mm. On May 20th, almost all of the new deposited larvae were between 26 and 34 mm. Two weeks later, on June 3, all of the 30 fire salamander larvae had total lengths between 26 and 36 mm. In contrast to May 20th, there were a few larger larvae. A bigger difference to the previous data recordings can be seen on June 16th. On this date the smallest larvae were over 30 mm and the largest had a total length of up to 44 mm. Two thirds of these 30 individuals were between 34 and 40 mm. The fire salamander larvae also became larger by June 1st. Two thirds of them were larger than 40 mm. On July 13th, there were also a few larger larvae than two weeks ago. Two thirds were between 42 and 48 mm. The biggest difference to the previous data was on July 27th. All larvae had a total length of up to 38 mm and most of the 30 captured individuals were between 46 and 56 mm. At the last data acquisition, on August 10th, we had in contrast to the data two weeks ago, more larvae that were over 48 mm.

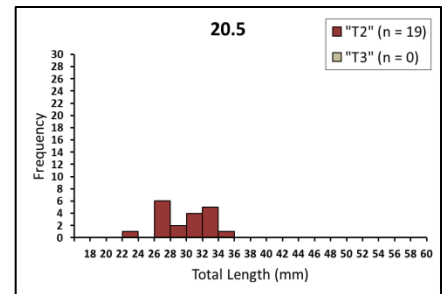
At the first data collection at “T3”, on March 13th, all fire salamander larvae were between 26 and 34 mm. At the second data recording only 14 individuals were caught, the half of them had total lengths of 28 to 32 mm. Two of the captured larvae were smaller and the other five larger than 32 mm with total lengths of up to 38 mm. After this data sampling, “T3” completely dried out. Due to the rain at the beginning of June this pond was filled again so that the next possible data collection was on June 3rd. On this day approximately two thirds were between 26 and 30 mm. The others were larger with total lengths of up to 38 mm. On June 16th, now two thirds of the 30 captured individuals were between 30 and 36 mm but there were also a few smaller and also larger ones with a total length of up to 42 mm. Two weeks later, on June 1st, more than the half of the 30 larvae were between 38 and 42 mm. The smallest ones had a total length over 32 mm and the biggest ones of up to 48 mm. At the last

data acquisition before “T3” dried up again most of the captured fire salamander larvae were between 38 and 44 mm. The largest ones had a total length of up to 48 mm (Fig. 14).



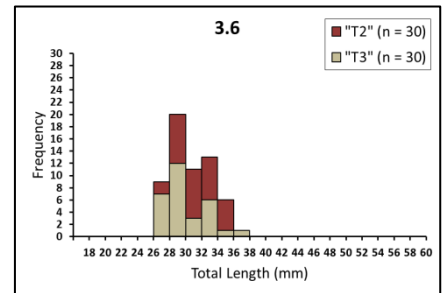
„Schwarzenbergpark“
11.5
→ no data collection

„Maurer Wald“
18.5
→ no data collection

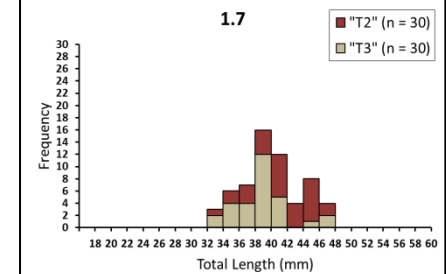
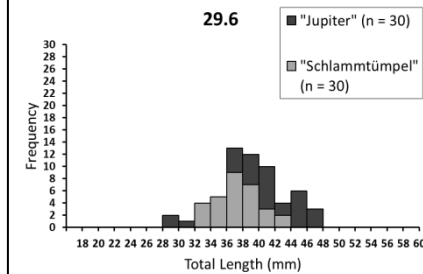
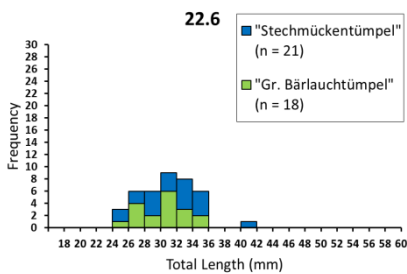
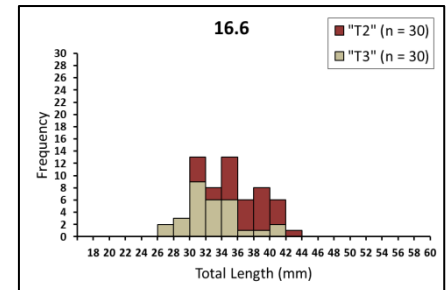
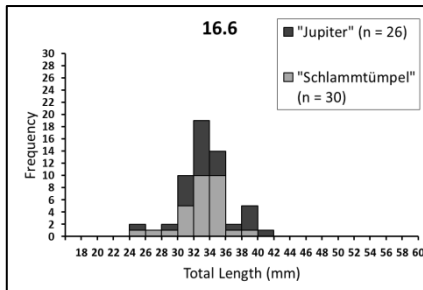


„Schwarzenbergpark“
25.5
→ no data collection

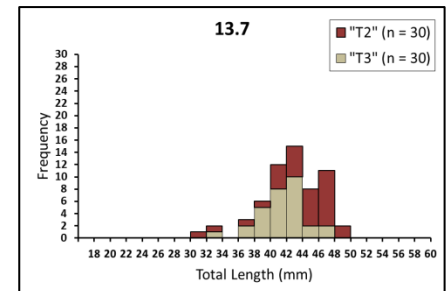
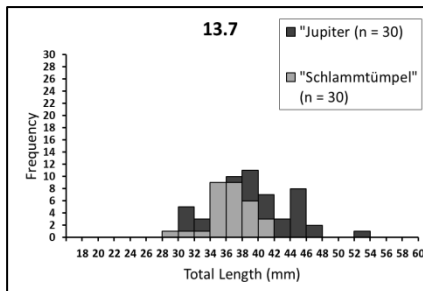
„Maurer Wald“
1.6
→ no data collection



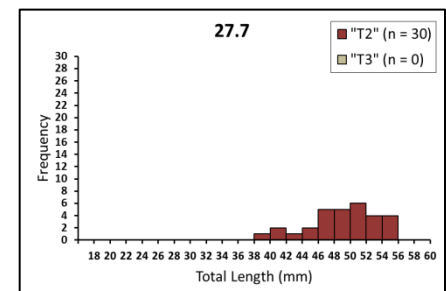
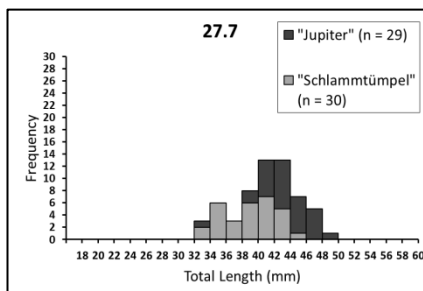
„Schwarzenbergpark“
8.6
→ no data collection



„Schwarzenbergpark“
6.7
→ no data collection



„Schwarzenbergpark“
20.7
→ no data collection



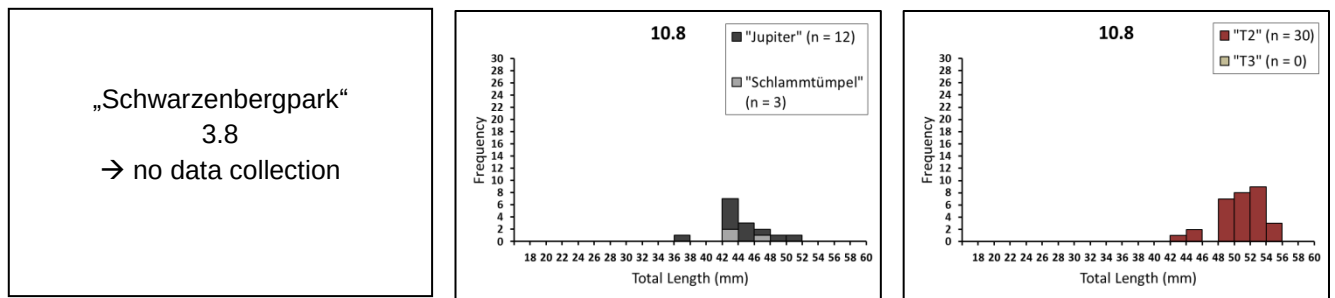


Figure 14: Synthetic histograms of the total lengths (mm) of the fire salamander larvae which were caught of the ponds at “Schwarzenbergpark”, “Maurer Wald” and “Lainzer Tiergarten”(n = number of samples, number of captured fire salamander larvae).

Flowing waters

The data recordings at “Eckbach” started on March 4th, exactly the same way as at “Schwarzenbergpark”, but the larvae were only deposited later (first data from March 31). In general, fewer fire salamander larvae were found at “Eckbach” and due to the weather - especially the increased rain - many were probably washed out of the stream. The last data collection where larvae were found was on June 22nd. At “Moosgraben”, the first data were from March 6th. That was also the only day on which 30 larvae were not caught. The data collection at “Lainzer Bach” started on March 13th. After April 22nd this stream dried out but due to the rain a further data acquisition was possible on June 3rd until it dried out again.

“Eckbach”

On March 31st, the first possible data collection, where only six fire salamander larvae were found, all of them had a total length between 28 and 32 mm. Two weeks later, 30 larvae had already been caught. Two thirds of the individuals were between 28 and 34 mm, but there were also a few smaller as well as larger ones which were already around 40 mm. On April 27th, almost all larvae had a total length between 28 and 38 mm, one third from 28 to 32 mm and one third from 34 to 38 mm. On May 11th, all fire salamander larvae which were caught were between 28 and 44 mm. Two weeks later, on May 25th, only 10 individuals were found. Four of them were between 28 and 34 mm and the other six had a total length over 42 and up to 50 mm. On June 6th only eight fire salamander larvae were caught. Six of them had a total length between 26 and 30 mm and the other two between 50 and 52 mm. The last day where fire salamander larvae could be found was on June 22nd. Three of the four captured larvae had a total length of 36 to 40 mm and one individual of 46 to 48 mm (Fig. 15).

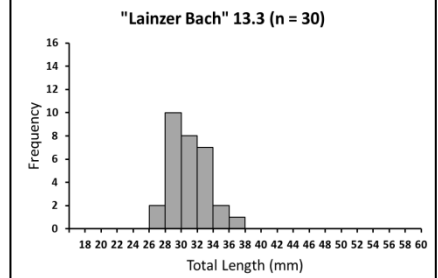
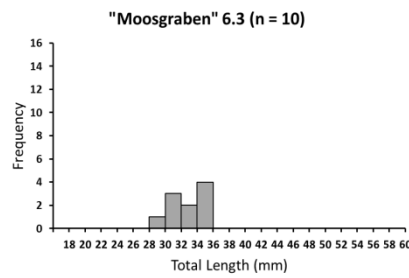
“Moosgraben”

On March 6th, the only day on that 10 and not 30 fire salamanders were found, all of them were between 28 and 36 mm. On March 19th, most of the 30 captured individuals had a total length 28 and 34 mm. There were also a few smaller and also larger ones with total lengths of up to 38 mm. Two weeks later, on April 1st, almost the half had a total length between 32 and 34 mm. As well as on March 19th there were also a few smaller and larger ones with total lengths of up to 38 mm. Six of the 30 individuals were between 34 and 36 mm. At the next data collection on April 15th, all fire salamander larvae were between 28 and 38 mm but two thirds of them had a total length between 30 and 34 mm. On April 29th, more than two thirds were between 28 and 36 mm and most of them had a total length between 30 and 32 mm. The largest one had a total length of up to 42 mm. At the next data acquisition on May 13th, there were larger larvae between 30 and 38 mm. Most of them had a total length between 34 and 38 mm. The largest one had a total length of up to 42 mm again. On May 27th, more than the half of the 30 captured individuals had a total length between 30 and 36 mm. There were also a few smaller ones and larger ones with total lengths of up to 50 mm. Two weeks later on June 10th, the larval sizes were approximately the same but there were more larger ones than two weeks ago. One fire salamander larvae even had a total length of up to 56 mm. On June 24th, none of the larvae were smaller than 32 mm. Most of the 30 individuals were between 38 and 48 mm. Two larvae had total lengths of up to 52 mm. At the next data collection on July 8th, about two thirds were between 40 and 46 mm. There were also a few smaller ones with a total length of 34 to 38 mm and also larger ones. The largest larvae had a total length of up to 52 mm. On July 21st, most of the 30 caught fire salamander larvae had a total length between 42 and 46 mm. The largest one had a total length of up to 54 mm. At the last data sampling on August 4th, we had a very even size distribution with a total length from 34 to 56 mm but most of them were between 40 and 52 mm. Two larvae had a total length of up to 56 mm (Fig. 15).

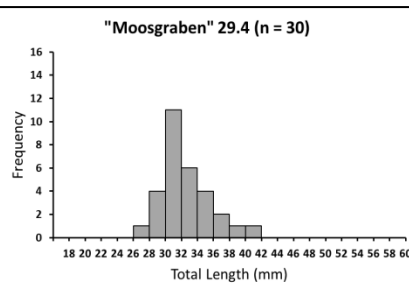
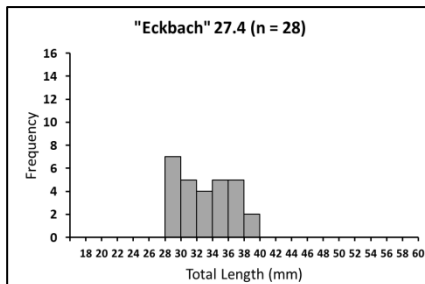
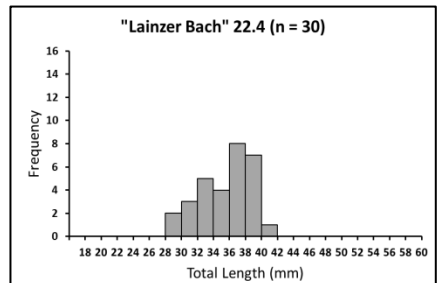
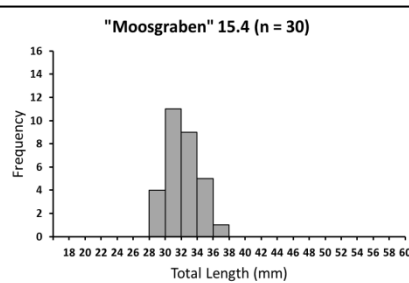
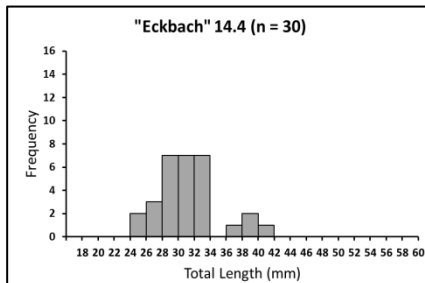
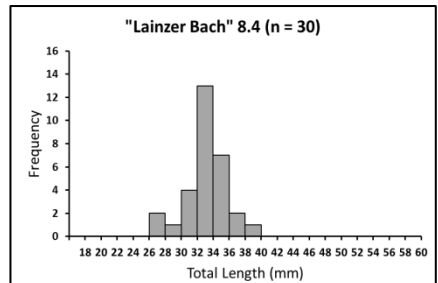
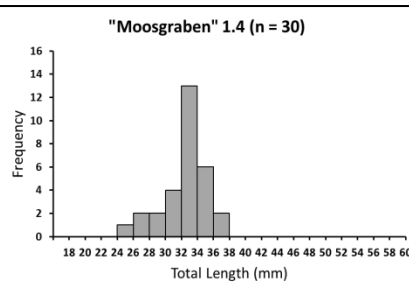
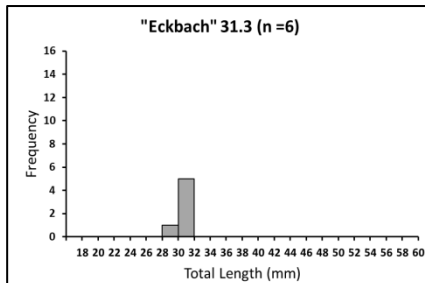
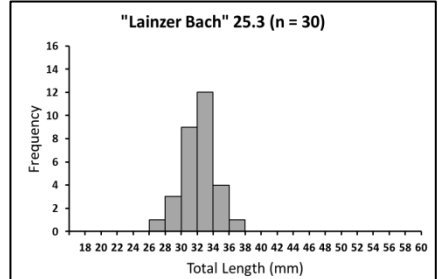
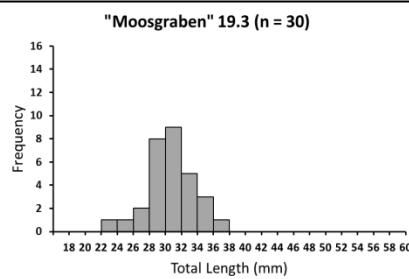
“Lainzer Bach”

On March 13th, most of the captured individuals had a total length between 28 and 34 mm. Two weeks later, on March 25th, two thirds of the larvae were between 30 and 34 mm. On April 8th, two thirds of the fire salamander larvae were between 32 and 36 mm. At the last data collection, on April 22nd, until this stream was dried out, the half of the larvae had a total length of 36 to 40 mm. On June 3rd, when some parts of “Lainzer Bach” were filled again most of the individuals were around 30 mm (Fig. 15).

