

CHAPTER 14-6

SALAMANDERS AND ADAPTATIONS

Janice M. Glime and William J. Boelema

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CHAPTER 14-6

SALAMANDERS AND ADAPTATIONS



Figure 1. **Four-toed Salamander** (*Hemidactylium scutatum*), predominantly a moss dweller, in a bed of mosses. Photo by John D. Willson, with permission.

Caudata (Urodela) – Salamanders

The term Caudata refers to having a tail (Figure 1), so the Caudata are the amphibians with tails. Caudata have four legs positioned at right angles to the body, and moist, smooth skin (except in newts). Some live entirely in the water, some live part of their life cycle in water and part on land, and others are entirely terrestrial or **arboreal** (in trees). Newts are salamanders that spend part of their adult life on land and part in the water.

Many salamanders live among bryophytes, and many live in areas where bryophytes form a dominant feature of the landscape. Others live in places where bryophytes are present, but scattered. Casual observations include finding salamanders in bryophyte collections, but we seldom know if this is a casual/accidental association, or if salamanders actually prefer the bryophyte habitat. Does the bryophyte offer any advantage to the salamander? There is no collection of data on the broad role of bryophytes, and most information is observational, thus not providing preferences or causality. The salamander sub-chapters represent an attempt to challenge researchers to make detailed studies on the relationships between bryophytes and salamanders.

In an attempt to be consistent with a worldwide fauna, Latin nomenclature in this chapter follows Frost (2011). English names are mostly based on the SSAR names list (Crother 2008) for North America north of Mexico, and

AmphibiaWeb (Sandmeier 2010) or Frost (2011) for species that do not occur in North America north of Mexico. The order of families follows proposed phylogeny presented by Pearson and Pearson (2010), but the species presented do not, but rather one of related habitats and of convenience.

Distribution

The majority of species of salamanders occur in North America, with the largest family, Plethodontidae, being almost restricted to the western hemisphere. Of the ten families, only the Plethodontidae have a significant number of species that live in areas outside the temperate regions, *i.e.*, in the Neotropics.

If you live in the North Temperate Zone of North America, it is difficult to imagine that large parts of the world do not have salamanders. As somewhat late arrivals on the tree of life, salamanders are absent in Australia (Marc P. Hayes, pers. comm. 26 March 2011; Stan A. Orchard, pers. comm. 27 March 2011; Frost 2011) and in most of India, South America, Africa (Marc P. Hayes, pers. comm. 26 March 2011), and parts of Southeast Asia [Edmund (Butch) Brodie, Jr., pers. comm. 7 June 2011] and of course Antarctica (Frost 2011). The most species-rich areas are the Appalachian and Ozark Mountains, USA,

the Pacific coast of North America, western Europe, Japan, and China (Wake 2011). Only the Salamandridae extend into Northern Africa, southern foothills of the Himalayas, northern Vietnam, and southern islands of Japan.

The largest concentration of salamander species is in the Appalachian Mountains in eastern North America. Perhaps more striking is the distribution of the Plethodontidae, containing 70% of all salamander species. This large family is restricted to the USA, southern Canada, Mediterranean Europe, and the Korean Peninsula (1 species!). In Europe and Asia, the only plethodontids present are the limestone cave dwellers in the genus *Speleomantes*, and only one of these (*S. supramontis*) is known to be associated with a mossy habitat. So, salamanders do not have worldwide distribution, and my North American bias in this presentation is justified.

Descriptions of salamander habitats often seem to lack detail. This is partly justifiable in that often a single individual represents the species when it is described for the first time. Even in surveys, it is typical to describe the general habitat and mention logs and rocks, but omit any mention of bryophytes. Salamanders that hide under bryophytes in the soil are treated as soil organisms and the bryophytes may or may not be mentioned. Epiphytic bryophytes that must be crossed to traverse the arboreal habitat are likewise often not mentioned. In some cases, these omissions are probably true representations of absence, but often they are in old-growth forests, cloud forests, and rainforests where this is unlikely to be the case.

