

Transformers

The bizarre life history of Montana's barred tiger salamanders

BY PAUL J. DRISCOLL

At first glance, there's nothing remarkable about the Axolotl Lakes, ten small lakes and potholes that sit among subalpine meadows and dry, timbered slopes in southwestern Montana roughly 15 miles southeast of Ennis. It's a scenic area, to be sure, but nothing out of the ordinary in a state filled with beautiful landscapes.

Yet beneath the water surface of two lakes in the basin lives what may be the strangest creature in Montana. It's the axolotl, (*ack-suh-LOT-uhl*), a unique and biologically baffling form of the barred tiger salamander.

Barred tiger salamanders are, for the most part, ordinary amphibians. They live throughout the central United States, central Canada, and northern Mexico. In Montana they are found across the central and eastern parts of the state as well as in the Tobacco Valley near Eureka. ▶▶



ARRESTED DEVELOPMENT Shown here is the larval form of the barred tiger salamander. Some individuals remain like this throughout their life while also developing sexual organs. These sexually mature "teenage" salamanders are known as axolotls. The similar looking true axolotl is a different salamander species native to central Mexico.

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Salamanders such as the barred tiger species, as well as frogs and toads, are in the taxonomic class amphibia, which means “double life” in Greek (*amphi* for “two” and *bio* for “life”). Their first life stage occurs in water, usually as larvae that hatch from eggs. Like the tadpoles of frogs, salamander larvae then metamorphose, or alter form, into adults, which crawl up onto land to live out their lives.

It’s an ancient story stretching back hundreds of millions of years. Amphibians were among the earliest life forms to evolve from water creatures into terrestrial ones.

Over time, barred tiger salamander populations adapted to their unique environments in North America. For instance, those in the central Great Plains evolved to spawn in buffalo wallows and prairie potholes that temporarily filled with snowmelt in spring. Populations in the Rocky Mountain West evolved to spawn in high-elevation fishless ponds and lakes, such as those in the Axolotl Lakes Basin.

The larval phase of salamanders differs slightly from that of frogs and toads. The oxygen-filtering gills are external and look like fine feathers extending behind the head. Also, a salamander larva has tiny legs and feet at hatching, unlike limbless frog and toad tadpoles. Like those of frogs and toads, salamander larvae resemble small fish as they slice through their natal pool powered by a single caudal (tail) fin.

“After a few months, stress causes a release of hormones that trigger metamorphosis,” says Bryce Maxell, co-author of *Amphibians and Reptiles of Montana* and a senior zoologist with the Montana Natural Heritage Program. “Usually the stress comes from lack of food, or lots of predators, or crowded conditions as the pool where the larvae live dries up. The salamanders develop lungs and other adaptations in order to move to terrestrial habitats and away from these stressors.”

In some pothole breeding pools that quickly shrink in the hot summer sun,

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Maxell adds, the larvae resort to cannibalism to rapidly gain size and weight so they will metamorphose more quickly.

As a larva transforms its shape, the salamander’s trademark long tail begins to grow, and the legs and feet grow bigger. Internal lungs develop, external gills shrink and are absorbed into the head, and the caudal fin is absorbed into the growing tail. Eventually, the fully metamorphosed salamander emerges from the shallows onto dry land to live, normally returning to water only in spring to breed.

At least that’s the way it usually works.



SHAPE SHIFTERS This illustration shows the metamorphosis of a tiger salamander from the advanced larval stage (top) to the adult terrestrial phase (bottom). Stressors such as aquatic predators and shrinking natal pools cause a larva to release hormones that trigger the transformation. The amphibian’s caudal (tail) fin is absorbed into the growing tail, legs and feet grow larger, external gills disappear, internal lungs grow, and the animal crawls up onto land to live. Occasionally, developing salamanders remain in their larval form and stay in water but still become sexually mature. These are commonly known as axolotls.

In some deep-water lakes and ponds, larvae do not need to race through the larval stage to metamorphose. Because the breeding site never dries up and predators and other stressors aren’t present, they can take their time—and they do, often remaining in the aquatic larval form for two or more years.