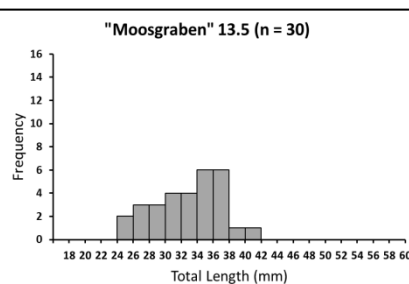
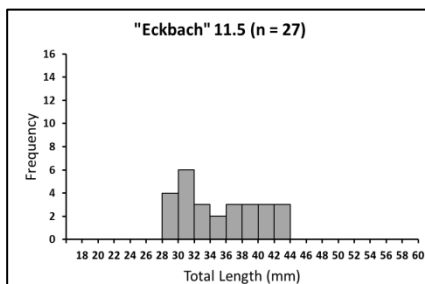
„Eckbach“
4.3
→ no data collection



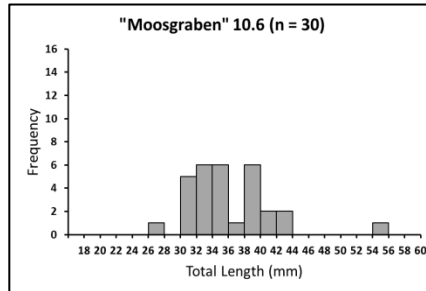
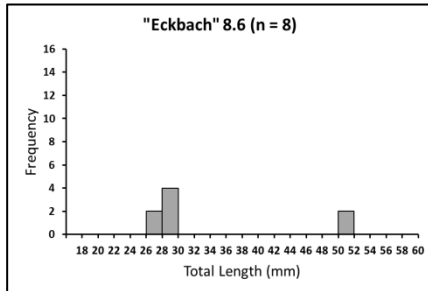
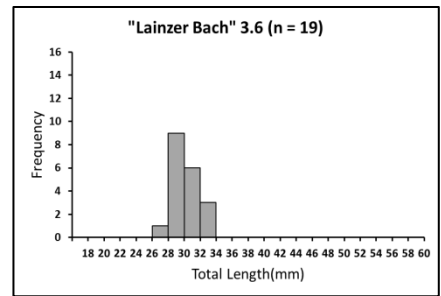
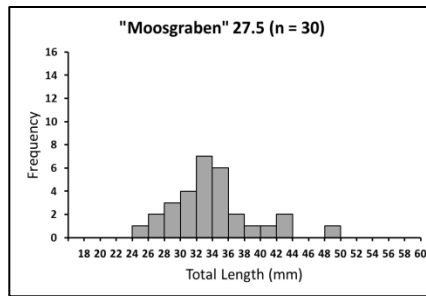
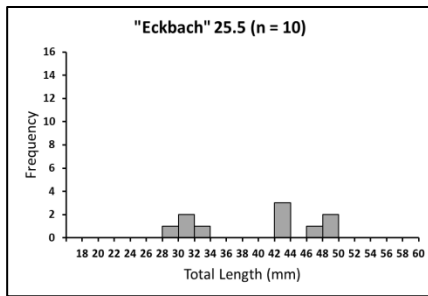
„Eckbach“
17.3
→ no data collection



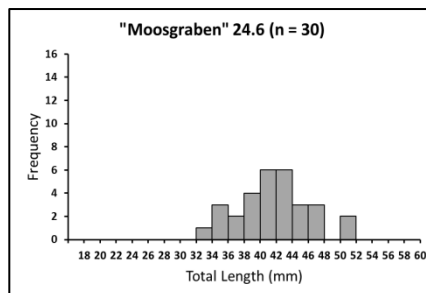
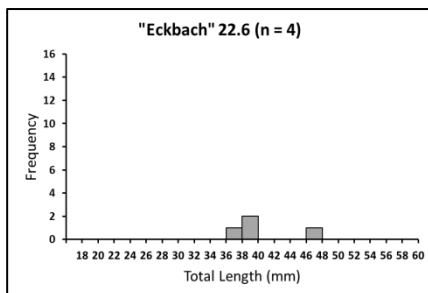
„Lainzer Bach“
6.5
→ no data collection



„Lainzer Bach“
20.5
→ no data collection

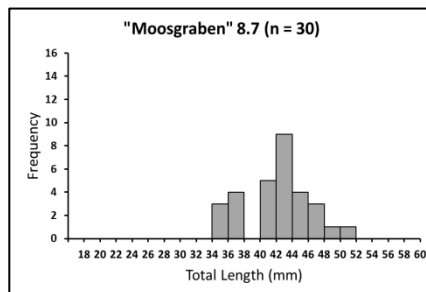


„Lainzer Bach“
16.6
→ no data collection



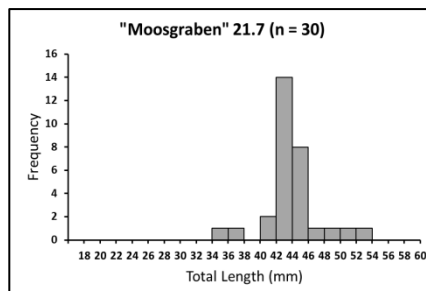
„Lainzer Bach“
1.7
→ no data collection

„Eckbach“
6.7
→ no data collection



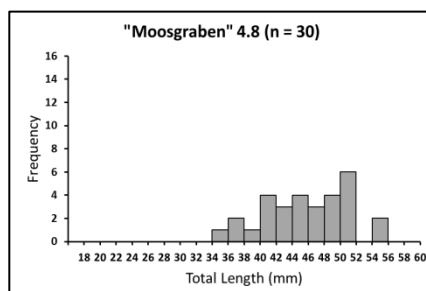
„Lainzer Bach“
13.7
→ no data collection

„Eckbach“
20.7
→ no data collection



„Lainzer Bach“
27.7
→ no data collection

„Eckbach“
3.8
→ no data collection



„Lainzer Bach“
10.8
→ no data collection

Figure 15: Histograms of the total lengths (mm) of the fire salamander larvae caught at “Eckbach”, “Moosgraben” and “Lainzer Bach” (n = number of samples, number of captured fire salamander larvae).

Comparison of the individual waters and between standing and flowing waters

The total length showed a significant deviation from a normal distribution (Shapiro-Wilk test, $W = 0.948$, $p < 0.01$). If we look at the data in the specific time periods, we can see that the total length is also not normally distributed here.

At the first data collection at the beginning of March (March 4th – March 13th), the largest fire salamander larvae were at “Kleiner Tümpel beim Wilden Berg” followed by “Moosgraben”. This is also proven statistically because total length significantly varied between the different water bodies (Kruskal-Wallis test, $n = 143$, $H(6) = 49.251$, $p < 0.01$). Individuals born at “Kleiner Tümpel beim Wilden Berg” (“Maurer Wald”) were significantly larger than those at “Lainzer Tiergarten” (“T2”, “T3”, “Lainzer Bach”), “Schwarzenbergpark” (“Stechmückentümpel”) and the other filled pond at “Maurer Wald” (“Schlammtümpel”) (Dunn-Bonferroni test, $p < 0.01$). In addition larvae of “Moosgraben” had significantly a larger total length than those of “T2” (Dunn-Bonferroni test, $p = 0.026$).

At the second data acquisition (March 17th – March 25th), total length also significantly varied between the different water bodies (Kruskal-Wallis test, $n = 174$, $H(6) = 24.468$, $p < 0.01$). Larvae at “Schlammtümpel” were significantly larger than those from “T2” and “Moosgraben” (Dunn-Bonferroni test, $p < 0.01$).

At the third data collection at all water bodies (March 31st – April 8th), total length significantly varied between the different water bodies (Kruskal-Wallis test, $n = 97$, $H(4) = 14.975$, $p < 0.01$). Individuals from “Schlammtümpel” were significantly larger than those of “Eckbach” (Dunn-Bonferroni test, $p < 0.01$).

At the fourth data acquisition (April 14th – April 22nd) at the respective locations before some waters dried up the smallest individuals were at “T2” and the largest ones at “Lainzer Bach” where the larvae had a mean total length of 35.7 mm. Total length significantly varied between the different water bodies (Kruskal-Wallis test, $n = 152$, $H(5) = 40.628$, $p < 0.01$). Fire salamander larvae from “T2” had a significantly lower total length than those of “Jupiter” (Dunn-Bonferroni test, $p = 0.029$), “Schlammtümpel” and “Lainzer Bach” (Dunn-Bonferroni test, $p < 0.01$). In addition individuals from “Lainzer Bach” were significantly larger than those of “Eckbach”, “Moosgraben” (Dunn-Bonferroni test, $p < 0.01$) as well as “Jupiter” (Dunn-Bonferroni test, $p = 0.035$).

Six weeks later, by far the largest larvae were caught at “Eckbach” with an average size of over 40 mm but a standard deviation of about 8 mm. After that, the fire salamander larvae approximately grew equally fast and equally large at each location but fastest and largest at “T2”. Furthermore the new deposited fire salamander larvae of the dried up ponds had roughly the same total length and grew faster than the larvae which were deposited first at the last possible data collection before the water bodies completely dried out.

Likewise, these larvae that were deposited the second time grew a little faster than the larvae in the streams.

At the first data collection in June (8th – 16th), total length significantly varied between the different water bodies (Kruskal-Wallis test, $n = 154$, $H(5) = 26.1$, $p < 0.01$). Individuals of “T2” had significantly a larger total length than those of “T3” and “Schlammtümpel” (Dunn-Bonferroni test, $p < 0.01$) as well as “Eckbach” (Dunn-Bonferroni test, $p = 0.015$).

At the next data sampling (June 22th – July 1st), total length also significantly varied between the different water bodies (Kruskal-Wallis test, $n = 193$, $H(7) = 96.568$, $p < 0.01$). Fire salamander larvae at both ponds at “Schwarzenbergpark” were significantly smaller than any other water bodies (Dunn-Bonferroni test, $p < 0.01$) with the exception of “Eckbach”. Furthermore individuals from “Schlammtümpel” were significantly smaller than those of “T2” (Dunn-Bonferroni test, $p = 0.018$) and “Moosgraben” (Dunn-Bonferroni test, $p = 0.013$). At the first data collection in July (8 – 13), total length significantly varied between the different water bodies (Kruskal-Wallis test, $n = 154$, $df = 4$, $p < 0.01$). Larvae from “Schlammtümpel” had significantly a smaller total length than those from all other water bodies (Dunn-Bonferroni test, $p < 0.01$).

At second data sampling in July (21st – 27th), total length also significantly varied between the different water bodies (Kruskal-Wallis test, $n = 118$, $H(4) = 60.489$, $p < 0.01$). Individuals from “Schlammtümpel” were significantly smaller than those of “Jupiter”, “T2” and “Moosgraben” (Dunn-Bonferroni test, $p < 0.01$). Furthermore fire salamander larvae of “T2” were significantly larger than those of “Jupiter” and “Moosgraben” (Dunn-Bonferroni test, $p < 0.01$).

2018

In total a number of 1344 fire salamander larvae were caught, measured and analysed in the three spatially disconnected study areas (“Maurer Wald” $n = 677$, “Neuwaldegg” $n = 517$ and “Moosgraben” $n = 150$). At “Neuwaldegg” 392 of the 517 fire salamander larvae were from the ponds at “Schwarzenbergpark” and 125 larvae from “Eckbach”.

Table 3: Overview of the water levels of the water bodies in 2018. Each month was divided into two halves (1: Day 1 – 15, 2: Day 16 – 31). ●... Water body filled, ◐... Water body less full, ○... Water body dried out.

Water body	April		May		June	
	1	2	1	2	1	2
“Stechmückentümpel	●	●	●	◐	○	
“Bombentrichter”	●	○	○	◐	○	
“Matschtümpel”	●	●	○	◐	○	
“Kl. Bärlauchtümpel“	●	●	○	○	○	
“Gr. Bärlauchtümpel”	●	●	●	◐	○	
“Eckbach”	●	●	●	●	●	
“Moosgraben”	●	●	●	●	●	
“Jupiter”	●	●	●	●	◐	
“Gr. T. b. WB”	●	●	●	◐	○	
“Schlammtümpel”	●	●	●	◐	◐	
“Saturn”	●	●	●	◐	◐	
“Pappeltümpel”	●	●	◐	○	○	

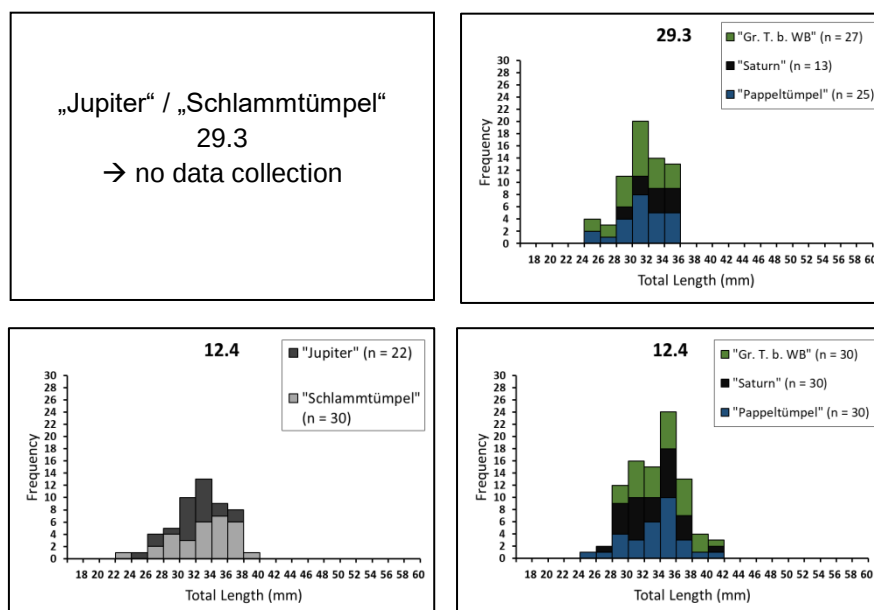
Stagnant waters

We started with the data collection at “Maurer Wald” on March 29th. “Schwarzenbergpark” was visited for the first time one week later, on April 3rd. At both study sites, 30 fire salamander larvae could not always be caught at all ponds. In the course of this study, at “Maurer Wald”, “Großer Tümpel beim Wilden Berg” and “Pappeltümpel” dried up. At “Schwarzenbergpark”, all the ponds had dried out until July, “Matschtümpel”, “Bombentrichter” and “Kleiner Bärlauchtümpel” even dried out in April. “Matschtümpel” and “Bombentrichter” refilled due to heavy rain, but later dried up again (Fig. 16).