I found it encouraging that Bryce A. Maxell (2005) of the Wildlife Biology Program, University of Montana, Missoula, MT, USA, not only recommended looking on and under bryophyte mats for amphibians, but the sample data sheet for *Plethodon idahoensis* specifically listed it among the habitats to record:

under wood/vegetation
under 4-20cm rock fragments
under >20cm rock fragments
under bryophyte mat
on bryophyte mat
in rock fracture
other_____

This list would insure that habitat information on the bryophytes would be included in any survey using the form. On the other hand, encouraging searching of bryophytes could be seriously destructive to the bryophyte habitat. This seems to be a tricky problem.

Adaptations to Bryophytes

If you have to move through moss mats, it doesn't hurt to be shaped like a worm (Figure 2). For a salamander, that includes having short legs on an elongate body (Figure 2). Your diet necessarily changes to the mites, ants, beetles, and other small invertebrates (mostly arthropods) available. And if you wiggle and move, you attract attention, so your color should either blend in with the bryophytes or you should warn predators to beware by having bright colors that suggest you are poisonous. And if you fail to blend

and someone grabs your tail, disengaging your tail while you run off can confuse your predator (Figure 3-Figure 5) (Wikipedia 2011a), especially if the detached tail continues to wiggle.



Figure 2. *Oedipina pacificensis* showing its small size, reduced appendages, and wormlike body that adapt it to maneuvering among mosses. Photo by Vide Ohlin, with permission for education.

Of these adaptations, most are adaptations to terrestrial living in general. Small size, short limbs, and cryptic (camouflage) coloration are the most bryological. Need for moisture is not an adaptation, but it increases the utility of the bryophytes in some habitats.

Tail Autotomy

Tail autotomy is the ability to drop the tail. Often if the salamander tail is simply dropped, it can continue to move and wiggle (Figure 3), providing a distraction that might permit the rest of the body to escape (Jim McCormac, pers. comm. April 2011). Not only that, but apparently some predators prefer the tail; consumption of the disengaged tail permits the remainder of the body more time for escape (Beneski 1989).



Figure 3. The Greenmountain Slender Salamander, *Batrachoseps altasierrae*, with a waving disarticulated tail on the left and the escaping body in the upper left of the photo. Photo by Gary Nafis, © Gary Nafis at CaliforniaHerps.com, with permission.

And it doesn't hurt to be able to regenerate lost parts. But regeneration requires energy, and this apparently results in loss of reproductive capacity, at least in the salamander *Batrachoseps attenuatus* (California Slender Salamander; Maiorana 1977). On the other hand, Smits and Brodie (1995) demonstrated that in the moss-dwelling *Oedipina uniformis* (Cienega Colorado Worm Salamander) it does not appear to cause any increase in

respiratory cost. They measured respiration before and after activity of this salamander with and without an autotomized tail. Results suggest that the tail accomplishes the oxygen exchange/respiration the tail needs, but the tail is not needed to supply the rest of the salamander.



Figure 4. *Bolitoglossa lincolni*, Lincoln's Mushroomtongue Salamander, with a complete tail. Note the constriction at the base of the tail that permits it to release. Photo by Sean Michael Rovito, with permission.

Salamanders have remarkable abilities to regenerate lost tissues (Figure 5), including other limbs as well as the tail (Endo *et al.* 2007; Keim 2009; Garza-García 2010). The exposed tissue after losing a tail is undoubtedly subject to bacterial infection, but following this self-amputation (**autotomy**), epidermal tissue migrates within 12 hours to cover the remaining stump (Mullen *et al.* 1996; Bryant, *et al.* 2002). In as little as twelve weeks after tail loss, some salamanders are able to achieve coordinated swimming behavior with their newly developing tails (Davis *et al.* 1990). It appears that the only serious price is loss of reproduction.



Figure 5. *Bolitoglossa lincolni* with short tail, suggesting it has been attacked by a predator and lost its tail, which is now regenerating. Photo by Sean Michael Rovito, with permission.

