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Reproduction and Development in Salmanders

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Opinion Article

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DESCRIPTION

Many salamanders do not use vocalisations and in most species the sexes look alike, so they use olfactory and tactile cues to identify potential mates, and sexual selection occurs. Pheromones play an important part in the process and may be produced by the abdominal gland in males and by the cloacal glands and skin in both sexes. Males are sometimes to be seen investigating potential mates with their snouts. In Old World newts, Triturus spp., the males are sexually dimorphic and display in front of the females. Visual cues are also thought to be important in some Plethodont species.

Except for terrestrial species in the three families Plethodontidae, Ambystomatidae, and Salamandridae, salamanders mate in water. The mating varies from courtship between a single male and female to explosive group breeding. In the clade Salamandroidea, which makes up about 90% of all species, fertilization is internal. As a general rule, salamanders with internal fertilization have indirect sperm transfer, but in species like the Sardinian brook salamander, the Corsican brook salamander, the Caucasian salamander and the Pyrenean brook salamander, the male transfer his sperm directly into the female cloaca.

For the species with indirect sperm transfer, the male deposits a spermatophore on the ground or in the water according to species, and the female picks this up with her vent. The spermatophore has a packet of sperm supported on a conical gelatinous base, and often an elaborate courtship behavior is involved in its deposition and collection. Once inside the cloaca, the spermatozoa move to the spermatheca, one or more chambers in the roof of the cloaca, where they are stored for sometimes lengthy periods until the eggs are laid. In the Asiatic salamanders, the giant salamanders and Sirenidae, which are the most primitive groups, the fertilization is external. In a reproductive process similar to that of typical frogs, the male releases sperm onto the egg mass. These

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salamanders also have males that exhibit parental care, which otherwise only occur in females with internal fertilization.

Three different types of egg deposition occur. Ambystoma and Taricha spp. spawn large numbers of small eggs in quiet ponds where many large predators are unlikely. Most dusky salamanders (Desmognathus) and Pacific giant salamanders (Dicamptodon) lay smaller batches of medium-sized eggs in a concealed site in flowing water, and these are usually guarded by an adult, normally the female. Many of the tropical climbing salamanders (Bolitoglossa) and lungless salamanders (Plethodontinae) lay a small number of large eggs on land in a well-hidden spot, where they are also guarded by the mother. Some species such as the fire salamanders (Salamandra) are ovoviviparous, with the female retaining the eggs inside her body until they hatch, either into larvae to be deposited in a water body, or into fully formed juveniles.

In temperate regions, reproduction is usually seasonal and salamanders may migrate to breeding grounds. Males usually arrive first and in some instances set up territories. Typically, a larval stage follows in which the organism is fully aquatic. The tadpole has three pairs of external gills, no eyelids, a long body, a laterally flattened tail with dorsal and ventral fins and in some species limb-buds or limbs. Pond-type larvae may have a pair of rod-like balancers on either side of the head, long gill filaments and broad fins. Stream-type larvae are more slender with short gill filaments, narrower fins and no balancers, but instead have hind limbs already developed when they hatch. The tadpoles are carnivorous and the larval stage may last from days to years, depending on species.

Sometimes this stage is completely bypassed, and the eggs of most lungless salamanders (Plethodontidae) develop directly into miniature versions of the adult without an intervening larval stage. Not all species of salamanders follow this path. Neoteny, also known as paedomorphosis, has been observed in all salamander families, and may be universally possible in all salamander species. In this state, an individual may retain gills or other juvenile features while attaining reproductive maturity. The changes that take place at metamorphosis are under the control of thyroid hormones and in obligate neotenes such as the axolotl (Ambystoma mexicanum), the tissues are seemingly unresponsive to the hormones.

In other species, the changes may not be triggered because of underactivity of the hypothalamus-pituitary-thyroid mechanism which may occur when conditions in the terrestrial environment are too inhospitable. This may be due to cold or wildly fluctuating temperatures, aridity, lack of food, lack of cover, or insufficient iodine for the formation of thyroid hormones. Genetics may also play a part. The larvae of tiger salamanders (Ambystoma tigrinum), for example, develop limbs soon after hatching and in seasonal pools promptly undergo metamorphosis. Other larvae, especially in permanent pools and warmer climates, may not undergo metamorphosis until fully adult in size. Other populations in colder climates may not metamorphose at all, and become sexually mature while in their larval forms. Neoteny allows the species to survive even when the terrestrial environment is too harsh for the adults to thrive on land.

By the end of the larval stage, the tadpoles already have limbs and metamorphosis takes place normally. In salamanders, this occurs over a short period of time and involves the closing of the gill slits and the loss of structures such as gills and tail fins that are not required as adults. At the same time, eyelids develop, the mouth becomes wider, a tongue appears, and teeth are formed. The aqueous larva emerges onto land as a terrestrial adult.