“Maurer Wald”

On March 29th, fire salamander larvae were found at “Großer Tümpel beim Wilden Berg”, “Saturn” and “Pappeltümpel”. Most of the larvae there were between 28 and 36 mm and almost the half of the larvae from “Großer Tümpel beim Wilden Berg” were between 28 and 34 mm. Two weeks later, on April 12th, fire salamander larvae were also caught at “Jupiter” and “Schlammtümpel”. At “Jupiter” more than the half of the captured fire salamanders was

between 30 and 34 mm. At “Schlammtümpel”, “Saturn” and “Pappeltümpel” mostly of the animals had a total length between 32 and 38 mm. The biggest individuals were caught at “Großer Tümpel beim Wilden Berg” where more than the half had a total length of over 34 mm. On April 27th, the largest larvae were at “Schlammtümpel” where most of them had a total length between 38 and 42 mm and some up to 46 mm. At “Jupiter” and “Pappeltümpel” most of the larvae were between 34 and 38 mm. At “Saturn” more than the half of the captured fire salamander larvae had a total length between 34 and 40 mm. The smallest ones were caught at “Großer Tümpel beim Wilden Berg” where only few of them had a total length over 34 mm. Two weeks later, on May 9th, a significantly larger number of larger individuals than in the previous dates were found at “Schlammtümpel”, “Jupiter” and “Saturn”. More than the half of the captured fire salamander larvae at “Schlammtümpel” was between 40 and 46 mm. At “Jupiter” and “Saturn” more than the half of the larvae had a total length between 36 and 40 mm and a few had total lengths of up to 50 mm. At “Pappeltümpel” and “Großer Tümpel beim Wilden Berg” most of the captured individuals were between 30 and 36 mm. On May 22nd, almost all animals had a total length over 40 mm and more than the half of them was between 44 and 52 mm. At “Großer Tümpel beim Wilden Berg” only a few of the larvae had a total length over 40 mm. At “Saturn” two thirds of the fire salamander larvae were over 38 mm. “Pappeltümpel” was already dried out. Two weeks later – at the last data collection – on June 6th, only few larvae could be found at “Schlammtümpel”. About the half of them were between 42 and 48 mm. At “Jupiter” almost all the captured fire salamander larvae had total lengths over 42 mm, the largest ones until 52 mm. At “Saturn” two thirds of the individuals were between 30 and 36 mm. At this date, some larvae were caught shortly before or even during metamorphosis (Fig. 16).



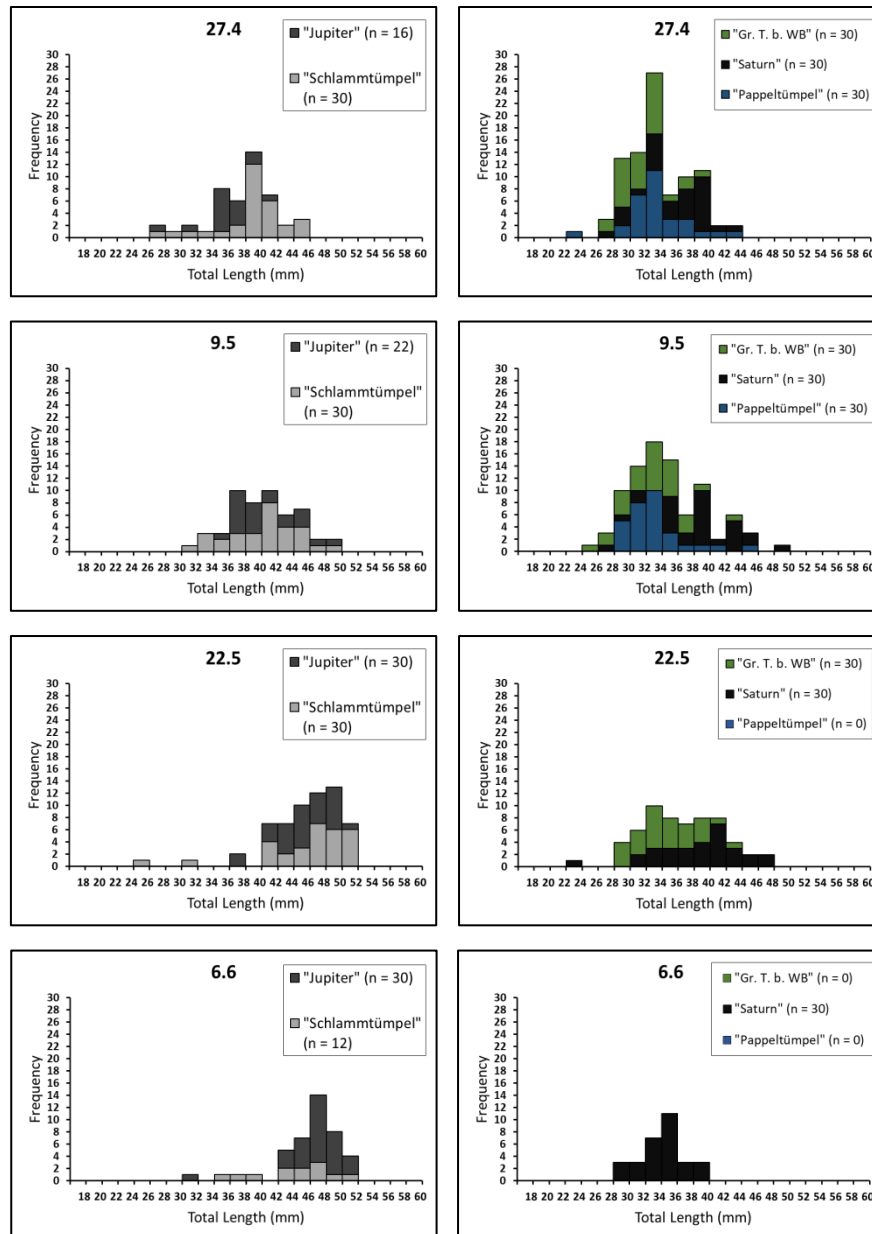
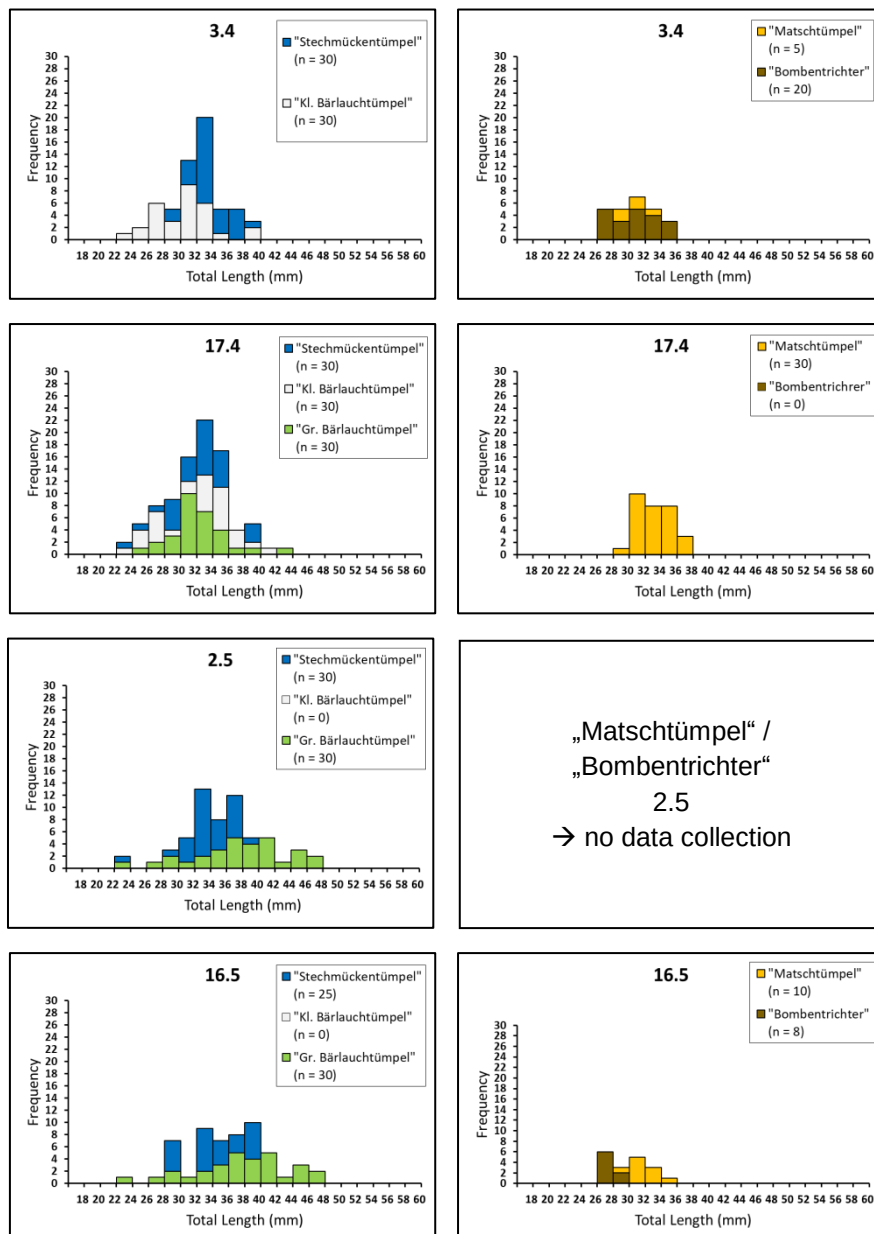


Figure 16: Synthetic histograms of the total lengths (mm) of the fire salamander larvae caught at “Maurer Wald” (n = number of samples, number of captured fire salamander larvae).

“Schwarzenbergpark”

On April 4th, two thirds of the captured fire salamanders at “Stechmückentümpel” were between 30 and 36 mm. At “Bombentrichter” and “Kleiner Bärlauchtümpel” most of the individuals had a total length between 28 and 34 mm. Two weeks later, on April 17th, most of the captured larvae of all ponds had again total lengths between 28 and 34 mm. “Bombentrichter” was already dried out. On May 2nd, in addition to “Bombentrichter”, also “Kleiner Bärlauchtümpel” and “Matschtümpel” were dried out. At “Stechmückentümpel” and “Großer Bärlauchtümpel” most of the larvae were between 32 and 38 mm. Two weeks later, on May 16th, almost all fire salamander larvae were between 32 and 40 mm. At “Großer

Bärlauchtümpel” two thirds had total lengths over 36 mm. At “Bombentrichter” and “Matschtümpel” new animals were deposited again. All these larvae had a total length below 36 mm. The largest ones had a total length of up to 48 mm. At the last data acquisition, on May 29th only “Stechmückentümpel” and “Großer Bärlauchtümpel” were filled. At “Stechmückentümpel” more than the half of the captured individuals had a total length over 36 mm. The largest ones had total lengths of up to 48 mm. At “Großer Bärlauchtümpel” two thirds of the larvae were over 36 mm and more than the half were larger than 40 mm.



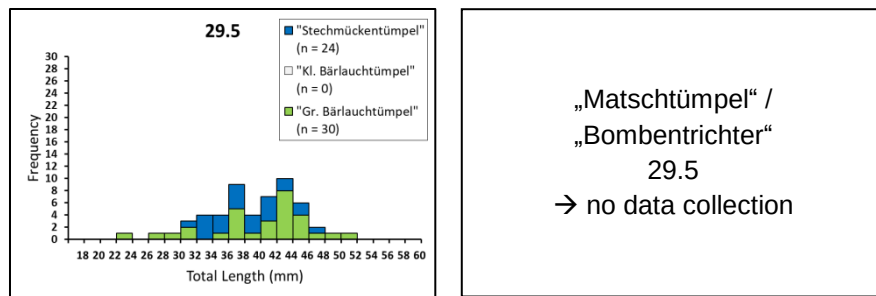


Figure 17: Synthetic histograms of the total lengths (mm) of the fire salamander larvae caught at “Schwarzenbergpark” (n = number of samples, number of captured fire salamander larvae).

Flowing waters

The data acquisition at “Moosgraben” started on April 10th, at “Eckbach” one week later, on April 17th. With the exception of May 29th and June 14th, on each examination day 30 fire salamander larvae caught. On May 29th and June 14th fewer larvae were found due to thunderstorms at “Eckbach” (Fig. 18).

“Moosgraben”

On April 10th and also two weeks later on April 25th, two thirds of the captured fire salamander larvae were between 30 and 36 mm. On May 9th, a few of the individuals had a total length between 24 and 28 mm. All the others had a total length over 28 mm in which the most of them were between 28 and 36 mm again. Two weeks later, on May 22nd, about the half of the captured fire salamander larvae had again a total length between 28 and 36 mm. But on this day larger individuals with a total length up to 52 mm were found. At the last data collection on June 6th, about the half of the individuals had a total length between 28 and 36 mm again. The other half were between 40 and 52 mm but the most of them had a total length between 40 and 46 mm (Fig. 18).

“Eckbach”

At the first data acquisition on April 17th, size distribution was roughly the same as at the first data collection at “Moosgraben” with the only difference that there a few larger larvae. Two weeks later, on May 2nd, more than the half of the captured animals were already larger than 36 mm. On May 16, more than the half were between 30 and 36 mm but there were also larger larvae with a total length up to 50 mm. Two weeks later, on May 29th, approximately the half of the individuals was larger than 40 mm but just like as “Moosgraben” there were also smaller fire salamander larvae with a total length below 34 mm. At the last data

collection, on June 14th, only one individual was smaller than 30 mm. The others had a total length of over 36 mm. The largest ones had a total length up to 54 mm (Fig. 18).