Toxicity

Living on land can often make salamanders more vulnerable to predation. They are more easily seen and more easily caught by small mammals, birds, and snakes than those in water where glares, shadows, and silt can make visibility poor. The salamanders have varying degrees of being poisonous through glands in their skin, and many either have no poison or it is too weak to be effective [Edmund (Butch) Brodie, Jr., pers. comm. 22 April 2011]. Fortunately for herpetologists, the poison is

not a contact poison, but must be eaten to become noxious or dangerous. But when a snake flicks its tongue against this would-be dinner, it feels the effects of the poison from the more toxic ones.

Unfortunately for the salamander, it appears that not every snake is affected by the poison. In some cases, one or more species occurring in the same range, and with historically overlapping habitats to the salamander, have evolved immunity to the poison (Brodie *et al.* 2002; Williams *et al.* 2003; Ridenhour *et al.* 2004). For example, the garter snake (*Thamnophis* spp.) has developed resistance to the neurotoxin **tetrodotoxin** (TTX). This resistance seems to have evolved independently in both related and unrelated snakes. The Sierra Gartersnake, *Thamnophis couchii*, has elevated resistance to TTX, a toxin present in the **sympatric** (having overlapping distribution) newt *Taricha torosa* (California Newt, Salamandridae; Brodie *et al.* 2005). But the distantly related *Thamnophis sirtalis* (Common Gartersnake) also coevolved with its very poisonous sympatric newt prey, *Taricha granulosa*, **Rough-skinned Newt**. These multiple predator-prey co-evolutions in *Thamnophis* seem to result from the simplicity of the genetic structure of TTX resistance in that genus, permitting the evolution of "extreme phenotypes" (Feldman *et al.* 2010), in this case, TTX resistance.

Not only does the *Thamnophis* snake with immunity have a broadened diet that includes newts, it becomes endowed with a bit of protection of its own! Some of these highly resistant snakes are able to ingest multiple newts safely in one meal (Williams *et al.* 2004). Williams *et al.* (2010) found that after consuming only one newt of *Taricha granulosa*, the Common Gartersnake *Thamnophis sirtalis* retained significant amounts of active TTX in its liver for one month or more. The 42 µg in the liver that remained after three weeks is sufficient to incapacitate or even kill avian predators, and possibly also mammalian predators (Williams *et al.* 2010). Hence, the bryophytes in the ecosystem, through their housing of newts, could increase the number of snakes in the area through these interactions. *Taricha torosa*, and all *Taricha* species, can dwell in bryophytes [Edmund (Butch) Brodie, pers. comm. 7 June 2011]. It is likely that other bryophyte-dwelling salamanders could be victims or promulgators of similar, as yet unexplored, relationships.

Several authors have attempted to determine the origin of the poison TTX. Possible sources include diet of poisonous arthropods, bacteria that manufacture the poison within the salamander, and manufacture by the salamander itself.

Some arthropods living among mosses are poisonous when eaten, especially mites and ants, and we know these can impart their poisons to some of the poisonous frogs that consume them (Daly & Myers 1967). Although Cardiff (2011) states that the same is true for salamanders, few salamanders eat the beetles, mites, or ants that are poisonous (David Wake, pers. comm. 21 April 2011), and no peer-reviewed study seems to be published to support this poison transfer claim.

Lehman *et al.* (2004) examined the possibility of bacterial origin of the poison TTX. Using PCR primers that amplify 16S rRNA genes, they were unable to detect any bacterial DNA in skin samples from the toxic *Taricha*

granulosa. This provides a strong suggestion that bacteria are not involved.

Hanifin *et al.* (2002) examined the ability of *Taricha granulosa* to manufacture its own TTX by maintaining the newts in captivity. These newts were fed non-toxic earthworms, *Tubifex* worms, and crickets weekly. The levels of TTX actually increased by 20.7% after one year. Since none of these food items is poisonous, these results suggest that the newts manufacture their own poisons. Cardall *et al.* (2004) supported this view by stimulating the release of TTX in *Taricha granulosa* with a mild electric stimulation. Following reductions of 21-90% in TTX levels, these newts regenerated their original TTX levels in the skin during the next nine months in captivity.

