



Endurance Test

A salamander is a living paradox in a world of heat and drought.

Story and Photographs
by Christopher J. Norment

On a hot desert day in September, when water is mostly fantasy, an Inyo Mountains slender salamander feels like the epitome of contradictions. Hold one in the palm of your hand: it seems as vulnerable as a naked, newly hatched sparrow. What is it doing here, among the radiant rocks and cacti, the brittle bursage and torrents of light? A lungless salamander that breathes only through its moist skin, the species was not discovered until 1973. It is one of only two desert salamander species in the world. Providing almost no barrier to the evaporation of water, its skin is thin as parchment, and yet it hides a wonderful toughness. Lungless salamanders are very good at taking their time and hanging on. They need little, tolerate much, and can endure.

The Inyo Mountains slender salamander (*Batrachoseps campi*) occupies a total of about fifty acres of stream-side and trickling spring habitat scattered in twenty rugged canyons on the eastern and western slopes of the Inyo Mountains. This desert range rises to an elevation of 11,000 feet east of—and thus in the rain shadow of—California's Sierra Nevada. Each population of the species appears to be completely isolated from others of its kind, restricted by the heat and dryness of the surroundings. And the species has been separated from closely related salamanders for millions of years. It has survived the folding and faulting of desert ranges, volcanic eruptions, the advances and retreats of Pleistocene glaciers, and a great drought some 7,500 to 4,500 years ago. Walk up a heat-soaked *bajada* (alluvial slope) deep into the scorched

mountains and you will understand something of this anomaly and of the lovely, heartbreaking tenacity of life.

The two dozen or so species in the slender salamander genus share several morphological traits, including four digits on the hind feet and a large gap between the dorsal bones of the skull. A complex molecular analysis suggests that the genus originated some 80 million years ago. Within the genus *Batrachoseps*, evolutionary biologists have identified two subgenera, designated subg. *Plethopsis*, to which the Inyo Mountains species belongs, and subg. *Batrachoseps*. Molecular evidence suggests they went their separate ways at least 20 million years ago. Species in the larger lineage, subg. *Batrachoseps*, are mostly restricted to California, from the western slopes of the Sierra Nevada to the coast, whereas subg. *Plethopsis* has a more northerly and inland

View west from the rugged slopes of California's Inyo Mountains, which reach up to 11,000 feet in elevation, reveals the still higher Sierra Nevada in the distance. In the arid habitat, small populations of the Inyo Mountains slender salamander live in isolation from one another.

distribution. In addition to *B. campi*, subg. *Plethopsis* includes the Oregon slender salamander, *B. wrighti*, found farther north, on both sides of the Oregon Cascades, and the Kern Plateau salamander, *B. robustus*, which occurs to the west and south, in the southeastern Sierra Nevada. The discontinuous distribution suggests that other species

and populations in the subgenus must have disappeared. Mutational differences in the mitochondrial DNA of the Oregon, Inyo Mountains, and Kern Plateau slender salamanders place their separation at roughly 10 million years ago. One puzzle is that although the Oregon and Inyo Mountains species are separated by 600 miles, and





Although lungless salamanders breathe only through their skin, they nevertheless survive in places where conditions are favorable, such as this moist microhabitat. They can retreat deep into rock crevices during time of drought and remain there for long periods of time without nourishment.

the Kern Plateau and Inyo Mountains species only by the narrow trough of the Owens Valley, the genetic differences among the three species are about equal. As the raven flies it is only about twenty-three miles across the Owens Valley, but as the salamander crawls the ranges of the two species might as well be a continent apart, across terrain that for a salamander is death. Even in good habitat *Batrachoseps* salamanders don't move around very much, and so the scattered populations of Inyo Mountains slender salamanders, which may be separated from one another by only a few miles of dry and rugged country, show genetic subdivisions greater than reported for any mammal species.

One day, after climbing to near the crest of the Inyo Mountains and absorbing as much of this country as I can, I make my slow and difficult way into a jumbled canyon where Inyo Mountains slender salamanders live. I move carefully through rough and trail-less terrain, edging across steep bands of

loose rock and down slopes covered with sagebrush and Mormon tea, then descend a seam spilling off a steep ridge, one that hammers my aching knees and thighs until it bottoms out in a narrow gorge. There is water in the canyon, and a ribbon of native thistles and seep willow, wildflowers and grasses. I begin flipping rocks, looking for the salamanders that shelter beneath them, carefully replacing each rock before moving on.

After fifteen minutes of searching I am lucky enough to find a salamander tucked under a small rock at the edge of the water, wedged into a narrow, muddy slot. It is a big one, about four inches long from snout to tail tip, its dark-brown back sprinkled with a thick band of silver-green dots. I take a few measurements and then set it down. The salamander hesitates briefly, then begins walking deliberately toward water. It travels with a slightly sinuous side-to-side motion, in the manner of a swimming fish. A running mouse or lizard moves nothing like a salamander; modifiers such as “scuttle” or “scamper” have no place in the lexicon of words we might use to describe how a terrestrial salamander travels. This aquatic pattern of movement in a terrestrial species is an essential aspect of the Inyo Mountains slender salamander's primordial nature, its life of inherited slowness.