Occasionally, some barred tiger salamanders actually stay in the larval form while becoming sexually mature and able to reproduce. These atypical permanent larvae

are commonly known as axolotls.

Axolotls survive well in certain aquatic habitats, usually deeper waters without competition from egg-devouring crayfish or predation by trout or other fish. They average 6 to 10 inches long and can grow up to a foot—much larger than an adult barred tiger salamander, which rarely reaches 7 inches long.

Because they retain the external gills and caudal fin of the larval stage, even while attaining mature reproductive organs, axolotls are considered by scientists to be “paedomorphs” (from the Greek *paedo* for “child” and *morph*)—sexually mature animals that retain juvenile physical characteristics. Axolotls are also sometimes described as “neotenes”—animals in natal form with sexually mature organs.

Some axolotls eventually continue their development and become terrestrial, while others remain in their larval aquatic form all their lives. It depends on the environment. “Axolotls are found in high-elevation lakes that don’t have a lot of good terrestrial habitat,” says Maxell. He explains that for some barred tiger salamanders in these challenging environments, it’s better to live out their lives in water as larvae rather than take their chances on land.

A barred tiger salamander’s axolotl form is similar to but not exactly the same as the more famous true axolotl, a unique salamander species found only in several mountain lakes near Mexico City. This salamander, which almost always stays locked in its larval form, has a large head, lidless eyes, external gills, and limbs with thin digits. In the ancient Aztec language, axolotl is loosely translated as “water dog” or “water monster.”

True axolotls of central Mexico differ from the axolotl form of Montana’s salamanders in one key respect. The Mexican species is not a temporary phase. Instead, it is hardwired to its permanently larval life and will never metamorphose into an adult terrestrial salamander under natural conditions.

The Mexican axolotl has long commanded the attention of scientific researchers, particularly those investigating evolution and species development.

True axolotls are nearly extinct in their native habitat. Human development has pol-



SEPARATE SPECIES The terrestrial adult barred tiger salamander (above) is found near ponds and wetlands across central and eastern Montana. The true Mexican axolotl (below), though appearing identical to the larval form of the barred tiger salamander, is a separate species and remains in a permanent aquatic larval form. The axolotls in Montana are a life form of the barred tiger salamander and sometimes continue to metamorphose and become terrestrial.



CLOCKWISE FROM LEFT: PUBLIC DOMAIN/JOSÉPHE HUÉT, 1866; JIM HERRLY; JOHN P. CLARE/CAUDATA.ORG

luted their lake and canal habitats, while imported tilapia fish eat the vegetation where they lay their eggs. Yet in laboratory aquariums around the world, true axolotls are thriving. For more than a century, scientists have propagated breeding lines in order to study another amazing aspect of this species: its ability to perfectly regenerate severed limbs, tails, and select body parts. Not surprisingly, a great deal of medical research focuses on this rare attribute.

According to Maxell, barred tiger salamanders remain common throughout much of Montana. James Collins, an expert on the global decline of amphibians and co-author of *Extinction in Our Times*, told me he thinks barred tiger salamanders in the American West may be among the species that end up surviving the viruses and fungi causing the disappearance of many other amphibians. Because these salamanders have “developmental flexibility”—such as the ability to become cannibalistic as larvae or take on the axolotl form—they have been able to survive in many different climate zones and terrain. “Barred tiger salamanders may be among the lucky ones,” Collins said.

Still, areas with barred tiger salamanders exhibiting the axolotl life strategy are quite rare. In Montana, they are known to occur only in the Axolotl Basin and a few small lakes near West Yellowstone. Recent surveys conducted by the Montana Natural Heritage Program and Bureau of Land Management found axolotls in only two of the ten lakes and potholes in the Axolotl Basin and none in the one actu-

ally named Axolotl Lake. That lake and perhaps others in the basin historically contained axolotls, but trout transplanted there more than a century ago apparently wiped them out.

Whether the Axolotl Basin continues to house its namesake inhabitants into the future will likely depend on the ecological health and stability of a few small lakes in this remote corner of Montana. 🐸