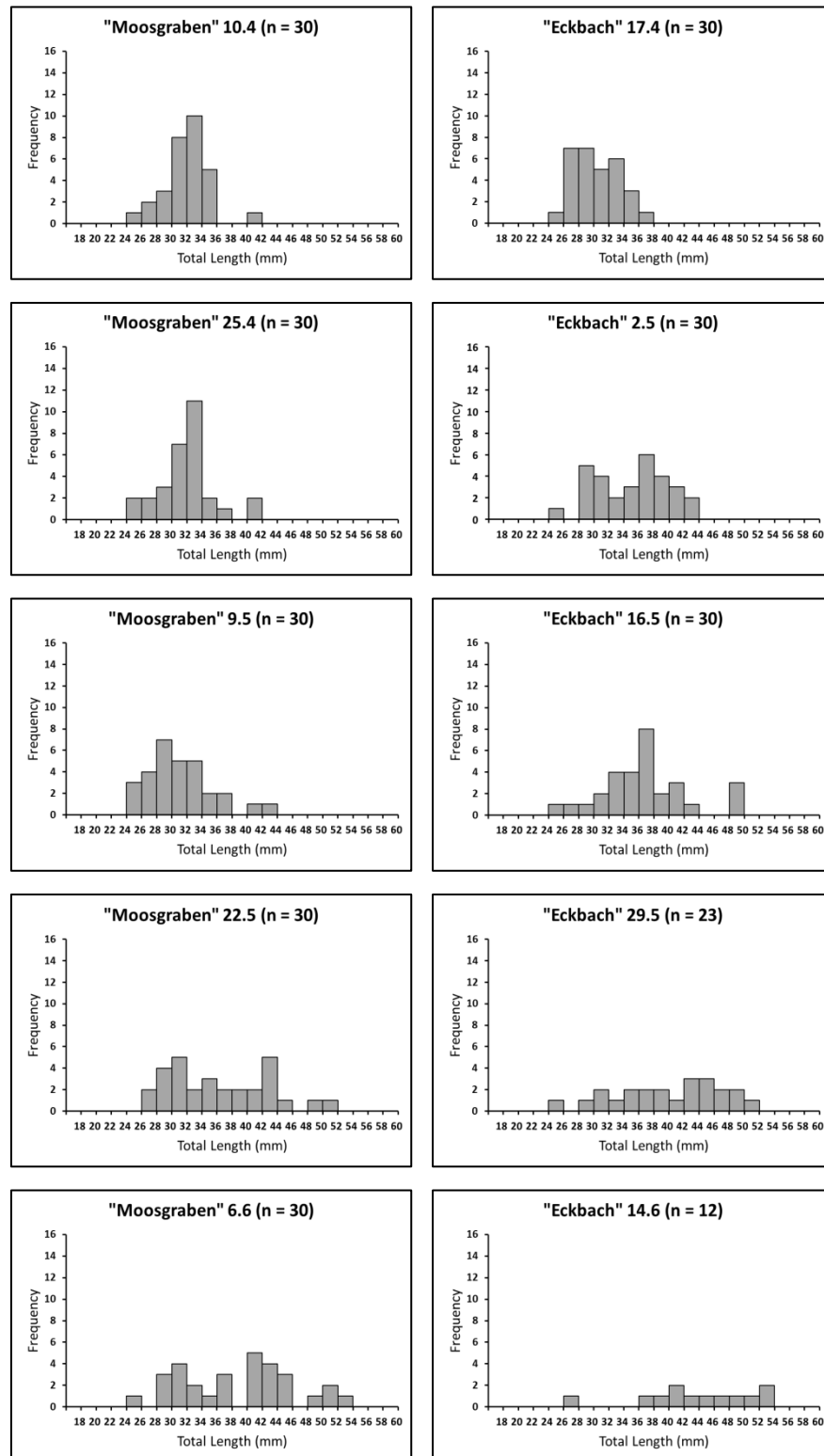


Figure 18: Histograms of the total lengths (mm) of the fire salamander larvae caught at “Moosgraben” and “Eckbach” (n = number of samples, number of captured fire salamander larvae).

Comparison of the individual waters and between standing and flowing waters in 2018

At the first data collection, the largest individuals were found at “Stechmückentümpel” but the differences were small.

At the second data acquisition at all water bodies (between April 12 and 25), total length significantly varied between the different water bodies (Kruskal-Wallis test, $n = 322$, $H(10) = 25.735$, $p < 0.01$). Larvae at “Eckbach” had significantly a smaller total length than those of “Großer Tümpel beim Wilden Berg” and “Pappeltümpel” (Dunn-Bonferroni test, $p < 0.01$).

At the third data collection the largest individuals were again at “Schlammtümpel”. This is also proven statistically because at all water bodies (between April 27 and May 9), total length significantly varied between the different water bodies (Kruskal-Wallis test, $n = 256$, $H(8) = 66.194$, $p < 0.01$). Larvae at “Großer Tümpel beim Wilden Berg” and “Moosgraben” were significantly smaller than those of “Jupiter”, “Schlammtümpel” and “Saturn” (Dunn-Bonferroni test, $p < 0.01$). Furthermore individuals of these two water bodies had a smaller total length than the larvae of “Eckbach” (“Großer Tümpel beim Wilden Berg”, Dunn-Bonferroni test, $p = 0.042$; “Moosgraben”, Dunn-Bonferroni test, $p = 0.025$). In addition fire salamander larvae of “Schlammtümpel” were significantly larger than those of “Pappeltümpel”, “Stechmückentümpel”, and “Großer Bärlauchtümpel” (Dunn-Bonferroni test, $p < 0.01$).

At the fourth data sampling (between May 9 and May 22), total length also significantly varied between the different water bodies (Kruskal-Wallis test, $n = 275$, $H(10) = 88.825$, $p < 0.01$). Larvae from “Bombentrichter” were significantly smaller than those of “Jupiter”, “Schlammtümpel”, “Saturn”, “Großer Bärlauchtümpel”, “Eckbach” and “Moosgraben” (Dunn-Bonferroni test, $p < 0.01$). Individuals from “Matschtümpel”, “Großer Tümpel beim Wilden Berg” and “Pappeltümpel” had significantly a lower total length than those of “Jupiter”, “Schlammtümpel” and “Saturn” (Dunn-Bonferroni test, $p < 0.01$) as well as “Großer Bärlauchtümpel” (Dunn-Bonferroni test, $p = 0.048/p = 0.026/p = 0.027$). Furthermore fire salamander larvae of “Stechmückentümpel” had significantly a lower total length than those of “Jupiter” (Dunn-Bonferroni test, $p = 0.017$) and “Schlammtümpel” (Dunn-Bonferroni test, $p = 0.015$). So the largest individuals were at “Jupiter” and “Schlammtümpel”.

At the fifth data collection (between May 22 and June 6), total length significantly varied between the different water bodies (Kruskal-Wallis test, $n = 275$, $H(7) = 75.059$, $p < 0.01$). Larvae of “Jupiter” and “Schlammtümpel” were significantly larger than those of “Großer Tümpel beim Wilden Berg”, “Stechmückentümpel”, “Saturn” and “Moosgraben” (Dunn-

Bonferroni test, $p < 0.01$). Furthermore these two ponds had significantly a higher total length than the individuals of “Großer Bärlauchtümpel” (“Jupiter”: Dunn-Bonferroni test, $p = 0.026$; “Schlammtümpel”: Dunn-Bonferroni test, $p < 0.01$).

At the last data acquisition (between June 6 and June 14), the largest fire salamander larvae were at “Jupiter” and “Schlammtümpel” again. Total length also significantly varied between the different water bodies (Kruskal-Wallis test, $n = 84$, $H(3) = 48.953$, $p < 0.01$). Fire salamander larvae from “Saturn” were significantly smaller than all other three water bodies (“Jupiter”, “Schlammtümpel” and “Eckbach”: Dunn-Bonferroni test, $p < 0.01$).

Comparison of data from 2018 and 2020

The first data collection this year was at the beginning of March. In contrast, the first of 2018 was at the end of March.

At “Schwarzenbergpark”, a data comparison is not useful at both of these ponds because there are too few data.

At “Jupiter” and “Schlammtümpel” at “Maurer Wald”, the first larvae in 2018 were only deposited until April 12th. In 2020 the first fire salamander larvae were already deposited until March 24th at “Jupiter” and until March 10th at “Schlammtümpel”. On the first data acquisition, when the first individuals were deposited, there were hardly any differences in total length between 2018 and this year. Four weeks after the first data sampling at “Jupiter”, the larvae in 2018 grew much faster and were larger than these in 2020. But if we compare the growth of the fire salamander larvae from 2018 with the second larvae – that individuals which were deposited after this pond had been refilled, we see roughly the same growth in the respective data recordings. At “Schlammtümpel”, the growth of the first deposited fire salamander larvae was also much lower in 2020 than in 2018. The individuals that were newly deposited this year after the pond had dried up grew faster than the first but not as quickly as those in 2018.

At “Eckbach” the data collection started later in both years compared to the other locations, but in 2018 a bit later than in 2020. At the start of the data recording the fire salamander larvae were roughly the same size in both years but in 2018 the individuals grew faster than in 2020. Overall, however, despite a much longer study period, fewer larvae were caught this year than in 2018.

At “Moosgraben”, the data collection in 2018 started one month later than this year. There were only very small differences in size growth in that the larvae grew slightly faster in 2018 than in 2020 (Tab. 4).

Table 4: Mean values as well as the standard deviation of the total lengths (mm) of the fire salamander larvae at the various locations on the respective day (marked in bold) from 2020 and from 2018.

Standing waters													
"Schwarzenbergpark"													
"Stechmückentümpel"		4.3	17.3	31.3	14.4	27.4	11.5	25.5	8.6	22.6	6.7	20.7	3.8
2020	Mean	31,00	32,08							31,22			
	SD	3,68	2,03							3,72			
				3.4	17.4	2.5	16.5	29.5	14.6				
2018	Mean			33,53	32,42	33,88	34,63	38,40					
	SD			2,27	3,80	3,06	3,54	4,32					
"Großer Bärlauchtümpel"													
2020	Mean	4.3	17.3	31.3	14.4	27.4	11.5	25.5	8.6	22.6	6.7	20.7	3.8
	SD									30,34			
										2,95			
				3.4	17.4	2.5	16.5	29.5	14.6				
2018	Mean				32,33	33,21	37,73	39,77					
	SD				3,38	3,60	5,98	6,62					
"Maurer Wald"													
"Jupiter"		10.3	24.3	6.4	20.4	4.5	18.5	1.6	16.6	29.6	13.7	27.7	10.8
2020	Mean		32,74	33,20	32,70				34,01	40,52	40,82	43,35	44,63
	SD		1,82	2,52	1,71				3,55	4,73	5,56	3,14	3,71
2018	Mean		29.3	12.4	27.4	9.5	22.5	6.6					
	SD			31,84	35,76	40,45	45,24	46,55					
				2,89	3,42	3,80	3,54	3,70					
"Schlammümpel"													
2020	Mean	10.3	24.3	6.4	20.4	4.5	18.5	1.6	16.6	29.6	13.7	27.7	10.8
	SD	31,42	33,70	35,48	33,17				32,96	37,30	36,61	39,00	44,27
		2,80	2,82	3,00	2,19				2,76	2,83	2,81	3,18	2,61
2018	Mean		29.3	12.4	27.4	9.5	22.5	6.6					
	SD			32,96	38,67	40,12	45,69	44,12					
				3,50	4,29	4,52	5,84	4,54					
Flowing waters													
"Eckbach"													
2020	Mean	4.3	17.3	31.3	14.4	27.4	11.5	25.5	8.6	22.6	6.7	20.7	3.8
	SD			30,77	31,12	33,16	35,22	40,04	34,20	39,93			
				0,80	3,86	3,17	5,06	7,83	10,00	4,70			
				3.4	17.4	2.5	16.5	29.5	14.6				
2018	Mean				30,31	35,05	36,61	39,84	43,65				
	SD				2,89	4,72	5,79	7,11	7,47				
"Moosgraben"													
2020	Mean	6.3	19.3	1.4	15.4	29.4	13.5	27.5	10.6	24.6	8.7	21.7	4.8
	SD	33,02	30,82	32,55	32,20	32,70	32,81	34,20	36,19	41,79	42,29	43,82	45,90
		1,84	3,01	2,73	2,16	3,02	3,97	5,14	5,45	4,49	4,07	3,26	5,16
					10.4	25.4	9.5	22.5	6.6				
2018	Mean				31,93	32,18	31,18	36,36	38,93				
	SD				2,97	3,67	4,36	6,49	7,44				

Discussion

2020

At the start of the data collection all fire salamander larvae had a total length between 26 to 36 mm which is in line with the findings of Mayerhofer (2013) and Thiesmeier (2004). Because some of the previously dried up ponds were filled again, it can be said that fire salamander larvae were deposited at least by mid-June, and probably even longer until the end of June.

On one side there was no growth in size at the beginning until these ponds dried out. Due to the low temperatures and the changing conditions, some larvae may have died, either suffocated under the ice or due to the shock like for example those at “Kleiner Tümpel beim Wilden Berg”. Another reason could be that all ponds were filled with less water. So, the individuals had less hiding options and crows were also sighted these days which could have reduced the density. Therefore fewer fire salamander larvae were found at these ponds. For example the animals at “Schlammtümpel” survived partially buried in the mud. Maybe the larger ones had died because they already needed more water and oxygen.

On the other side, the growth at „Jupiter“ and „Schlammtümpel“ as well at “T2” and “T3” was very interesting because the larvae which were deposited second until mid-June, after these ponds were refilled, had approximately the same size or at "Jupiter" they were even slightly larger than the individuals that were measured during the last data collection before the ponds dried out. It is therefore likely that the animals continue to grow in the womb and consumed the yolk of the egg (Kopp & Baur, 2000). Some other studies, for example from Portugal or Israel, have even written that in unfavourable conditions the larvae can be kept in the uterus for several months up to five years and are only deposited when the conditions are better (Rebelo & Leclair, 2003, Warburg, 2010). If this behaviour is just as extreme or if this data can be compared with the fire salamander species in Central Europe is debatable.

In addition, these larvae also grew much faster than the first deposited ones, especially at “T2”. The growth could also be seen at “Schlammtümpel”, but significantly slower than in the other ponds. Since it was later in the year, this could of course have something to do with the rising temperature. Reinhardt (2014) said that with the increasing temperature also the growth rates increase. Caspers et al. (2015) pointed out that females which deposited their offspring in ponds enabled them to deposit larger larvae towards the end of the deposition period and that these individuals grow faster.

Generally, the most relevant factor influencing growth increment for amphibians is next to the temperature also food availability (Ryan 1986). So food availability plays an important role in this study because due to the water bodies dried out, all animals died. When larvae were then deposited again, it was observed that there were far fewer other animals, especially those used as food by fire salamander larvae. This resulted that there is more cannibalism towards the individuals (Keckeis, 2013, Reinhardt, 2014, Manenti et al., 2015) which were seen twice at "Jupiter" as well as "Schlammtümpel" and that the larvae were spending considerable time floating close to the surface to consume terrestrial arthropods (Blaustein et al., 2013).

When comparing stagnant and flowing waters it turned out that at the beginning of the data collections there were no big differences in total length of the individuals between these two water bodies. The largest ones were at "Kleiner Tümpel beim Wilden Berg" where there was already a great abundance. It is possible that these larvae were already deposited in autumn or that the size was related to the mass of the females because heavier mothers produced longer and heavier offspring (Mayerhofer, 2013, Caspers et al., 2015).

At the fourth data collection at each location about mid-April the largest larvae were caught at "Lainzer Bach". The reason was that the ponds, in particular, had to cope with unfavourable conditions, such as drying out or freezing.

It can definitely be confirmed that the larvae in the ponds were deposited at least by mid-June. The last ones were deposited at "Schwarzenbergpark" in the two newly filled "Stechmückentümpel" and "Großer Bärlauchtümpel". Therefore, the individuals from these two ponds were significantly smaller than those of the other water bodies at this time.