It appears that toxins may be rare among the members of the largest family of salamanders, the Plethodontidae. Brandon and Huheey (1981) were the first to identify the composition of a skin toxin in the family Plethodontidae, a family with many bryophyte-dwelling species. This toxin, identified by them in *Pseudotriton ruber* (Figure 13) and *P. montanus*, occurs in the skin and some organs but is most concentrated on the **dorsal** (back) surface. They determined this to be a **pseudotritontoxin**, a proteinaceous **neurotoxin**. When they experimented with its effects on mice, the mice responded by exhibiting hyperextension of their hind legs and lower back, having severe **hypothermia** (body temperature below normal), prolonged debility, coma, and death usually in 12 to 48 hours. Larger doses caused convulsions and death within as little as one hour. Young chickens, perhaps a closer model for their natural predators of reptiles and birds, had convulsions and death within minutes.

But reports of toxins in other plethodontid salamanders are rare. These salamanders are not as easy to experiment with as newts because of their small size, and for many tropical species, rarity. Brodie *et al.* (1991) have found toxicity in *Bolitoglossa huehuetenanguensis* (formerly *B. rostrata*), and *B. subpalmata* (Figure 6-Figure 7), so poisons may exist elsewhere.

Bolitoglossa subpalmata not only produces toxins, but also has behavioral responses to predators (snakes) that deter the predator (Brodie 1977; Ducey & Brodie 1991). In this case, the salamander rolls onto its back. Those salamanders from alpine areas where there were no snakes were less likely to respond with this behavior when making contact with a snake tongue.



Figure 6. *Bolitoglossa subpalmata* on its back in a defensive posture. Photo by Edmund (Butch) Brodie, with permission.



Figure 7. *Bolitoglossa subpalmata* adult with eggs. Photo by Edmund (Butch) Brodie, with permission.

Predator Avoidance

There is some suggestion that some sort of chemical cues may exist that warn other salamanders because at least some members of the family Plethodontidae are sensitive to skin chemicals from other salamanders, both their own species and others in their genus, that have been attacked. These are not documented as being poisonous, but rather elicit avoidance behavior in those salamanders sensing this danger signal (Lutterschmidt *et al.* 1994). Lutterschmidt *et al.* (1994) demonstrated this response for *Desmognathus ochrophaeus* (sometimes a moss-dweller) toward other *D. ochrophaeus* and also to others in its genus, but not to *Plethodon richmondi* skin extracts. This chemical does not seem to be present in the viscera of the salamanders or in damaged mealworms. Recognition of the released chemical from attacked individuals signals the nearby salamanders to flee or take cover.

Warning Coloration and Mimicry

A type of mimicry known as **disruptive coloration** helps to hide organisms in plain view and involves having a color pattern that resembles their surroundings. This is well known in the clothing worn by soldiers who need to blend with their surroundings. You probably noticed that the colors changed when the soldiers started fighting in desert habitats with little vegetation. Greens were replaced by grays.

For bryophyte-dwelling salamanders mimicry can involve resembling the bryophytes that surround them. Disruptive patterns of green, brown, and black give them the appearance of the bryophytes (Figure 8), at least from a distance. Nevertheless, most bryophyte-dwelling salamanders do not seem to mimic bryophytes. Instead, the non-colorful ones are typically shades of brown, instead mimicking the soil, bark, or a stick. This is perhaps reasonable since they could move within moss mats with little visibility, but would be conspicuous on the soil or bark where catching dinner may dictate surface movement. And brown salamanders on green moss do resemble a stick from a distance. I have not located any information to indicate that any salamanders have outgrowths that resemble moss or lichen growths, such as those seen on some frogs.



Figure 8. *Aneides aeneus* (Green Salamander) juvenile somewhat resembling its mossy habitat. However, one could argue that the blackish and yellow colors are also warning colors. Photo by Bill Peterman, with permission.