The desert and the limitations of the salamanders

themselves have forced them into what looks like an evolutionary dead end. There are no salamander pasturelands waiting just downstream, only heat and light and dust and rock. Slender salamanders are very sedentary; the maximum extent of their home ranges over months or years may be less than fifteen yards. Their skin is extremely porous and must remain moist in order to exchange respiratory gases. Evaporative water loss from the skin of a lungless salamander is equivalent to evaporation from the surface of a shallow pool; place a wide bowl of water under the desert sun and watch the water disappear—essentially the same thing will happen to any exposed salamander.

Although hot, dry air is absolutely lethal to salamanders, they are remarkably tolerant of dehydration. A relative of the Inyo Mountains slender salamander, the California slender salamander, can survive until water loss approaches 30 percent of its body weight. A comparative value for humans is roughly 15 percent, although severe mental and physical impairment kicks in at about 10 percent loss. While *Batrachoseps* can survive levels of dehydration that would kill most mammals or birds, another general aspect of their biology must help them through the leanest times. Salamanders, including lungless species, have an extraordinarily low resting metabolic rate and need little energy to survive. Vertebrate ectotherms—animals that do not use metabolic heat production to regulate their body temperature—require much less energy than do endotherms such as mammals, which use most of their metabolic energy to generate heat.

Although all ectotherms use less energy than equivalent-size endotherms, salamanders are masters of energy efficiency. Their resting metabolic rates are about 60 percent that of other air-breathing vertebrate ectotherms, and they need only one-eighth to one-thirtieth of the energy required by birds and mammals. And because ectotherms do not defend their body temperature in the same way that endotherms do, surface-to-volume ratios are of less consequence, and they can be very small. Adults of about 65 percent of all salamander species weigh 5 grams (0.175 ounce) or less, while 20 percent weigh less than 1 gram. Take three moderate-size raisins and cup them in your hand; that's roughly the weight of a full-grown Inyo Mountains slender salamander, about a twentieth of an ounce.

Given their low metabolic rates, small lungless salamanders require very little of their invertebrate prey to get by. One study of dusky salamanders (a lungless species found in eastern North America) estimated that a 1-gram female needs about 1.2 grams of food *per year* to survive and reproduce. Finally, when faced with heat, drought, and lack of food, many amphibians enter a state of decreased metabolic activity known as estivation, when their steady-state metabolic rate decreases to about 25 percent of the normal resting rate. The low energy demands of lungless salamanders, combined with further decreases during estivation, make them extremely tolerant of both starvation and low oxygen levels, or hypoxia. Lungless salamanders can persist for long periods without eating anything; in one lab population of *Batrachoseps*, 74 percent survived at room temperature for one year without food.

Never having adopted the need to maintain a constant body temperature, salamanders are free to use much of



An Inyo Mountains slender salamander uncurls from its defensive posture. An adult of the species measures about two inches long (from snout to vent, the typical measurement for salamanders) and weighs roughly one-twentieth of an ounce.

their food energy for growth and reproduction instead of for staying warm. In small vertebrate endotherms the percentage of food energy used for adding biomass is typically 0.5 to 6 percent, but it runs as high as 50 to 80 percent in lungless salamanders. And so, when long pulses of killing conditions—waves of drought, volcanic ash,

heat, and cold—visited the Inyo Mountains, decimating salamander populations, the survivors must have retreated deep underground, where some could have lived for years on lipid reserves stored in their tails. They are that slow. Tightly wedged in the moist and absolute darkness of deep oxygen-deprived cracks, bereft of all food, the salamanders—the ultimate subterraneans—would have drowned away the days, weeks, months, years.

But when the world did brighten, the survivors would have crawled from the rocks. Perhaps they would have surfaced along tiny streams, in the riparian sweetness of some rainy desert night. There they would have found sufficient food and enough of their kind to mate and grow the eggs that, developing directly into miniature replicas of adults, would carry the population into the future.

How many Inyo Mountains slender salamanders could possibly live in the fifty acres that they

have, given the harshness of the surrounding desert and the isolation of their tiny habitat islands? Perhaps many more lived in the mountains back in the Pleistocene, when there was more rain, when the streams and springs ran strongly and extended their reach far down lush canyons. There would have been more cottonwoods and willows, abundant leaf litter beneath the trees, and pockets of soil rich with humus and invertebrate prey. Perhaps conditions once were moderate enough so that the salamanders did not retreat as often or as deeply into their cloistered crevices to await the next respite. Although I very much doubt it, once there could have been as many slender salamanders in prime Inyo Mountains habitat as there are lungless salamanders in the deciduous woods of New Hampshire—up to 4,000 per acre. There, salamander biomass may equal that of small mammals and be two times greater than that of breeding birds. There, salamanders play important roles in the ecosystem, both as highly concentrated protein packets for predators and as regulators of invertebrate populations on the forest floor.