How long females deposited larvae in streams cannot be precisely said but due to the growth of the animals, possibly not as long as in ponds. But what can be said is that various aspects of larval deposition behaviour and maternal investment differ between females from these two habitat types (Caspers et al., 2015, Hendrix et al., 2017). Pond-adapted females, which are faced with more unpredictable and unstable environment, had a more pronounced bet-hedging strategy than stream-adapted ones because they are characterised by a more frequent and longer time period for larval deposition (Reinhardt, 2014). Caspers et al. (2015) said that the lengthened deposition period enabled pond-adapted females to deposit larger larvae towards the end of the deposition period. He also stated that over successive deposition events, the body condition of larvae deposited by stream-type females decreased faster than these which were deposited in ponds. So pond-adapted females might extend their deposition period to

give their embryos, especially the later batches, the opportunity to grow more prior to birth and increasing their probability of surviving to metamorphose because larger larvae could probably compete for food more successfully and undergo metamorphosis earlier (Semlitsch et al., 1988, Rowe & Ludwig, 1991, Krause et al., 2011) or have a lower size threshold for metamorphosis (Czypionka et al., 2018). Alcobendas et al. (2004) also found in their study that the size at deposition is positively correlated with survival until metamorphosis, especially at higher water temperatures. Weitere et al. (2004) said in their study that under natural conditions, these responses/adaptations include a greater larval mass at birth and the ability to thrive on lower-quality food. So fire salamander larvae which were deposited and developed in ephemeral habitats show several habitat specific adaptations – that optimize survival and reproduction – which are absent in stream-adapted ones (Hendrix et al., 2017). For example, when larvae occupy ephemeral aquatic habitats, life cycles have adapted to water availability and dehydration risk (Caspers et al., 2015).

Moreover, the fire salamander larvae which were deposited at second grew a little faster than the larvae in the streams. These results are also in line with Kopp and Baur (2000) they said that larvae born in ponds grow faster due to the short duration of the pond (Kopp & Baur, 2000). This can be attributed to the different thermal regime between these two habitats (Reinhardt et al., 2015) – especially at this time – because the higher temperatures in the ponds (as was also the case in this study) impact the growth rate and activity of the larvae (Beachy, 1995, van der Have & de Jong, 1996, Alcobendas et al., 2004, Grant et al., 2014). So individuals from water bodies with higher temperature were larger and heavier and partially showed morphological signs of metamorphosis – for example appearing yellow knee patches and degeneration of gills (Czypionka et al., 2018, Sanchez et al., 2018). A more precise comparison between standing and flowing waters is not possible because the ponds were not completely filled through the season.

2018

At the start of the data collection in 2018 all fire salamander larvae had a total length between 26 to 36 mm which is in line with the findings of 2020, Mayerhofer (2013) and Thiesmeier (2004). In 2018 also some ponds dried out and filled again between the beginning of May and mid-May. So we could say that fire salamander larvae were deposited at least until mid-May. This event based on the statement by Steinfartz et al. (2006) they said that females deposit their larvae until mid-May.

At “Jupiter” and “Schlammtümpel” where significantly the largest larvae with total lengths over 46 mm were found, the water levels remained approximately constant. All the other ponds which fell sharply in the course of spring or led to complete drying out contained significantly fewer larger larvae than these two stagnant waters, especially from May onwards. The reasons for the larger individuals at “Jupiter” and “Schlammtümpel” could be beside the constant water level also the muddy underground which leads to that the water becoming cloudy and hinders predators (Krause et al., 2011). In general, we could say that the larger total length of almost all captured individuals were due to the favorable growth conditions, e.g. a large supply of food at these two ponds (Reinhardt, 2014). At “Saturn” significantly larger larvae were also found in the course of spring compared to the other ponds. But these individuals were significantly smaller than those of “Jupiter” and “Schlammtümpel”. This could be due to the clarity of the water and the significantly smaller size of the pond, which led to a lack of hiding places and less protection from predators especially at the end of spring. At the last data collection at “Saturn” the fire salamander larvae were significantly smaller than in the previous weeks, which can be explained by the fact that this pond only had a very low water level and there was no food available but a very high population density at that time. Likewise, the larger animals could not have survived the low water level due to the decreasing hiding options against predators (Krause et al., 2011) or some already undergo the metamorphosis. Although “Großer Tümpel beim Wilden Berg” was by far the largest pond only a few larvae were found over 38 mm. Possible reasons for this could be that it was not very deep and housed an excessive number of fire salamander larvae. As I mentioned before, a high population density could have led to food shortages and cannibalism in the animals (Reques and Tejedo, 1996, Reinhardt, 2014) which impeded growth.

The fire salamander larvae at “Jupiter” and “Schlammtümpel” were also significantly larger than those of the streams. This could be because larvae are still being deposited in flowing waters until late spring. For example at “Eckbach” the depositing period started later than at the other water bodies. In streams they would still have a good chance of survival at the end of spring due to the many possibilities for spreading (Caspers et al., 2015). Possibly smaller larvae may be more likely to be deposited in streams than in ponds because there they have a greater chance of survival. Mayerhofer (2013) also showed that newly deposited fire salamander larvae at “Maurer Wald” were slightly larger than those at “Eckbach” and “Moosgraben”. As I mentioned before the total length at birth was related to the mass of the

females because heavier mothers produced longer and heavier offspring. But this could also be a reproductive strategy of the females to protect the smaller new deposited individuals which could have been eaten by the larger ones.

Comparison of data from 2018 and 2020

Due to the strongly changing weather pattern in 2020, the data analysis was very different to them from 2018 because the water bodies dried out even faster this year and in the short frost period many larvae died – maybe they suffocated under the layer of ice, for example “Kleiner Tümpel beim Wilden Berg”. Nevertheless it can be said that the fire salamander larvae from 2020 were deposited earlier than in 2018. A possibly reason could be that it was warmer at the beginning of spring this year than two years ago. Furthermore, the ponds dried up faster this year but due to rainfalls these were refilled and larvae were deposited again. Probably the larvae had been deposited later than two years ago but no careful attention was paid in 2018. But due to the available data and the different weather conditions it can be assumed. Cabela et al. (2001) said in their study that in Europe larval density usually peaks at the end of April/beginning of May, followed by a continuous decline. Due to the weather and the constant drying up of the ponds this had been postponed this year because in early June, a large number of larvae were deposited. The fact that the fire salamander larvae in some water bodies grew a little bit faster in 2018 than in 2020 can also be explained by the weather, especially by the temperature.

If we compare for example the data of 2018 and 2020 from “Eckbach” we see however, despite a much longer study period, fewer larvae were caught in 2020. A possible reason for this cannot be safely said because the rainfalls were not much more than in 2018. Maybe the corona pandemic could have an impact on this because due to the restrictions there were much more people in the forest this year than two years ago. “Eckbach” is right next to a well-frequented footpath which could disturb the females in their rest and keep them from coming near it (Hamer & McDonnell, 2008, Manenti et al, 2009b, Price et al., 2011). Adult fire salamanders had never been seen along this stream in 2020. Presumably that is why they retired to the dense and less frequented forest.

In general, it has been shown that the larvae in streams in 2018 grew faster than in 2020. At "Moosgraben" it would be interesting to have a longer data acquisition in 2018 in order to compare the data from this year with them to see how the growth would continue. At the ponds it was harder to compare because they dried out very fast and were no filled at the same

time like in 2018. The fire salamander larvae which were deposited first this year grew slower than these two years ago but if we compare the data from 2018 with these from the larvae 2020 which were deposited after the ponds were refilled, we do not see big size differences. So it can be assumed that the weather and therefore also the temperature play a very important role. It is possible that the first larvae which were deposited in the ponds at the beginning of March 2020 grew slower because they were affected by poor conditions and in the short frost period, in addition to the numerous larvae, also other animals, which the fire salamander larvae used as food, died.

But if we look at the data from 2018, it can also be assumed that most of the ponds at “Maurer Wald” and “Schwarzenbergpark” partly dried out very quickly due to the lack of precipitation. This meant that they could not offer optimal development conditions, which was reflected in the small size of the captured fire salamander larvae in spring. However, two ponds at “Maurer Wald” lost significantly less water than the other ponds. In these two ponds (“Jupiter” and “Schlammtümpel”) the highest number of large individuals was found over the course of spring compared to the other ponds.

If we compare the results from 2018 and 2020 with those of Keckeis (2013), who found that fire salamander larvae from temporary stagnant waters were larger than those from flowing waters, we could say that in 2020 only the individuals of “T2” and in 2018 only “Jupiter” and “Schlammtümpel” were larger than those of the streams. The total length of the larvae of the other ponds at “Maurer Wald”, “Schwarzenbergpark” and “Lainzer Tiergarten” hardly differed from those of the larvae from the streams. However, the fire salamander larvae of the stagnant waters had to struggle with the loss of water and the resulting excessive population density, which led to a lack of food and so probably severely impaired the growth of the animals. Despite the suboptimal conditions, the individuals of the ponds were not smaller than the ones of the streams, which may be related to the conjecture by Schulte (2008), who claimed that larvae from ponds have longer tail fins because these are helpful for a quick escape from predators, while shorter tail fins are advantageous in streams so that the animals are not carried away with the water flow. But if we only compare the growth of the fire salamander larvae in 2020, it can be said that the individuals in the ponds grew much faster than these in the streams. As I mentioned before, this is due to the higher temperature in the ponds.

Females also could deposit larvae in more different ponds, with each pond providing an independent chance of larval survival (Reinhardt, 2014). Ponds exhibit a greater risk of

oxygen depletion and dehydration, so that all the deposited larvae could die (Reinhardt et al., 2013). Furthermore, stagnant water bodies contain less food, which increases the likelihood of cannibalism (Reinhardt, 2014). Crump (1983) said that cannibalism is often a result of limited alternative food resources or high conspecific density. Due to that the population density in ponds is bigger than in streams (Reinhardt, 2014) females could delay their larval deposition to wait until there are fewer individuals in this pond to increase their chances of survival (Eitam et al., 2005) because later born larvae face a higher risk to be eaten by the bigger ones (Manenti et al., 2015, Reinhardt et al., 2015). Caspers et al. (2015) pointed out that females can control larval deposition and potentially have different options regarding when, where and how many larvae they deposit.

But it is unknown if females decide only for a habitat type or if they also deposit larvae in flowing and stagnant waters during one season. Hendrix et al. (2017) described in their study that a genetic analysis of salamander larvae suggested that one population has genetically differentiated into two subpopulations associated with the two larval habitat types inhabited (streams vs. ponds) (Steinfartz, 2007). So that would mean that females do not switch between streams and ponds when they deposited their offspring. It is not known whether this will change if, for example, all the ponds in the vicinity have dried up or whether the pond-adapted females wait until the ponds filled again. A good example is “Neuwaldegg” because at “Schwarzenbergpark” the ponds were rarely filled in 2020 but in the nearby “Eckbach” there were not more larvae deposited in them in contrast to 2018.

Considering the high energetic demand at a top-position within the aquatic food web, the risk of resource overexploitation exists, especially in small habitats like ponds because they confine the larvae on a small area and maintain high larval densities throughout the season. Due to the low aquatic food availability after the ponds refilled and the resulting high intraspecific competition for food, the larvae acquire alternative substitutes of their diet (Reinhardt, 2014). I observed that aquatic prey at streams, especially at “Moosgraben”, was in contrast to the ponds much higher during the larval growth season. Therefore fire salamander larvae were more often seen on the surface of ponds compared to streams to prey on drowning or ovipositing insects and their eggs (Blaustein et al., 2013, Reinhardt, 2014). In streams where food availability is abundant, the consumption of terrestrial insects would not provide a good alternative. Floating on the water surface is very risky for the fire salamander larvae because it could lead to increased predation by terrestrial predators (Reinhardt, 2014) and also to downstream drift (Thiesmeier and Schuhmacher, 1990). Moreover, terrestrial prey is only

available when they are drifting by, but in the ponds they are on the surface for a longer time. So, larvae probably consumed active terrestrial insects in ponds in the same way as aquatic prey with the sit-and-wait strategy in streams (Reinhardt, 2014). Manenti et al. (2013) also showed that salamander larvae modified their behaviour in response to environmental conditions and that predators often show strong plasticity of optimal foraging strategies. These two strategies are most effective under opposite environmental conditions. So active predators being favoured over sit-and-wait predators when prey is scarce and their detection difficult (Huey & Pianka, 1981, Manenti et al., 2013).

In general, this reproduction mode would be beneficial for larval survival because drift is used as a strategy to overcome population density for example when larval crowds lead to local starvation. This behaviour prevents extremely high densities and thus reduces the intraspecific competition for food (Thiesmeier, 1992).

One general reason why larvae had not been seen on the surface is because they often remain near rocks to hide and reduce the risk of being detected by predators (Krause et al., 2011) and also that their activity rate increases at night. Fire salamander larvae demonstrate UVB avoidance behaviour by preferring shady spots and seeking deeper water regions during day (Scheessele, 2007, Schauer et al, 2012). On one hand lack of light reduces the possibility of detecting prey but on the other hand also reduces the risk of being spotted by predators (Manenti et al., 2013). It would be very interesting whether more larvae could be seen during the night, like Schauer et al. (2012) found in their study or whether the size ratio to the animals which were caught during the day varies. Other several factors which can influence the detectability of the individuals are animal activity patterns, air and water temperature, rainfall, unpredictable seasonal events such as dryness or floods, moon phase, as well as prey and predator activity (Jung et al. 2004). For example, Manenti et al. (2013) found in their study that the movements were higher in food-deprived larvae and in the presence of prey compared to fed larvae and when the prey was absent.

So the detection probability could also affect the results. A good example is the second data acquisition at “Moosgraben” in 2020 because more larvae with lower total lengths were caught compared to the first ones. But on this day the sample size was much smaller and only ten individuals were found. Maybe no or only a few fire salamander larvae were deposited before the first data collection and the few larger ones are still from autumn. Kopp and Baur (2000) said that larvae could stay up to one year in the aquatic habitat. The problem is that the

data could be correlated with the detection probability because larger individuals are more likely to be seen. In addition, due to the different habitats in a stream, the bias can drift in both directions because smaller larvae could be caught in shallow areas and vice versa. Furthermore there are big differences between standing and flowing waters as in streams the probability is higher to catch not always the same individuals.

As I mentioned before, in comparison to “Moosgraben” and “Lainzer Bach” (as long as this was not dried out), less individuals were found at “Eckbach” this year. At the first two field trips no fire salamander larvae were found. Maybe no larvae or only a few ones were deposited until this date. At the first possible data collection at “Eckbach” at the end of March, the smallest larvae were caught there because they were deposited much later than the individuals of the other water bodies. After that there were an increase in total length until the end of May at this stream but then, fewer and fewer larvae were caught so that a comparison would be very difficult and not really useful. The cause for this was the flow velocity because it is known that a lower flow velocity with some riffle pool sequences positively influence salamander larvae abundance (Thiesmeier & Schuhmacher, 1990, Tanadini et al., 2012) and “Eckbach” had a very high flow speed this year with only less quiet places. Larvae absence or high extinction probabilities could also be a consequence of individuals that have been flushed away due to heavy rainfalls (Anderson & Lehmkuhl, 1963) – more likely at stronger flowing streams – or even early emigration to the terrestrial habitat after metamorphosis (Baumgartner et al., 1999). In particular from May 11th to May 25th, much fewer larvae were found, which is definitely due to the heavier rainfalls and storms at this time.

