

Identification of a New Stage in *Salamandra infraimmaculata* Metamorphosis

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Abstract

We examined various water bodies in which fire salamander (*Salamandra infraimmaculata*) larvae were growing and showed significant variation in growth rate and completion of metamorphosis depending on the habitat-seasonal pond, spring stream, or water hole. The phenomenon described herein involves larvae found in a water hole at a late stage of metamorphosis with highly developed gills, unable to leave the hole and complete metamorphosis. We hypothesize that the gills are an adaptation to the summer period, until the hole fills with water, allowing the larvae to complete metamorphosis and transition to terrestrial life.

Keywords

Salamandra infraimmaculata, Fire Salamander, Larval Development, Metamorphosis, Gill Retention, Habitat Variation, Seasonal Pond, Spring Stream, Water Hole, Amphibian Adaptation

1. Introduction

The genus *Salamandra* is widespread across Europe, North Africa, and the Near East. Numerous local populations have adapted to diverse climates and habitats, but their classification into species and subspecies remains controversial. [1] conducted a mitochondrial DNA analysis and proposed a taxonomy and distribution for *Salamandra* species in Europe and Mediterranean regions. Their phylogenetic analysis indicated six major monophyletic groups: *S. salamandra*, *S. algira*, *S. infraimmaculata*, *S. corsica*, *S. atra*, and *S. lanzai*, which collectively encompass over 14 subspecies [2]. According to their distribution, *S. algira*, *S. infraimmaculata*, and *S. corsica* located at the southern edges of their range encounter semi-arid conditions [3].

Although there are many aspects to *S. infraimmaculata* adaptation to dry conditions in semi-arid habitats [4] [5], relatively limited studies have been carried out on the effects of breeding places on that adaptation. The breeding places themselves, where larval development and complete metamorphosis take place, have been studied quite extensively, and those on the southern border of *S. infraimmaculata*'s distribution are described in detail [2]. However, relatively less information is available on metamorphosing and mature salamanders [2]. Two different metamorphosis activity patterns have been described for *S. infraimmaculata*: local year-round activity [6], and relatively long-distance migration to breeding places [7]. In the latter, the salamanders return to the same breeding places [2] or to new breeding places in the same area [7]. *Salamandra infraimmaculata* exhibits several adaptive traits that enable its persistence in highly variable and often ephemeral aquatic and terrestrial habitats across its range. Notable adaptations include phenotypic plasticity in larval development rates, allowing metamorphosis timing to adjust based on hydroperiod length [8]. Larvae can also exhibit extended gill retention and delayed metamorphosis under conditions of prolonged aquatic phases, which is especially relevant in isolated or seasonal water bodies [4]. Additionally, adults show behavioral adaptations such as site fidelity to reliable breeding sites and nocturnal activity patterns to minimize desiccation and predation risks [7]. These traits underscore the species' capacity for ecological flexibility and resilience in response to environmental unpredictability, making it an excellent model for studying habitat-driven developmental variation. In semi-arid habitats, there are many man-made water bodies that are suitable for *S. infraimmaculata* larval development and complete metamorphosis, but due to a lowering of the water level in the summer, the mature salamanders and metamorphosed juveniles are unable to move back to their terrestrial habitat; eventually, these salamanders die [2] [9]. *S. infraimmaculata* thus face a significant danger in semi-arid habitats where water bodies are limited and the many man-made pits are essentially traps. Estimations of damage to salamander populations are very important for nature conservation. In the present study, the breeding places of *S. infraimmaculata* are evaluated and described, along with the potential damage conferred by water pits as potential traps for mature salamanders.

[8] investigated various breeding sites of *S. infraimmaculata*, such as springs, streams, water holes, winter pools, and reservoirs. They found a high number of salamander larvae in springs and streams (503), and water holes (48), and relatively few in winter pools. They closely examined the water holes to assess the impact on *S. infraimmaculata*, where breeding sites are scarce. In Israel, salamanders breed during the fall and winter seasons. The larvae grow and undergo their transformation in the spring or early summer, contingent upon the ecological conditions of their aquatic environment [2]. During the summer, if salamanders become trapped in water pits, the larvae face unique conditions-increasingly warm water with low oxygen content; they are unable to leave the pit until the winter rains arrive. A fair number of articles have dealt with the adap-

tation of salamander larvae to different habitats and it seems that water temperature, oxygen, and food are the most important factors affecting metamorphosis.

