CHAPTER 14-1
AMPHIBIANS: ANURAN ADAPTATIONS

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Figure 1. ***Dendrobates tinctorius*** (Dyeing Poison Frog), perched on a bed of mosses. Many species in the tropics use bryophytes to maintain hydration. This species is named for the use of the poisons in its skin. Its specific name, *tinctorius*, refers to the way indigenous tribes of Amerindians of the Amazon drainage and the Guianas rub the frogs' skin or blood onto the skin of plucked parrots, toxifying the skin and causing the new feathers to develop with a variety of different colors (Métraux 1944). Photo © Henk Wallays, through Creative Commons.

Bryophytes and Amphibians Share Commonalities

In searching for information on bryophytes and their amphibian inhabitants (frogs, toads, salamanders; Figure 1), I ran into Wachman's (2010) interesting question: "In what way are the bryophyte plants and the amphibian animals alike?" Wachman points out that bryophytes have shared the planet with amphibians since the Carboniferous era. Both are transitional organisms from living entirely in water to living at least part of their life cycle on land, a shift that occurred around 360–290 mya. Wachman claims both need a moist environment (I think most bryologists would take exception to that claim, and many treefrogs likewise have found ways around that requirement, although they do use mosses and other moist places to keep their skin moist). While it is true that most amphibians must find water to reproduce, this can be the basin of a bromeliad or tree hole, and a number of them lay their eggs on mosses or other vegetation in trees or on the ground.

Bryophytes need water to maintain the viability of their male gametes (sperm) while they travel to female reproductive organs, taking advantage of rainwater or dew in most cases. Both bryophytes and most amphibians have two distinctive phases of development – bryophytes have haploid leafy gametophytes and diploid sporophytes with a capsule; amphibians have larvae (not always free-living; usually known as tadpoles in frogs and toads) and adults. (But certain salamanders are neotenic in that they stay aquatic and have gills all their lives. Newts have three life phases: larva, then eft, then aquatic adult. They are somewhat able to go back to the eft stage if the standing water disappears – their skin becomes less permeable to water.) And both bryophytes and amphibians thrive best when far from populated areas. But bryophytes seem to be well armed against disease by their secondary compounds, whereas amphibians seem very susceptible to diseases. Since bryophytes are able to grow well in some areas, becoming a major part of the flora, it is to their credit that they provide cover and moisture for the amphibians there.

But in one way, bryophytes differ greatly from amphibians. Bryophytes have tolerance to extreme cold, occupying the northernmost and southernmost locations on the planet, sometimes even surviving on glaciers, whereas amphibians have very poor cold tolerance and most cannot occupy areas with permafrost. In central Alaska, only the Wood Frog (***Lithobates sylvaticus***) and Boreal Toad (***Anaxyrus boreas boreas***) occur, surviving the winter buried in frozen mud (National Park Service 2013).

Anura – Frogs and Toads

The tailless amphibians (Figure 1) are in the order **Anura**, a word that literally means without a tail. These include the frogs and toads. Most of the more familiar temperate frogs were included in the family **Ranidae** in the genus ***Rana***. The family occurs on all continents except Antarctica. However, only the Australian Wood Frog (***Hylarana daemeli***) represents this family in Australia, where it is restricted to the far north. The family has been revised and many of the familiar species are no longer in the genus ***Rana***.

Standard English names used here are according to Crother (2008) for North American species. **Common names** are local and not at all standardized, whereas the **Standard English names** have legal standing through an official published list (Crother 2007, 2008). Scientific (Latin) names are based on Frost (2011), using classification concepts based largely on recent molecular studies. Where possible, I have tried also to provide the older, more familiar names.

Ranid frogs range in size from the Wood Frog (***Lithobates sylvaticus***, previously *Rana sylvatica*; 2.5-7 cm long; Figure 2) to the Goliath Frog (***Conraua goliath***; up to 45 cm long).

Figure 2. ***Lithobates sylvaticus*** on a bed of mosses, the smallest of the "true" frogs (Ranidae). Photo © John White, with permission.

Role of Bryophytes for Anurans

Amphibians utilize bryophytes in a variety of ways, from nesting sites to substrata for maintaining or replenishing moisture to perches for calling to winter hibernacula. One of the more amazing discoveries I have made is to pick up a moss clump in late fall and discover a torpid toad beneath it. Indeed, many herpetologists seek out mossy sites when they are on amphibian hunts, as I well remember from my undergraduate days when I had the privilege to go in the field with a well-known **herpetologist** (one who studies amphibians and reptiles). But often the use of the bryophytes is passive or difficult to perceive. The bryophytes grow in the same sorts of habitats where these amphibians can survive, but does the bryophyte really contribute?