“Moosgraben” is a nature reserve with very good conditions because this area offers a lot of shelter or hiding places for the adults and due to the sufficient flow rate this stream cannot dry out. *Salamandra salamandra* is strongly associated with forest cover because older forests or those with more deadwoods might be more suitable to support the occurrence (Manenti et al., 2009b, Ficetola et al., 2011). In contrast, at “Schwarzenbergpark” there are less hiding options for the adult fire salamander and this area is much more frequented by strollers, cyclists and especially children. This is also due to the playgrounds and chill areas along the “Eckbach” whereby the animals could be disturbed in their rest. “Neuwaldegg” was also the only study area where no adult fire salamanders were seen. Bänziger (2016) found that many features of the habitat are correlated with the change in occupancy of the populations and that the local extinction of fire salamanders is associated with the amount of deadwood. So there are also

the terrestrial variables alongside the aquatic ones which could affect fire salamander occupancy (Manenti et al., 2009b) and therefore the presence of the larvae. Deadwood and woodpiles which could be a consequence of forestry could induce stress (Price et al., 2006) but it is a very important energy source for many stream organisms that are preyed on by fire salamander (Davic & Welsh, 2004).

In fire salamanders, predation risk is highest during the larval and early post-metamorphic stage and almost by zero if they achieve adulthood (Thiesmeier, 2004, Reinhardt et al., 2013). The fact that the presence of some fish species reduced the density of fire salamander larvae can be neglected in this study because there were no fish in any of these waters. In these fishless stream systems, they can take over the role as top predators and so it can be said that the greatest danger comes from the conspecific. Other animals that count as predators are the crows. Especially at the ponds that were just before drying out, crows were often spotted in them and possibly look for aquatic prey. This supports the previously mentioned hypothesis that predators could limit larvae occurrence. What known is that fire salamander larvae – both as predators and prey – serve as a keystone species, which stabilises the balance of the ecosystem community (Baumgartner et al., 1999, Davic & Welsh, 2004).

Conclusion

It cannot be confirmed that larvae at birth of the ponds were larger than those of streams. Habitats had an important effect on the total lengths of the individuals. Differences in total length are the results of the constantly changing environmental conditions like temperature, food availability and various other factors.

In general, the pond habitat is characterized as a spatially and temporally highly unpredictable or impermanent habitat that may represent sub-optimal conditions for larval growth, survival and metamorphosis (Arntzen & Van Belkom, 2020). In contrast, streams provide in spite of the potential larval drift which can arise by heavy rainfalls or storms, a more stable environment for the development of larvae (Hendrix et al., 2017).

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Attachments

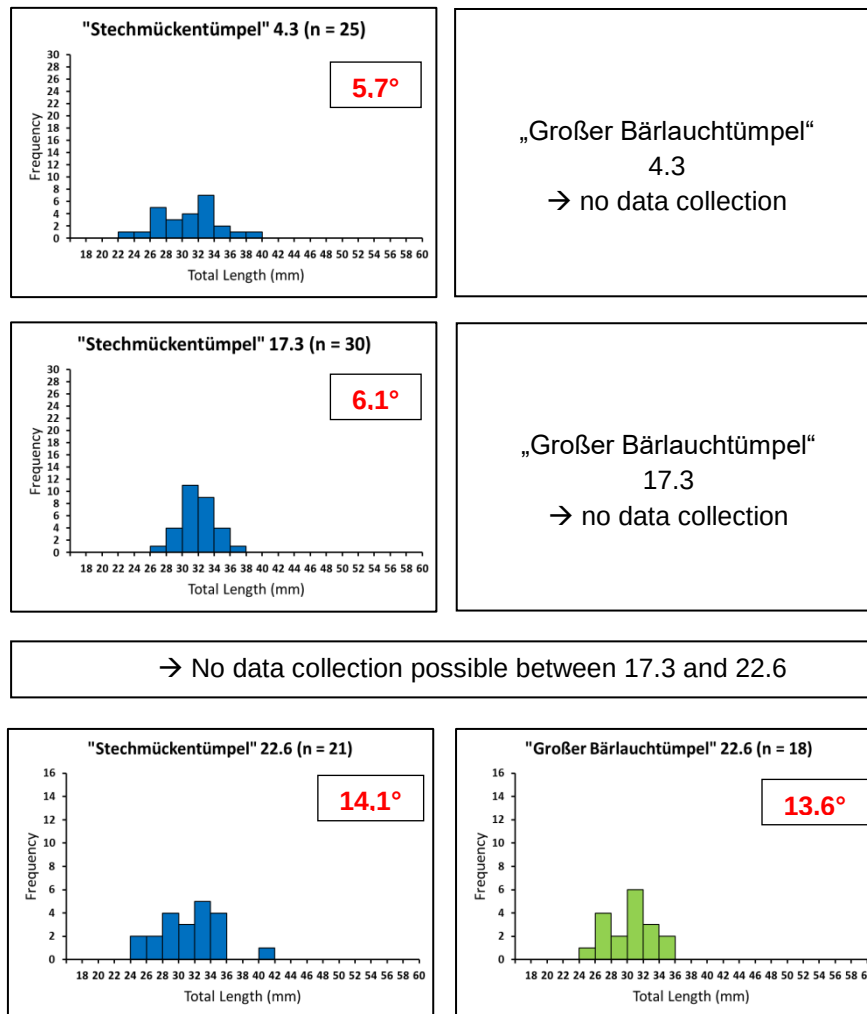
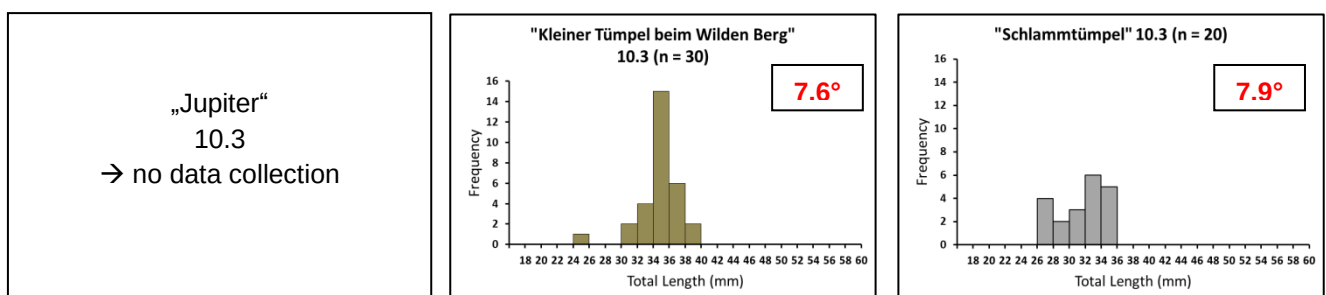
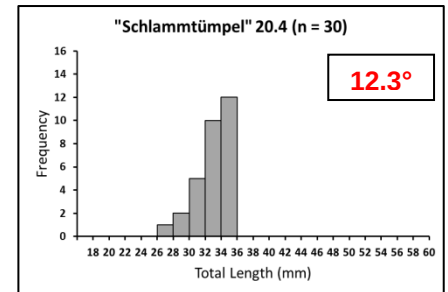
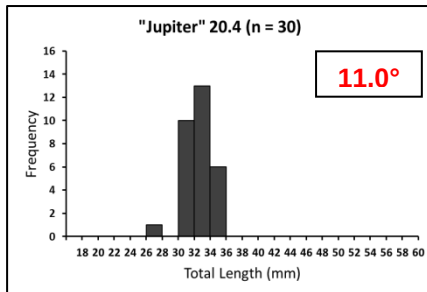
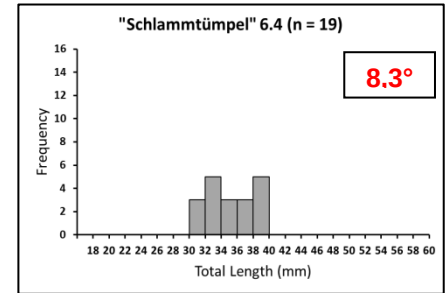
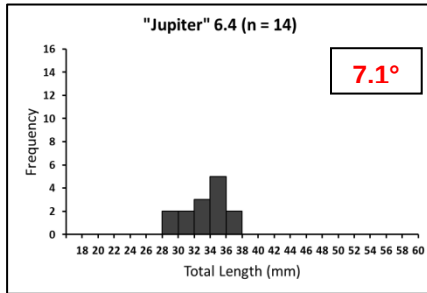
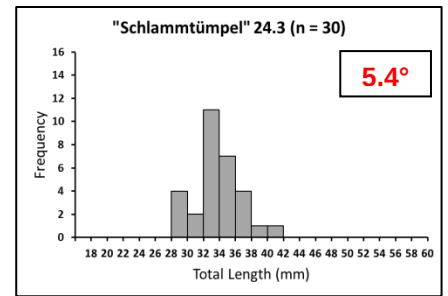
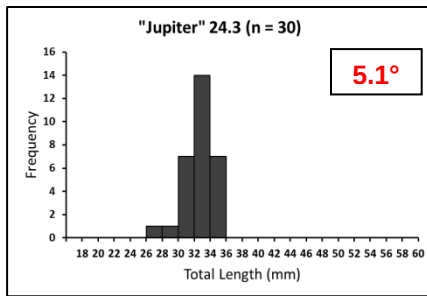
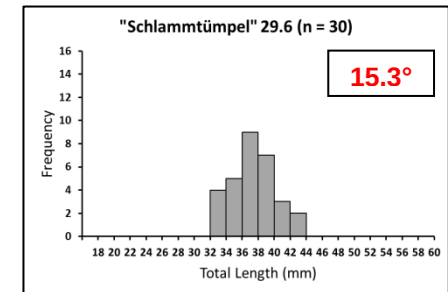
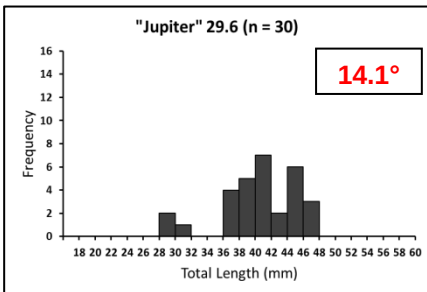
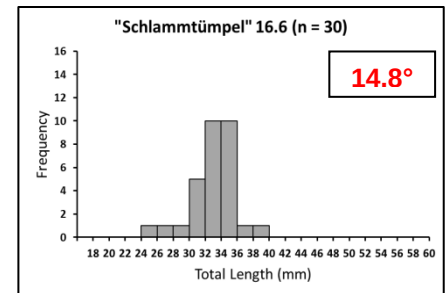
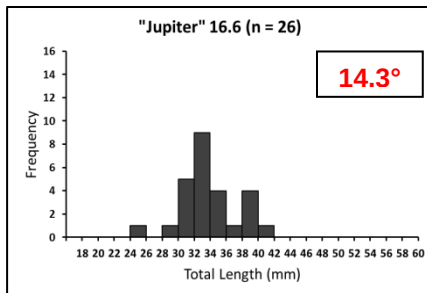


Figure 19: Individual histograms of the total lengths (mm) of the fire salamander larvae which were caught at “Schwarzenbergpark” (n = number of samples, number of captured fire salamander larvae).





→ No data collection possible between 20.4 and 16.6



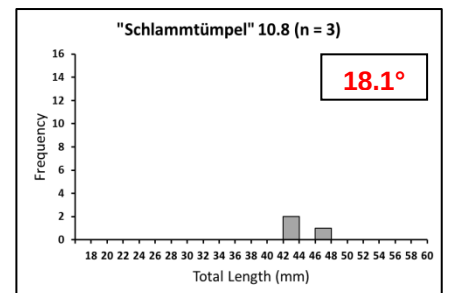
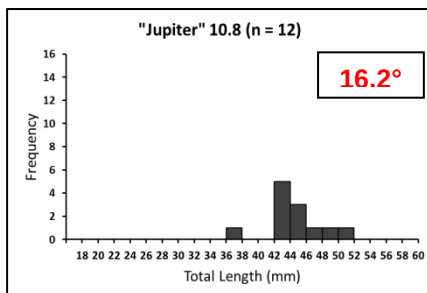
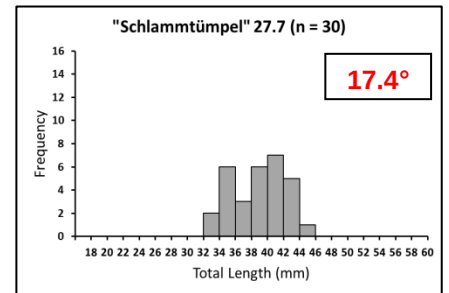
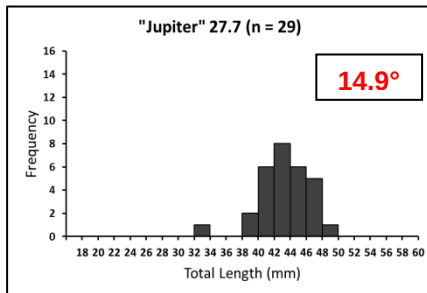
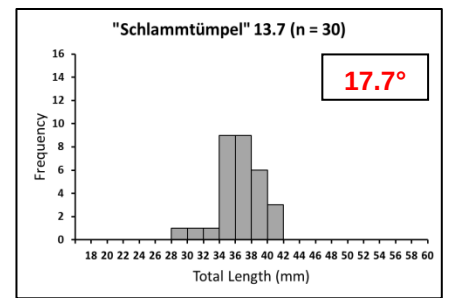
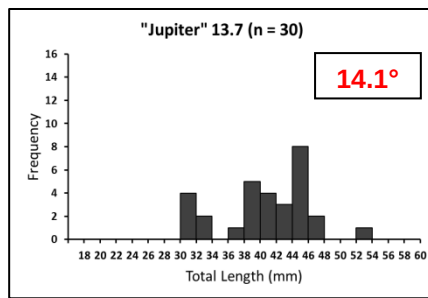
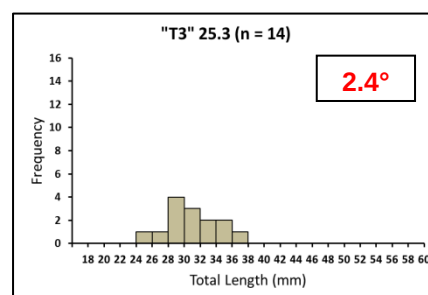
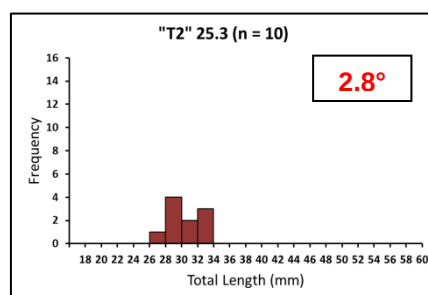
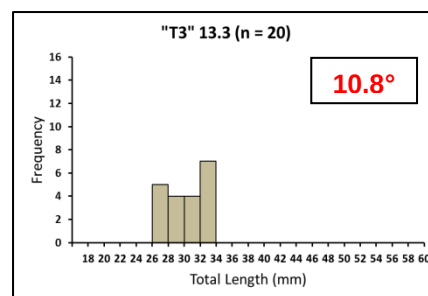
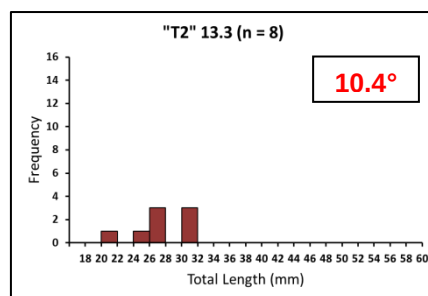
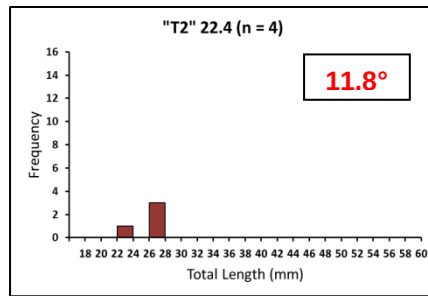
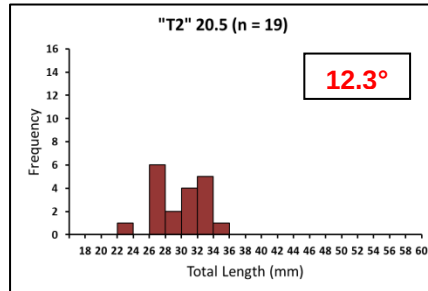


Figure 20: Individual histograms of the total lengths (mm) of the fire salamander larvae which were caught at “Maurer Wald” (n = number of samples, number of captured fire salamander larvae).