Research indicates that under hypoxic (low-oxygen) conditions, *S. infraimmaculata* larvae develop larger and denser external gills. In *Ambystoma tigrinum* larvae, this morphological change has been shown to facilitate gas exchange, compensating for the reduced oxygen availability in the environment [10]. The development of these structures is influenced by environmental factors, especially temperature and the availability of dissolved oxygen in the water. The external gills of amphibian larvae, particularly in species such as *S. infraimmaculata*, play a vital role in gas exchange. The increased surface area provided by larger gills allows for greater oxygen diffusion, which is essential for maintaining metabolic functions and overall physiological homeostasis [11].

An exceptionally large *S. infraimmaculata* larva with strikingly colorful gills was discovered in an artificial water well. This well lacked access to land, which hindered the salamander's metamorphosis, causing it to remain in its larval stage while developing adult coloration. It was likely to have consumed all of its siblings, as no other larvae were present in the water. It was relocated to a more natural habitat to prevent starvation. It should be noted that artificial water purification in pits that are used for the breeding of salamanders has been extensively described in Israel at the southern limit of *S. infraimmaculata*'s distribution [8] [12] [13].

2. Material and Methods

Based on a previous study of many water bodies in which salamander larvae were growing, one water hole was chosen in which there is water all summer long, but the salamanders cannot leave it because of its steep walls (Figure 1) [2] [14].

The breeding habitats of *Salamandra infraimmaculata* (fire salamander) in northern Israel, including the Upper Galilee and Golan Heights, often consist of temporary water bodies such as seasonal ponds, spring-fed streams, and particularly **water pits** or depressions that collect rainwater. These environments exhibit considerable seasonal and inter-annual variability in physical and chemical parameters (e.g., [4]-[6]).

Every 2 weeks, three samples were taken from the water body using a net with a pore size of 450 μm . The samples were collected from a depth of about 10 cm - 30 cm. The volume of water that passed through the net was determined by the net's dimensions and the area of the water that the net traversed [15].

The larval period refers to the time during which larvae emerge. In this study, the larval period was adjusted by ± 14 days, depending on how often we visited the breeding site. Every 2 weeks, we captured 5 - 7 larvae of each species from a depth of roughly 10 cm - 120 cm using a dip-net. These captures took place at three different locations within the water pit, totaling about 15 individuals per species [16]. We measured the full length of each larva with a caliper (± 0.5 mm) and immediately released it at the point of capture without marking it.



Figure 1. Various breeding locations of *S. inframaculata* in northern Israel. A. Sasa pond. B. Humma spring. C. Gush Halav pond. D. Dan stream. E. Water pits in northern Israel where salamander larvae were found.

3. Results

Figure 2 depicts the various stages of color and gill development in larvae from different water bodies, from spawning until just before metamorphosis.

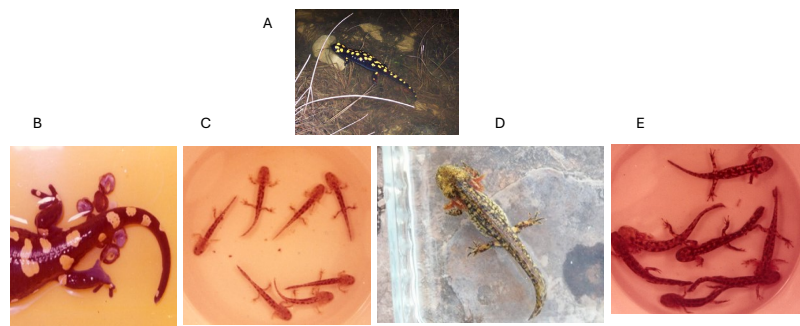


Figure 2. Different stages of larval color and gill development from spawning until just before metamorphosis. A. Salamander at spawning. B. Larvae released into the water. C. Young larvae after 1 to 2 weeks. D. Developed larvae with no signs of metamorphosis onset. E. Larvae at various stages of metamorphosis, showing initial coloration and gill degeneration.

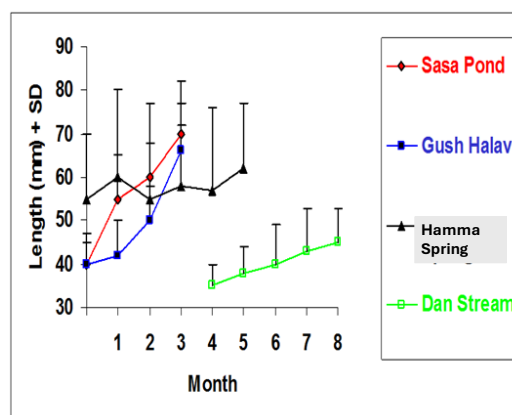


Figure 3. Salamander larvae spawned in different water bodies (winter ponds, springs, and streams) in northern Israel, and growing and completing metamorphosis at different times [2] [14].