Some salamanders take advantage of camouflage on top so they are not noticed from a distance, but if a predator draws near, they can rear up and show a bright warning color on the ventral (lower) side, such as that seen for *Taricha granulosa* in Figure 9, or roll over onto their backs (Figure 10-Figure 11). If the predator has had a bad experience with that color combination, it is likely to retreat.



Figure 9. Adult Rough-skinned Newt (*Taricha granulosa*) demonstrating a defensive posture that is practiced by a number of the larger salamander species. Photo © Gary Nafis at CaliforniaHerps.com, with permission.



Figure 10. The Cascade Torrent Salamander, *Rhyacotriton cascadae*, demonstrating the brown dorsal surface that blends with the twigs among the mosses. Photo © Henk Wallays, through Creative Commons.



Figure 11. The Cascade Torrent Salamander, *Rhyacotriton cascadae*. Behavior of rolling onto its back and revealing the warning color of yellow. Photo by Henk Wallays, through Creative Commons for educational use.

Müllerian mimicry is common among salamanders. **Müllerian mimicry** permits species that look like each other to protect each other through similar warning coloration. Less or non-poisonous species enjoy less predation because they look like a species that is highly poisonous. Thus a predator has a higher probability of encountering the highly poisonous common species first and learns to avoid things that look like it, including the less common weakly poisonous or non-poisonous species. Both relatively common, highly poisonous species and slightly poisonous species with small numbers can have varying degrees of red, yellow, and black warning color combinations. Interestingly, the same color combinations are prevalent among hurtful and toxic species elsewhere in the animal kingdom, including snakes, bees, and frogs.

Howard and Brodie (1971) first demonstrated the **Batesian mimetic** relationships of two toxic salamander species in the area at Highlands, North Carolina, USA. **Batesian mimicry** is the case where there is a toxic model and a non-toxic mimic that gains benefit by looking like a toxic species. It works best when the model is abundant and the mimic at least less abundant so that the predator is more likely to experience the model first. In the experiments by Howard and Brodie (1971), the highly toxic red eft (immature) stage of the **Eastern Newt**, *Notophthalmus viridescens viridescens* (Figure 12), a common moss visitor and a species that is both noxious and toxic, served as a model for the **Red Salamander**, *Pseudotriton ruber schencki* (Figure 13-Figure 15), a moss hibernator. After experiencing a noxious red eft, previously inexperienced chickens avoided the **Red Salamander** as well as the red eft. They still readily ate non-toxic species of *Desmognathus*. Brandon and Huheey (1981) suggested that a **Müllerian mimicry** complex exists that has a variety of palatability levels. In **Müllerian mimicry**, a number of species, often unrelated, resemble each other and thus gain predation protection when a predator experiences another member of the group. This enhances the effectiveness of **Batesian mimics** as well because it increases the size of the pool of models. In the study by Brandon and Huheey, the poisonous (Müllerian) group includes the red eft of the **Eastern Newt** and at least some members of the **Red Salamander**; the non-poisonous Batesian species include such moss dwellers as the **Spring Salamander**, *Gyrinophilus porphyriticus* (Figure 16).



Figure 12. Red eft stage, *Notophthalmus viridescens*, example of **Müllerian mimicry**. Photo by Alan Cressler, with permission.



Figure 13. *Pseudotriton ruber*, a salamander with a strong neurotoxin, a Müllerian mimic of the red eft. This species is known to hibernate under mosses in *Sphagnum* peatlands. Photo by Mike Graziano, with permission.



Figure 14. *Pseudotriton ruber*, where it is conspicuous on mosses. Photo by John White, through Creative Commons.



Figure 15. *Pseudotriton ruber* on mushrooms, where it is somewhat less conspicuous. Photo by John White, through Creative Commons.



Figure 16. *Gyrinophilus porphyriticus*, a non-toxic Müllerian mimic of *Pseudotriton ruber* (Figure 13-Figure 15), giving it the advantage of looking like a poisonous species. Photo by Todd Pierson, with permission.