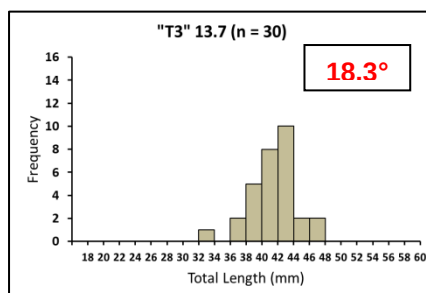
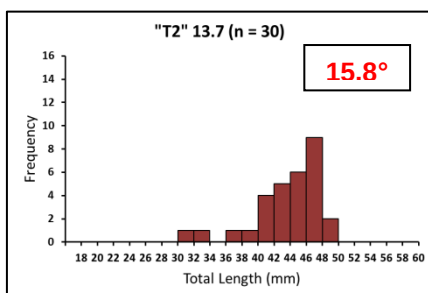
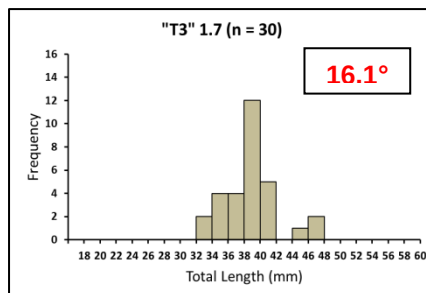
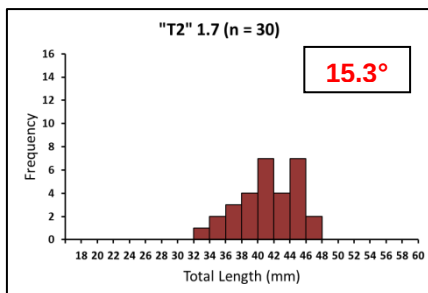
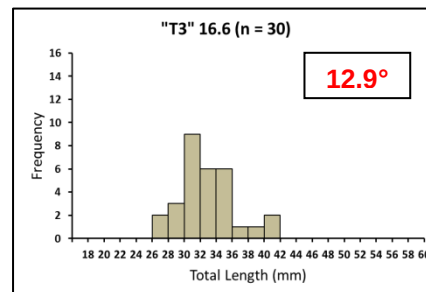
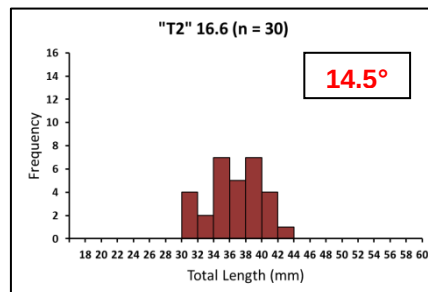
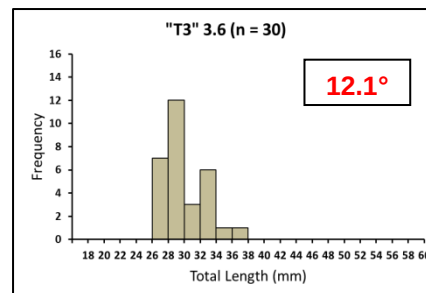
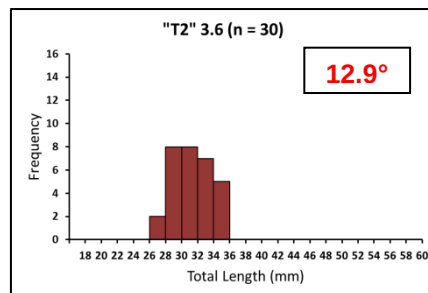




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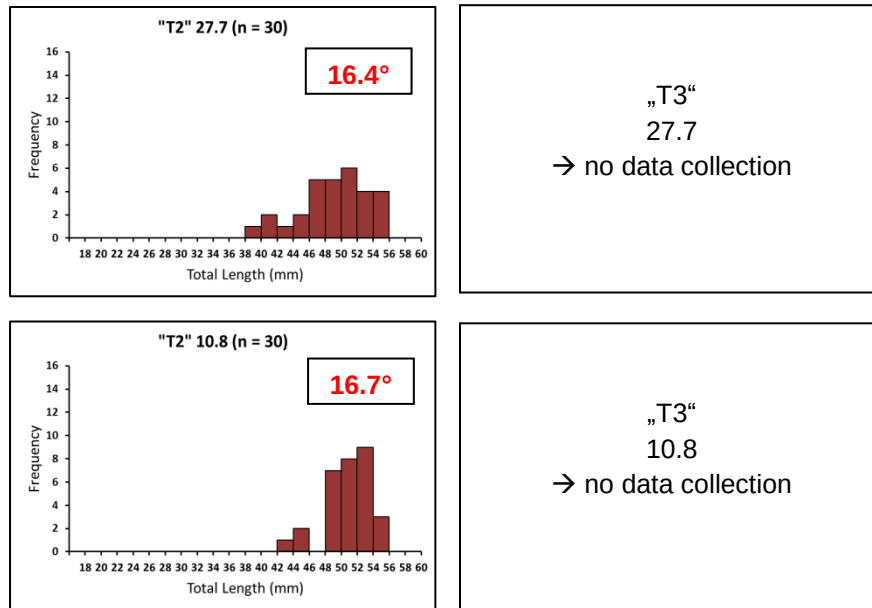
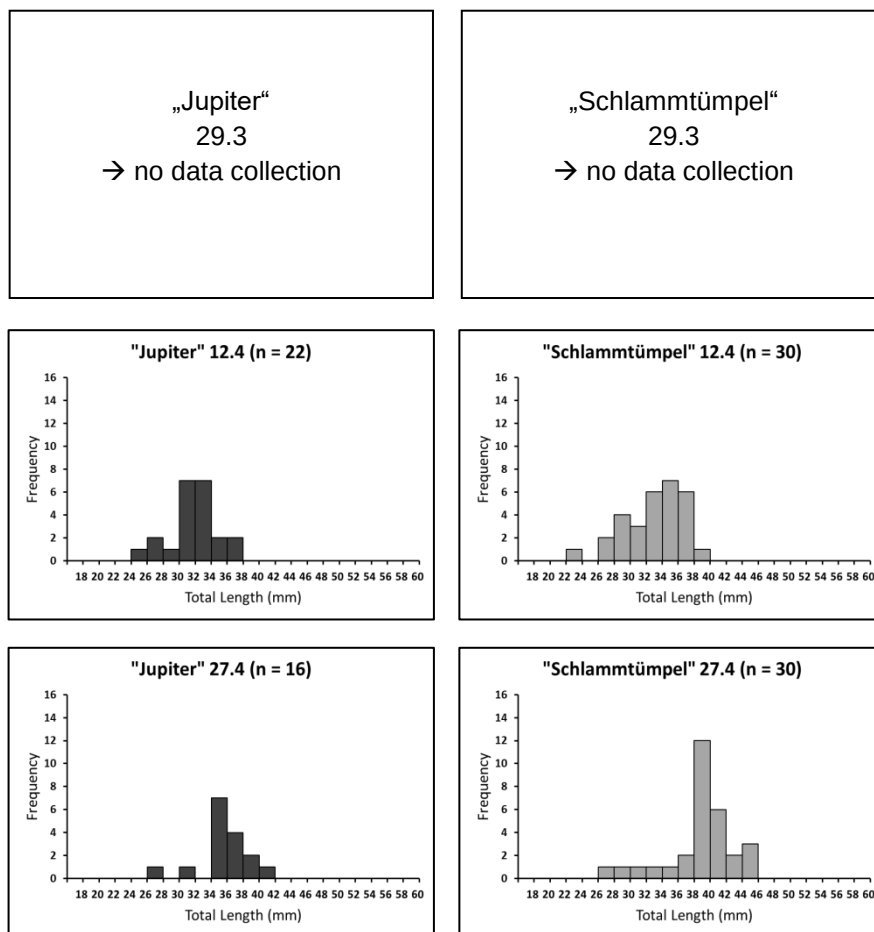


Figure 21: Individual histograms of the total lengths (mm) of the fire salamander larvae which were caught at "Lainzer Tiergarten" (n = number of samples, number of captured fire salamander larvae).



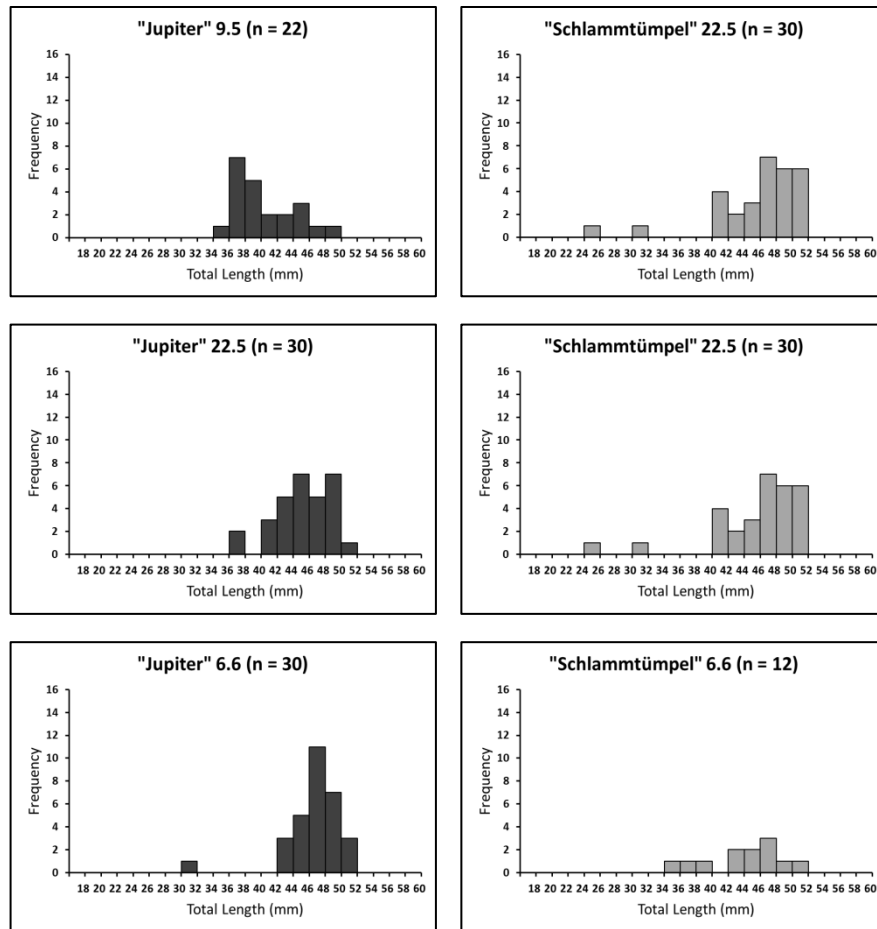
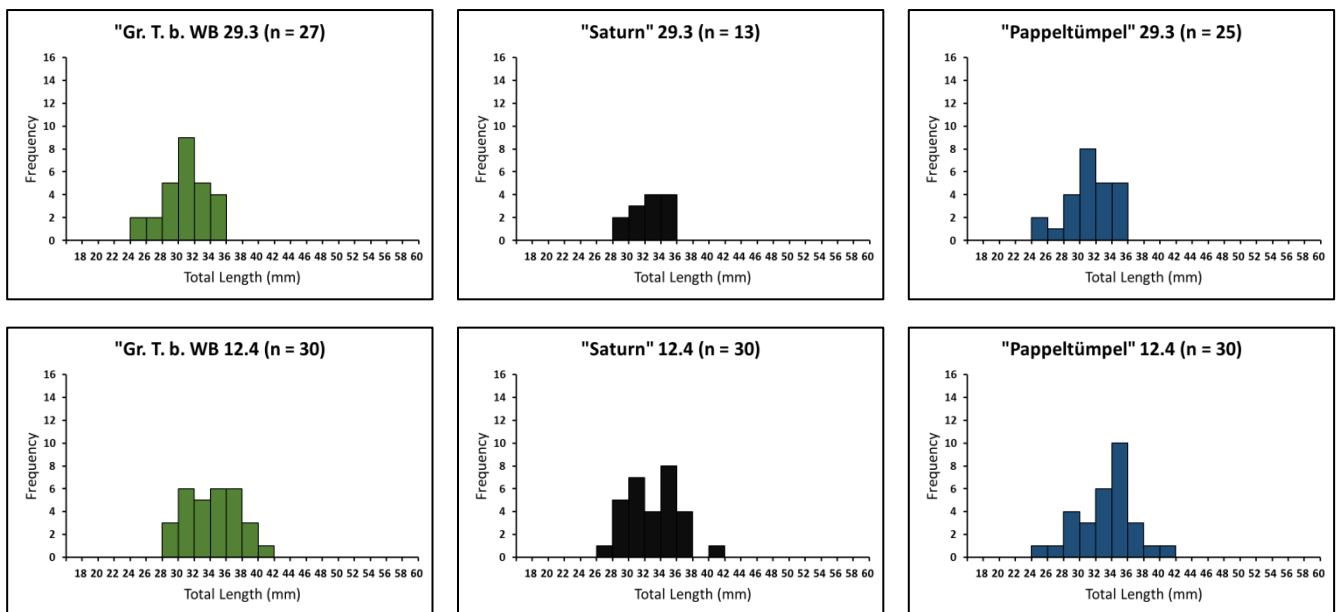


Figure 22: Individual histograms of the total lengths (mm) of the fire salamander larvae which were caught at “Jupiter” and “Schlammtümpel” (“Maurer Wald”) in 2018 (n = number of samples, number of captured fire salamander larvae).