Salamander larvae are spawned in northern Israel within a relatively small number of distinct water bodies, where environmental conditions influence their growth rate, metamorphosis, and coloration (**Figure 2** and **Figure 3**). Growth curves vary among these water bodies. In temporary winter ponds (such as those at Sasa and Gush Halav), growth is rapid—especially during the winter months—and typically lasts about three months. In contrast, in springs and streams, the growth period is extended, ranging from five to six months. The larger standard deviations observed, particularly in Humma Spring (**Figure 3**), indicate significant variation in larval length.

In waterholes where salamander larvae are unable to leave during the spring or summer metamorphosis period, the water temperature tends to be relatively high and the oxygen content low. If a larva survives and develops large gills, it may be able to complete its metamorphosis during the following autumn and winter, thereby completing its life cycle (**Figure 4**). That is based on studies by Degani *et al.* [17].



Figure 4. A salamander larva with post-metamorphosis colors and highly developed gills found in a water hole from which it cannot escape. A. Larva with adult colors and developed gills adapted to low oxygen uptake. B. Water hole in which a larva was found with metamorphosis colors and developed gills but no metamorphosis markers.

Water Pit Environment of *Salamandra infraimmaculata*:

The breeding habitats of *Salamandra infraimmaculata* (fire salamander) in northern Israel, including the Upper Galilee and Golan Heights, often consist of temporary water bodies such as seasonal ponds, spring-fed streams, and particularly water pits or depressions that collect rainwater. These environments exhibit considerable seasonal and inter-annual variability in physical and chemical parameters.

The size and concentration of external gills in *S. infraimmaculata* larvae are adaptive traits that respond dynamically to the oxygen concentration in their aquatic environment. Under low-oxygen conditions, these larvae exhibit a notable

increase in both size and density of their gills. This morphological adaptation is crucial for enhancing respiration efficiency, thereby improving the chances of survival in hypoxic environments.

4. Discussion

This study is the first to show a special adaptation of *S. infraimmaculata* to a water pit with ample water in the winter but low levels in the summer when the salamanders are metamorphosing, preventing them from moving onto land [2] [14]. The gills continue developing and apparently allow continued breathing in the water (Figure 4). When the first heavy winter rains fall [18] [19], the pit refills with water, and we hypothesize that the salamanders can then complete their metamorphosis and move to a full life on land. However, validation of this hypothesis requires further research, which remains difficult to carry out. Such pits in which salamanders spawn have been described in detail in several studies on *S. infraimmaculata* at the southern border of its distribution [2], but the adaptation of developed gills has not. An exceptionally large fire salamander (*S. infraimmaculata*) larva with vibrant, colorful gills was described by Ramy (Herpetology & Wildlife herpinglebanon). This salamander larva was found in an artificial water well that lacked access to land, similar to the present study, delaying its metamorphosis and causing it to stay in its larval stage while developing adult coloration (Figure 5).



Figure 5. The head of a salamander in a pit in Lebanon that underwent metamorphosis to an adult but the gills remained because it could not get out of the water and move onto land. <https://www.instagram.com/herpinglebanon/p/Cw5QI26sgmP/>

Thus, a new phase has been discovered in *S. infraimmaculata* larvae at the southern edge of their distribution range in a man-made water pit. After molting, the larva changes its coloration to match that of a mature salamander; however, its gills do not disappear, but rather become more developed. We hypothesize that the gills only disappear when the pit fills with rainwater, allowing the

young salamander to move onto land. This process contrasts with the many previous studies describing salamander metamorphosis, where the color change and gill disappearance occur simultaneously as the larva transitions to a terrestrial form (Figure 6).



Figure 6. Two developmental pathways of *S. infraimmaculata* larvae. A. The usual pathway described in many studies. B. In water cisterns, mostly man-made, larvae are found that have undergone metamorphosis but still have developed gills. These gills allow them to remain in the water, especially in the summer, until the cistern refills.

5. Conclusion

The ability of *S. infraimmaculata* larvae to modify their gill size and density in response to oxygen availability exemplifies an adaptive strategy to cope with environmental variability. This morphological plasticity underscores the importance of external gills in the survival and fitness of amphibian larvae in diverse aquatic habitats.

Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

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