If you have no warning coloration and you are edible, it is not a good idea to advertise your presence. Instead, being still works well. And if the predator gets too close, try to look bigger or more dangerous – or drop your tail and run!

Locomotion

Locomotion provides an interesting story for bryophyte-dwelling salamanders. Limbs provide means of climbing trees and running across rocks, with arboreal species at times having large footpads that help them to cling to slippery surfaces (Wake 2011). But they also use sinuous body movements for rapid locomotion. For example, the genera *Batrachoseps*, *Oedipina*, *Pseudoeurycea* (formerly in *Lineatriton*), and *Phaeognathus* have bryophyte-dwelling members with reduced limbs, and they use body movements for rapid locomotion. Some members of the often bryophyte-dwelling genus *Bolitoglossa* have highly webbed feet with nearly fused toes (Figure 17) that permit them to move across wet leaves and other smooth surfaces like bark. *Aneides*, *Chiropterotriton* (Figure 18), *Dendrotriton*, *Nyctanolis* (Figure 19), and *Pseudoeurycea* have bryophyte-dwelling species that are arboreal and use their long legs and toes with expanded tips to climb, but they are also aided by **prehensile tails** (tails that can be used to grasp, like that of a monkey) (Figure 18).



Figure 17. *Bolitoglossa* sp., illustrating the webbing on the foot that permits moving about on smooth surfaces. Photo by Ira Richling, <www.helicina.de>, with permission.



Figure 18. *Chiropterotriton* sp., demonstrating the long legs and prehensile tail that permit them to maneuver arboreal habitats. Photo by Timothy Burkhardt, with permission.



Figure 19. *Nyctanolis pernix*. Photo by Todd Pierson, with permission.

Life Cycle

Having a life cycle with no aquatic stage is critical for tree dwellers, but many other species are restricted to living near water where they can lay their eggs (Figure 20-Figure 21). This is particularly true for the larger salamanders (newts) in the Salamandridae. For completely terrestrial species, having eggs that hatch into young salamanders (**direct development**) instead of tadpoles (Figure 22) facilitates this terrestrial transition. Others lay eggs near water where the larvae can easily drop or slither in.



Figure 20. Breeding adult **California Newts** (*Taricha torosa*). Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Role of Bryophytes

“One does not know whether a man killing an elephant or setting fire to the grassland is harming others until one knows the total system in which his act appears.” Whereas this quote from Hardin (1968) was intended to illustrate the folly of our exploitations against whole ecosystems, it also characterizes our knowledge about the interaction of bryophytes with other members of the ecosystem. The salamanders are a group of organisms that is rapidly disappearing from the planet. As I researched this chapter, it became clear to me that for salamanders in particular, there is a huge gap in our knowledge. Many species live in “mossy” habitats, but little seems to be known about their use of the bryophytes.



Figure 21. Eggs of the **California Newt** (*Taricha torosa*). Photo © Gary Nafis at CaliforniaHerps.com, with permission.



Figure 22. Tadpole (aquatic) of **California Newt** (*Taricha torosa*). Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Pictures of salamanders on bryophytes abound on the web. But beware! Bryophytes are a favorite substrate for the photographers who often take these animals to the lab to be photographed. The bryophyte in the picture does not necessarily indicate that it is a preference for the salamander.

It is difficult to find documentation that salamanders actually depend on bryophytes, even when they are often found on or among mosses and liverworts (Figure 1). Others hide there in trees or peatlands. For example, Wilson (1992) reported finding one immature salamander

under a bryophyte mat at the base of a rock face in Idaho, USA. What does that really mean? Nevertheless, there is evidence that mosses can be beneficial to salamanders for maintaining moisture, camouflage, cover during hibernation and aestivation, nests, and in a few cases foraging sites.

Moisture

Salamanders have mucous-secreting glands that help to moisten and lubricate the skin. But these are insufficient to keep the skin moist in drier habitats, and not all salamanders are equally endowed with these glands.