Rates of population increase are affected by many factors, but two of the most important are age at sexual maturity and number of young per reproductive bout. What little data we have suggest that by both measures *Batrachoseps* salamanders are not fecund. No one knows how long it takes an Inyo Mountains slender salamander to reach sexual maturity, but the smaller California slen-

der salamander matures in three to four years and may live for eight years or more. Nor do we know how many eggs a female Inyo Mountains slender salamander lays, although clutch size in the Kern Plateau slender salamander is only four to six eggs, with no more than one clutch laid in a year. Compare these reproductive traits to those of a small endotherm such as the white-footed mouse, which reaches sexual maturity at two months of age, produces two to three litters of four young in a year, and then dies after only a year or so of life.

The Inyo Mountains slender salamanders also can endure because they are unimportant to the ecosystem and uncommon—no predator can specialize in them. They have entered into an evolutionary trade-off: slowness and survival in exchange for quickness and increase. Give them just the barest minimum of food and water in a world where there is little of either and they will get by, much as they always have. Mostly what they need

is to be left alone. Perhaps that is why the Inyo Mountains slender salamander is listed only as a “species of special concern” by the California Department of Fish and Wildlife, rather than as “threatened” or “endangered” by the state or by the United States Fish and Wildlife Service.

The character of the Inyo Mountains—little water, sparse vegetation, and apparently not much in the way of valuable mineral resources—contributes to our benign neglect of the species. In the past some of the springs and small streams that the salamanders depend upon were loci for mining and cattle grazing. But abandoned troughs and pipes, the scattered bits of

lumber and rusted machinery speak of a land too spare to offer much economic sustenance. Feral burros and cattle may have grazed and trampled their way through enough mountain canyons to decrease salamander populations in some places. And perhaps illegal collectors have taken too many salamanders from the few sites that offer relatively easy road access (I suspect this about two localities). But now few burros or cattle roam the Inyo



The home range of a slender salamander may be less than fifteen yards across.



The arid terrain leading into the Inyo Mountains is no place for a salamander.

Mountains, and most of the salamander populations have become more isolated than they once were as wilderness designation and the wear of water have pushed drivable roads farther away from where they live.

Just what good are Inyo Mountains slender salamanders? Why should people concern themselves with a species that few know about and even fewer will ever see? This question of worth nags me after a long hot day in the field, like the small stone lodged in my left boot, which I am too lazy to stop and remove but which gives my gait an irritating little hitch. I am mostly perplexed about possible answers to questions of value, but late in the afternoon I sense the outline of a possible answer.

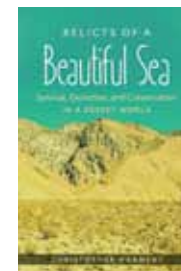
I stop at the Manzanar National Historic Site, just south of the small town of Independence in the Owens Valley. Manzanar was one of ten “war relocation centers” where Japanese Americans were imprisoned during World War II. It once held more than 10,000 “internees” crowded into 504 barracks. Most of the original camp structures have disappeared, but the National Park Service has renovated the auditorium as an interpretive center and erected replicas of several buildings, including barracks, a mess hall, and a guard tower.

Although the armed soldiers and barbed-wire fences are more than sixty years gone, Manzanar remains a place where the ghosts of the past wander with you, much as they do on the killing fields of Antietam in Maryland or at Little Bighorn in Montana. Suffering, pain, injustice, anger, death; these things are never far away as I work my way through the interpretive center. I think about fear, racism, hatred, and man’s inhumanity to man, and am

drawn into sadness and impotent anger. But then I happen to glance up and eastward toward the Inyo Mountains and the drainage where I found slender salamanders just a few hours before. Those tiny, tenacious creatures come to mind, with their patient slowness and the ways in which they have endured—and did even as the horrors of World War II unfolded.

I understand that nothing could ever repay the internees for their suffering, not even the belated Civil Liberties Act of 1988, which granted a \$20,000 payment to each surviving detainee and an apology to all former prisoners of Manzanar and other relocation camps. But I take some comfort in knowing that while

10,000 people were imprisoned at Manzanar, the Inyo Mountains slender salamanders were going about their business, much as they have for the last 10 million years. I do not pretend to understand much about the Japanese American experience in World War II, nor can I say how victims of any terrible injustice might come into forgiveness and peace. But like every person in this world I have lived through my own tiny Manzanars, my small imprisonments, pain, and sadness. And for me it is of some solace to know that, beyond the reach of human folly, Inyo Mountains slender salamanders have crawled and drowned their way through the millennia.



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