The evidence of bryophyte-amphibian interaction is modest and experiments to demonstrate the importance of the bryophytes are all but non-existent. Most of the reports on anurans only mention bryophytes casually. For example, Bosch and Martínez-Solano (2003) describe the factors that influence the presence of montane frogs in ponds and describe their study area as having moss with underwater caves. In many of the contacts I have made with herpetologists they have commented that the area (especially in the tropics) was covered with bryophytes and that surely the frogs make use of that habitat, but often published documentation is lacking. Nevertheless, it appears that loss of bryophytes could seriously impair many species in this highly vulnerable group of vertebrates that already are disappearing from the planet at an extraordinary rate.

Bryophytes provide a number of possible advantages to the anurans. For the tiny species, the bryophytes may be a full-time or part-time home where they can move about unseen by large predators like birds. As we wend our way through the many species that have been collected among the bryophytes, we will find that they provide mating and nesting sites, cover, calling sites, oxygen under water, and even food sources – both as food themselves and as sites for more traditional food items.

Bryophytes harbor many endangered species whose disappearance will increase with the loss of the bryophyte habitat. Some of these are tiny tropical anuran species that have not even been identified or named. Those that stay within the bryophyte mat are the least likely to have been collected (except perhaps by bryologists☺). Many occur on the IUCN (2011) list of endangered species.

Safe Sites

Safe sites, sometimes also known as predator-free sites, are important for amphibians, especially when they are calling or hibernating or nesting. Anurans are vulnerable to all sorts of predators, depending on their size. Large ones can suffer a brutal death by ducks that beat them to death on the water surface. Small ones can even become prey to insects, including those that can inhabit bryophytes, both on land (Figure 3) and in the water (Figure 4), or spiders (Figure 5) that lurk on ground and in the trees. Snakes lurk among the branches and leaf litter (Figure 6-Figure 7). For the amphibians, having colors of green, brown, and black can protect them when living among bryophytes, serving as camouflage. Furthermore, a large number of would-be predators are unable to maneuver among the small spaces provided among the bryophyte branches and leaves. Hence, for small frogs and salamanders the bryophytes provide safe sites. And for winter even larger amphibians can hide under them.

Figure 3. ***Pristimantis ridens*** that has fallen prey to an ant. This tiny frog most likely would have been just as vulnerable to ants within a mat of bryophytes, but would perhaps have been less obvious during its movements. Photo by Tobias Eisenberg, through Creative Commons.

Figure 4. ***Dytiscus*** (diving beetle) larva attacking the frog ***Xenopus***. This freshwater larva can be a threat to small frogs and tadpoles in pools and lakes. Photo by Brian Gratwicke, through Creative Commons.

Figure 5. Toad being eaten by spider in Costa Rica. Photo by Brian Gratwicke, through Creative Commons.

Figure 6. The Lora or Parrot Snake (***Leptophis ahaetulla***) eating the Evergreen Robber Frog (***Craugastor gollmeri***) with a much greater diameter than the snake. Photo by Brian Gratwicke, through Creative Commons.

Figure 7. ***Craugastor gollmeri***, a species adapted primarily for leaf litter, and resembling leaves. Photo by Brian Gratwicke, through Creative Commons.

Moisture and Temperature Conservation

Frogs and toads must maintain **moisture** without drowning, and mosses can provide that balance. As lung and skin breathers, it is more difficult for most anurans to obtain oxygen in water than in air, but the skin must remain moist to keep the cells functional and pliable. The moisture and temperature of the frogs are also important in attaining maximum jumping distance to avoid predators (Walvoord 2003).

Mosses can provide a moist environment at times when other habitats might be dry, playing a major role in the moisture conservation of many amphibians. Mazerolle (2001) demonstrated that the Wood Frog (***Lithobates sylvaticus***; Figure 2) had more predictable activity, based on weather, near the fragmented edges than in pristine bogs. This greater activity seemed to be more related to the amount of precipitation in the fragments than it was in the bogs, suggesting that the bogs are able to buffer the moisture changes for the frogs living there.

Walvoord (2003) demonstrated that for Cricket Frogs (***Acris crepitans*, Hylidae**) maximum jumping distance requires maintenance of appropriate interplay between temperature and hydration. In lab experiments at 30°C, jumping distances of frogs at hydration levels of 85-95% significantly exceeded those at 75%. Furthermore, when the temperature was lowered to 15°C, the frogs had significantly poorer performance. However, at 15°C and 85% hydration, the frogs jumped as well as those at 95% hydration at 30°C. Air temperature was the best predictor of frog body temperature, and sky condition (sunny, cloudy) was the best predictor of hydration. The frogs are able to behaviorally modify their body temperature and their hydration to near optimum by choosing their location, thus permitting them maximal jumping distance and increasing their chances to avoid predators. In the field, the mean body temperature of 55 Cricket Frogs was 28.0°C and hydration was 97.4%. As we shall see, some frogs burrow into mosses during the day or go underground or under mosses, presumably optimizing their temperature and state of hydration.

Calling Sites

In anurans, calling by males is used as a means to attract females. But it also calls attention them by would-be predators (not to mention humans). In the cypress swamps of Georgia, USA, frogs often perch on mounds of moss in summer, using these as locations for breeding calls (Wright 2002), and possibly increasing the distance the call will travel by using an elevated location. But in the tropics, calling sites are often elevated on tree branches and leaves (Figure 8), or even located **within** bryophyte clumps. Presumably, this affords a place to hide while the frog is otherwise making itself more noticeable by calling.