The need of salamanders for moisture suggests that the bryophytes might play a vital role, albeit in a spurious way. When the soil is moist and the air is cool, bryophytes may simply be there, occasionally stepped on, and probably more often avoided because the soil and litter are easier to traverse. But when conditions begin to dry, the bryophyte offers a place to replenish moisture or a wetter place to take cover. Even for those species living in the soil, a bryophyte reduces water loss, making the soil more hospitable.

Almost no experiments exist to support the role of bryophytes in the habitat of salamanders. Using the **California Newt *Taricha torosa*** (Figure 23-Figure 25), Brown and Brown (1980) demonstrated the usefulness of mosses in hydrating salamanders. This animal can be up to 20 cm long (Wikipedia 2011b), and water maintenance is important, as it is to all salamanders. In their experiments, Brown and Brown (1980) found that water uptake from wet moss equalled 66% of that in fully submersed members of the species. Furthermore, external movement of water occurred along skin channels from the ventral (lower) to the dorsal (upper) surface, suggesting that a damp substrate such as moss could hydrate an animal resting on it or walking across it (Figure 23-Figure 25).



Figure 23. Adult **California Newt (*Taricha torosa*)** posed on a bed of mosses. Photo © Gary Nafis at CaliforniaHerps.com, with permission.



Figure 24. Front view of adult **California Newt (*Taricha torosa*)** posed on a bed of mosses. Note its low profile, permitting the abdomen to contact the moss as it moves. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

Despite the wonderful pictures above by Gary Nafis, it appears that ***Taricha torosa*** often lives in habitats lacking bryophytes. David Wake (pers. comm. 31 March 2011) concurs. Nevertheless, some ***T. torosa*** and ***T. granulosa*** do indeed live where the forest is humid and epiphytic mosses are common. In these locations, this newt lives among the mosses (Gary Nafis, pers. comm. 27 April 2011; Edmund (Butch) Brodie, pers. comm. 7 June 2011). In general, however, it appears that ***Taricha torosa*** prefers less humid climates than many of the other newt species (Wikipedia 2011b). Too bad – there has been a lot of research on this species. ***Taricha torosa*** further conserves water by storing it in the bladder (Brown & Brown 1980).



Figure 25. Adult **California Newt (*Taricha torosa*)** posed on a bed of mosses where it is able to replenish its water supply. Note the rough skin. Photo © Gary Nafis at CaliforniaHerps.com, with permission.

This research on an animal of relatively dry habitats suggests that mosses could be critically important rehydration sources for other salamander taxa with higher moisture requirements. It is interesting that for their experiments Brown and Brown (1980) chose this species, which rarely encounters bryophytes in its California coastline and in the Sierra Nevada, USA, habitats. One must wonder if the species living in habitats with bryophytes have even better ability to make use of damp bryophytes for moisture regulation. Hopefully someone will investigate this role for salamanders in the "mossy" habitats occupied by amphibians, especially in the Neotropics.

Nesting Sites

Salamander nests are common among mosses, as well as grasses, sedges, and rotting logs (Wood 1955; Salthe 1967; Harris & Gill 1980). Studlar (Bryonet 8 September 2004) shared her observations that lungless salamanders (**Plethodontidae**) may lay their eggs in moss mats in the Appalachian Mountains, USA. Bryophytes help to maintain moisture as well as to provide cover that decreases visibility of the eggs. I wonder if they provide any antibiotic service? This could be especially helpful in preventing molds from developing on the eggs since many, perhaps most, bryophytes produce secondary compounds that have antibiotic properties. On the other hand, large areas of the eggs would not be in direct contact with the bryophytes and may, therefore, derive no antibiotic benefit from their bryological neighbors.

Food Source

As you will see later in this chapter, mosses are at least occasionally consumed by a few salamanders. But are they consumed as food, or merely ingested along with invertebrates or other food matter associated with them? No experimental work seems to be available to address this question.