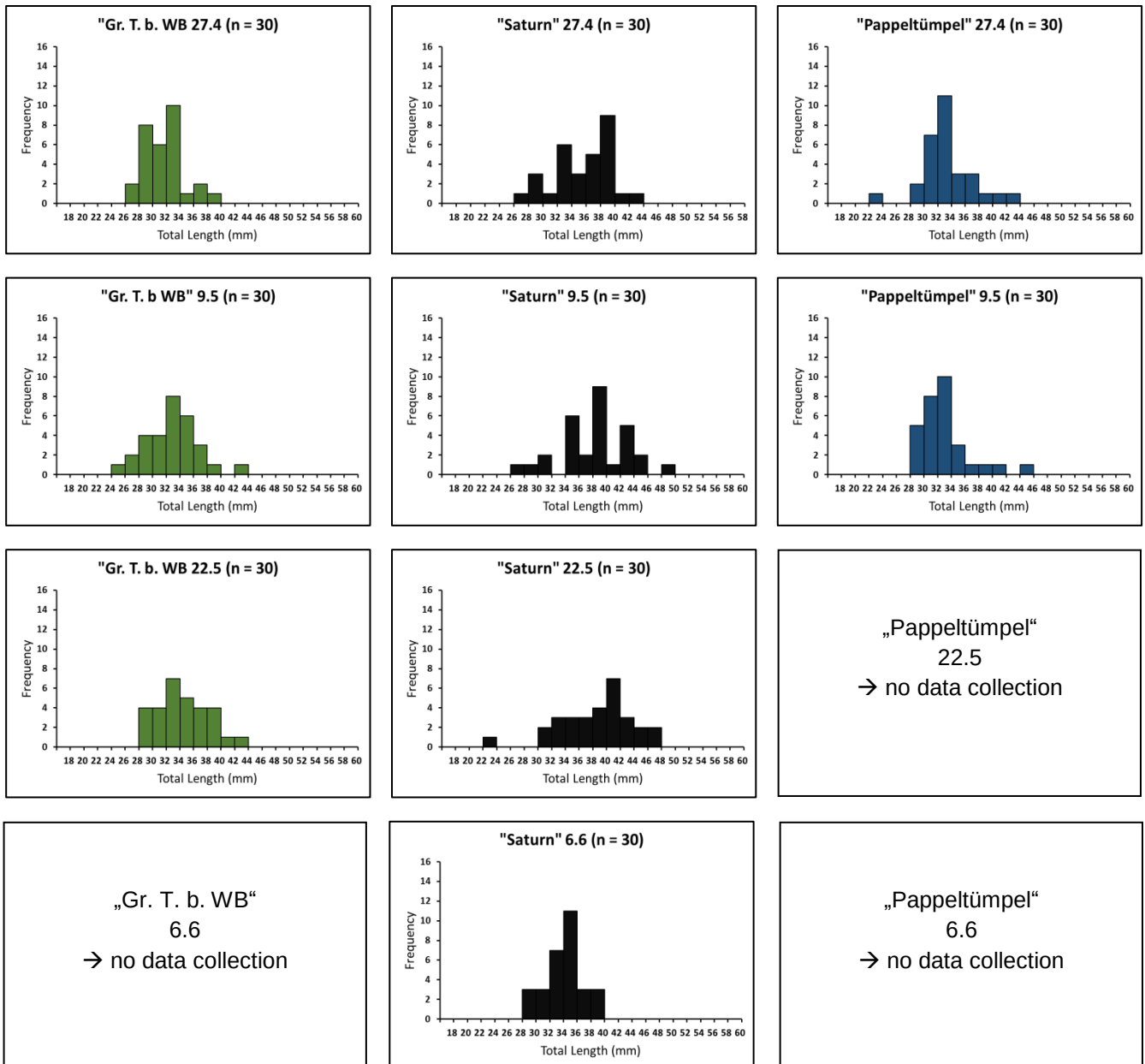
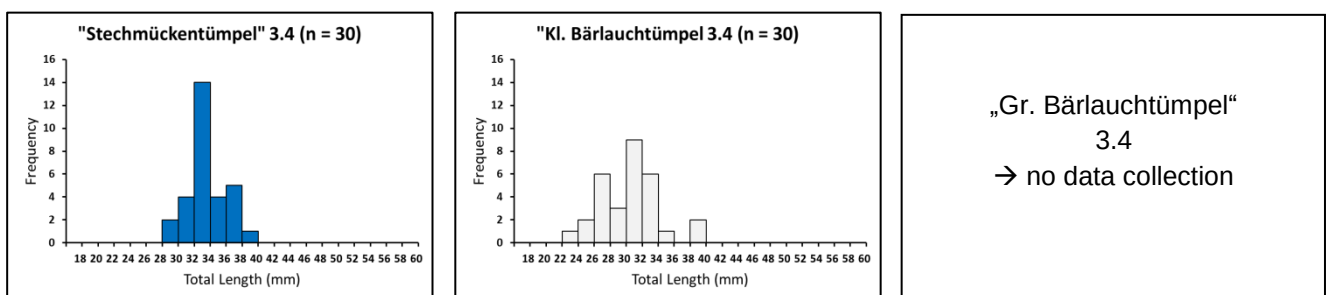


Figure 23: Individual histograms of the total lengths (mm) of the fire salamander larvae which were caught at “Großer Tümpel beim Wilden Berg” (“Gr. T. b. WB”), “Saturn” and “Pappeltümpel” (“Maurer Wald”) in 2018 (n = number of samples, number of captured fire salamander larvae).



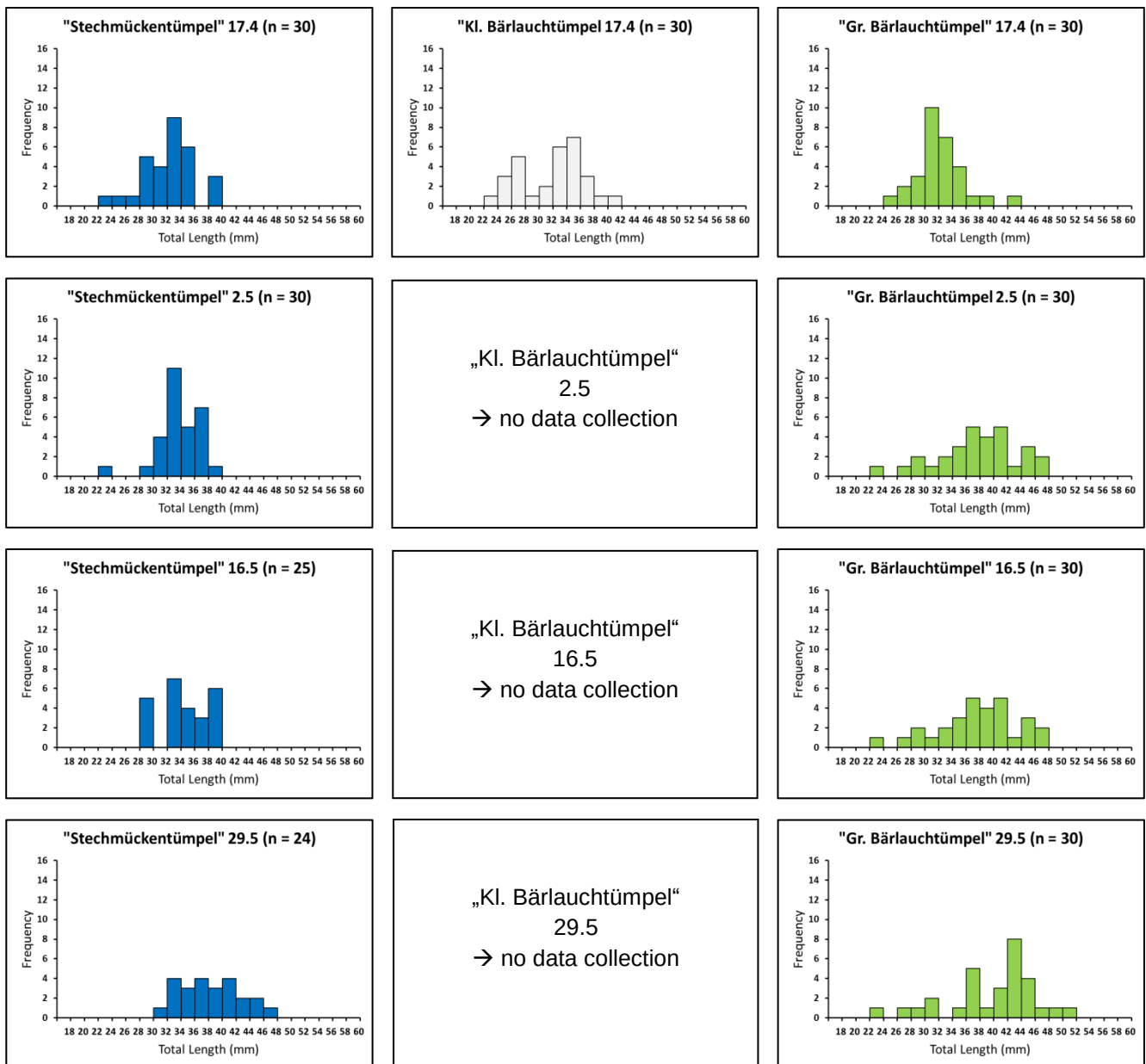
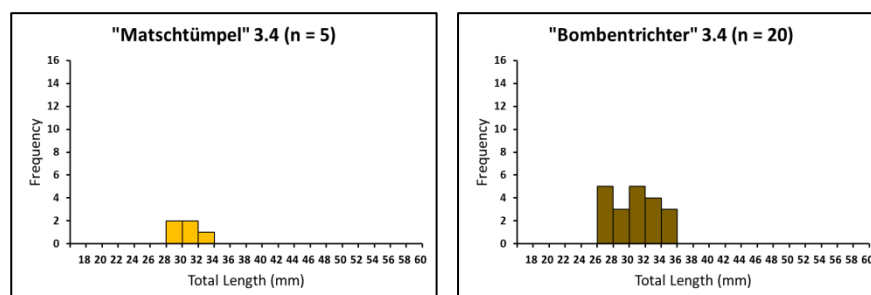


Figure 24: Individual histograms of the total lengths (mm) of the fire salamander larvae which were caught at “Stechmückentümpel”, “Kleiner Bärlauchtümpel” (“Kl. Bärlauchtümpel” and “Großer Bärlauchtümpel” („Gr. Bärlauchtümpel”) at “Schwarzenbergpark” in 2018 (n = number of samples, number of captured fire salamander larvae).



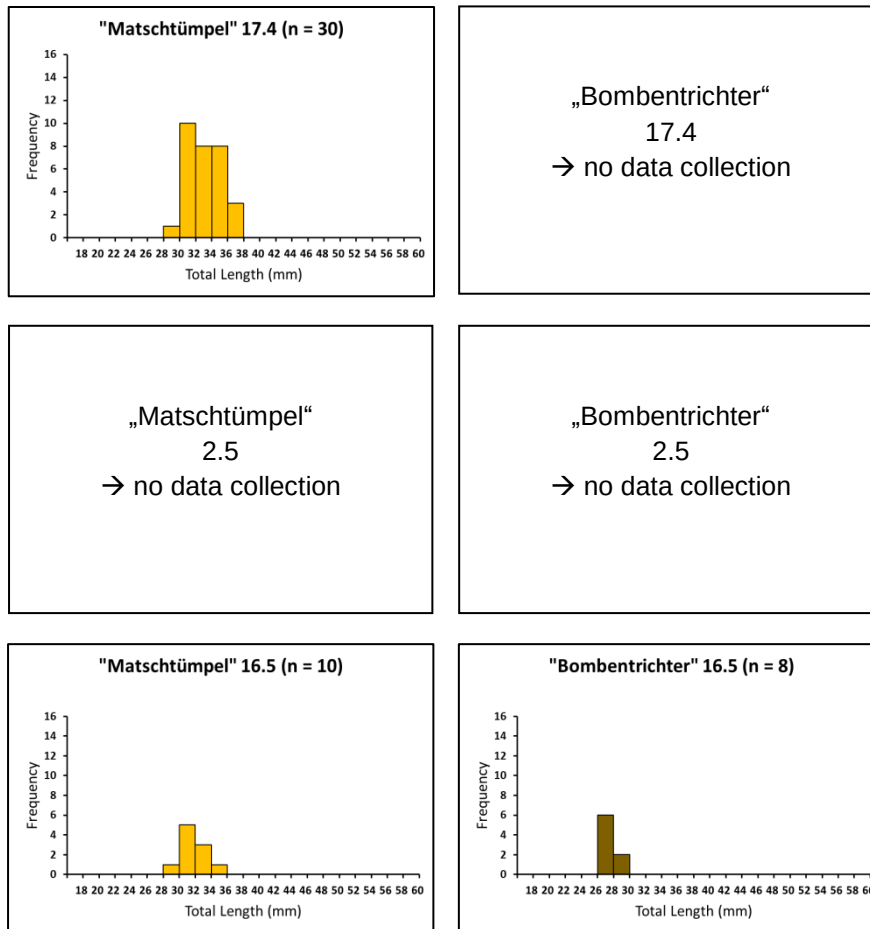


Figure 23: Individual histograms of the total lengths (mm) of the fire salamander larvae which were caught at “Matschtümpel” and “Bombenrichter” at “Schwarzenbergpark” in 2018 (n = number of samples, number of captured fire salamander larvae).

Zusammenfassung

Die Feuersalamanderlarven werden von weiblichen *Salamandra salamandra* in verschiedene aquatische Gewässer abgesetzt, wobei bei diesen hauptsächlich zwischen Still- und Fließgewässern unterschieden wird. Die vier räumlich getrennten Gebiete des Wiener Waldes waren der „Maurer Wald“, das „Neuwaldegg“ („Schwarzenbergpark“ und „Eckbach“), der „Lainzer Tiergarten“ („Auerochsengehege“ und „Lainzer Bach“) sowie der „Moosgraben“. Das Ziel dieser Studie war es die Größe der Larven aus diesen verschiedenen Gewässern zu untersuchen sowie die Daten von 2020 mit denen von 2018 zu vergleichen und mögliche Größenunterschiede zu erklären.

Die Feuersalamanderlarven wurden aus den verschiedenen Tümpeln sowie Bächen gefangen und fotografiert, um danach ihre Größe zu vergleichen. Die untersuchte Variable war die Totallänge, bestehend aus Körper- und Schwanzlänge. Aufgrund der stark wechselnden Wetterbedingungen vor allem dieses Jahr aber auch 2018 stellte sich heraus, dass die Larven mindestens bis Mitte Juni abgesetzt wurden. Im heurigen Jahr hatten die neu abgesetzten Individuen der wieder gefüllten Tümpel ungefähr die gleiche Gesamtlänge und wuchsen schneller – insbesondere im Tümpel „T2“ – als die erstabgesetzten Larven bei den Stillgewässern aber auch als bei den Bächen. Im Jahr 2018 gab es keine großen Unterschiede zwischen Feuersalamanderlarven aus Still- und Fließgewässern, mit Ausnahme der beiden Tümpel „Jupiter“ und „Schlammtümpel“ im „Maurer Wald“. Die Individuen aus diesen beiden Stillgewässern waren signifikant größer als die Larven aus den anderen aquatischen Lebensräumen. Im späteren Frühling wurden auch mehr kleinere Tiere in den Bächen als in den Tümpeln gefangen.

Allgemein waren die Feuersalamanderlarven aus einigen Tümpeln mit besseren Wachstumsbedingungen signifikant größer als aus anderen Gewässern. Es wurden keine großen Unterschiede zwischen den Individuen aus Still- und Fließgewässern festgestellt, mit Ausnahme des Größenwachstums der Larven von den wiedergefüllten Tümpeln. Ich gehe davon aus, dass die Unterschiede in der Gesamtlänge zwischen den Standorten und den verschiedenen Gewässern auf die Umweltbedingungen zurückzuführen sind vor allem in Hinsicht auf Temperatur sowie Futterverfügbarkeit.