On the other hand, bryophytes can be home to a number of food organisms, both in the water and on land. In peatlands, one attraction for salamanders in that mossy habitat is the presence of pools that harbor numerous insects, hence providing food (Desrochers & van Duinen 2006). Searching for the food available in the terrestrial bryophytes may impart cover as protection for them during foraging. Their predators may include reptiles, fish, birds, small mammals, and even spiders, with all but the latter being prevented from entering the small spaces within moss clumps.

Hibernation and Aestivation

When one considers **hibernation** (animal state of inactivity and metabolic depression, characterized by lower body temperature and slower breathing; used for passing winter) and **aestivation** (cessation or slowing of activity during summer, especially slowing of metabolism during a hot or dry period) sites, it appears that even less is known. Some salamanders in cooler climates hibernate in the winter and may seek the shelter of bryophytes for that purpose. However, as will be seen in the table at the end of this chapter, there seems to be documentation of this use for only a few species of salamanders. In many cases, the hibernation site is simply unknown.

Most salamander species are night-active. Some may spend the day among bryophytes, where they are less likely to be detected and where moisture is greater than on rocks or even in soil. In habitats where the summer is hot and dry most of the time, aestivation can occur. This likewise is not well documented, but at least a few species are known to use mosses as a summer refuge.

Bryophytes can help to buffer the temperature, maintaining a safer range for the salamanders. Vial (1968) found that *Sphagnum* in the mountains of Costa Rica maintained a relatively low range of stable temperatures (9.8-16°C). Peatland mosses, in particular, may help to cool the habitat through evaporative cooling. Gnaedinger and Reed (1948) found a temperature of 1.2°C under mosses while the air temperature was -3.3°C. The mosses apparently kept the soil from freezing, although the mosses themselves were frozen to a depth of 1 cm, as was the soil where mosses were absent.

This subchapter and the next will necessarily include a lot of anecdotal information and speculation in the hope that the information will stimulate further study. I hope in the following pages to suggest species that are worthy of further investigation to determine the role that bryophytes play in their life cycle – as hibernation sites, aestivation sites, remoistening sites, cover, and nesting sites.

Summary

Newts and salamanders are known as Caudata, a term referring to their tails. The majority are distributed in the Western Hemisphere. Lungless species (**Plethodontidae**) are almost completely restricted to North America and the Neotropics.

Salamander Adaptations: Arboreal bryophyte-dwelling salamanders tend to be small, shaped like a worm, with an elongate body and short legs. Their movements are often sinuous – they slither through a moss like a snake. And some have **prehensile tails** like a monkey, adding a fifth appendage for climbing, hanging, or clinging. Their colors are typically brown with various patterns of other colors (including **disruptive coloration**), and the ventral surface may be endowed with warning coloration. Hence, their defensive behavior may be to rear up or roll on their backs, exposing the **warning colors**. Some species are poisonous and colorful, and other species living in the same area may mimic their warning coloration (**Müllerian mimicry**). When attacked on the tail, salamanders can disarticulate the tail, which may continue wiggling, distracting the predator. They typically feed on ants, beetles, mites, and other small invertebrates. Their life cycle is either fully terrestrial, often with eggs hatching into young salamanders instead of tadpoles (**direct development**), or females locate their eggs near water where the larvae can easily drop or slither into the water when they hatch. Females often defend and tend the eggs, rotating them or cleaning them to reduce bacterial and fungal infection.

Role of Bryophytes: Bryophytes are important moisture reservoirs for salamanders, and at least some have channels in the skin that direct water, gained from bryophytes, upward to their backs. The plethodontid salamanders often lay eggs in mosses, thus satisfying their need for a wet or at least moist incubation environment. Some species use bryophytes exclusively for egg laying and are true **bryobionts**. Some use mosses for winter **hibernacula**, whereas others use them as summer retreats for aestivation. Thick bryophyte mats can buffer the temperature, providing soil that is frost-free longer, or cooled by evaporative cooling and shading. At least a few use the bryophytes as foraging sites.

Specific uses are often unknown, but the co-occurrence of certain salamanders with bryophytes in most of their known habitats suggests that the bryophytes may play an important role in their lives. At the very least, they can serve as indicators of the likely presence of salamanders.

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