Figure 8. ***Eleutherodactylus eileenae*** (Eileen's Robber Frog) perched on a tree leaf in Cuba to call during breeding season. Photo by Ariel Rodríguez, with permission.

One of the common genera calling from within mosses is ***Bryophryne*** (Figure 9). In southern Peru, at elevations of 3800-3850 m asl, Lehr and Catenazzi (2010) found ***Bryophryne abramalagae*** **(Strabomantidae)** calling from inside Peruvian feather grass clumps and in mosses at 11:00-13:00 hours. Likewise in Peru, ***Bryophryne cophites*** (Figure 9) calls from within moss clumps, despite its absence of a **tympanum** (exposed outer surface of ear drum).

Figure 9. ***Bryophryne cophites*** on a bed of mosses. Note the absence of a tympanum, the external evidence of an ear. Photo by Alessandro Catenazzi, with permission.

In the same location as ***Bryophryne abramalagae***, ***B. flammiventris*** called at 10:00-16:00 hours, again from within large moss mats (Lehr & Catenazzi 2010). Another species of ***Bryophryne*** (***B. gymnotis*****;** Figure 10) and a different genus of strabomantid (***Psychrophrynella*** sp.; Figure 11) also call from moss hideouts. These calls were often heard from the opposite side of the valley, suggesting that the moss cover was likely to be an important safe site during calling, protecting them against detection and possible predation when they were making such loud sounds.

Figure 10. ***Bryophryne gymnotis***, a Peruvian frog that calls from within moss mats. Photo by Alessandro Catenazzi, with permission.

In Bolivia, as in Peru, the genus ***Psychrophrynella*** (syn. = *Phrynopus***)** (**Strabomantidae**, formerly in Leptodactylidae) has a number of species that call from mosses (De la Riva 2007). At Cotapata, ***P. guillei*** begins as the mist rolls over the vegetation, calling from 5-10 cm deep within the mosses. ***Psychrophrynella iani*** calls from under stones and among the mosses. ***Psychrophrynella iatamasi*** (Figure 11) seems to stay in the forest floor mosses for its daytime calling (Aguayo & Harvey 2001). All of the Bolivian **páramo** ***Psychrophrynella*** species seem to call from secluded places such as mosses, with time of day or night depending on the species. The

páramo (Figure 12) is a misty alpine plateau with stunted trees and wide daily temperature fluctuations, creating a severe habitat. Luteyn (2011) describes the páramo as high, cold, inhospitable, wind and rain swept. I think I would seek shelter too.

Figure 11. ***Psychrophrynella*** (=*Phrynopus*) ***iatamasi*** on a bed of mosses. Photo by Ignacio de la Riva, with permission.

Figure 12. Chingaza páramo in the Eastern Cordillera of the Andes, Colombia. Photo by Andres Baron Lopez, with permission.

Peru seems to be one of the best-studied tropical countries for calling sites. ***Gastrotheca pacchamama*** (Ayacucho Marsupial Frog, **Hemiphractidae**; see Figure 13) males were found during the day, calling from moss-covered talus (Duellman 1987).

Figure 13. ***Gastrotheca testudinea***. Photo by Tiffany Kosch, with permission.

In east of Tanzania, from the moss forests at the summit of Morne Seychellois (1000 m), ***Sooglossus*** (=***Nesomantis***) ***thomasseti*** (**Sooglossidae**; Figure 16) calls from under objects, on cliff faces and boulders. Naomi Doak (pers. comm. 24 February 2011) reports that the three species of sooglossids that she studied [***Sooglossus sechellensis*** (Figure 14), ***S. gardineri*** (Figure 15), ***S. thomasseti*** (Figure 16)] call from mosses, and despite sooglossids being ground-dwelling frogs, they sometimes call from mosses on tree trunks.

Figure 14. ***Sooglossus sechellensis***, a species that sometimes calls from epiphytic mosses. Photo by Naomi Doak, with pernission.

Figure 15. Perhaps the world's tiniest frog, ***Sooglossus gardineri*** sits on a bed of moss in the Seychelles. Photo by Naomi Doak, with permission.

Figure 16. ***Sooglossus thomasseti*** sometimes calls from mosses on tree trunks. Photo by Naomi Doak, with permission.

In New Guinea, ***Choerophryne*** species (**Microhylidae**) call from steep, mossy-covered rocky cliff faces, as well as the forest floor and leaves of shrubs (Kraus & Allison 2001).

In a temperate forest in southern Chile, ***Eupsophus emiliopugini*** (Figure 17) (**Cycloramphidae,** formerly in Leptodactylidae**)** and its close relatives excavate burrows in mosses in bogs, from which they make their calls (Penna *et* *al*. 2005). This species also calls from burrows hidden in the moss ***Racomitrium*** (Figure 18-Figure 19) and grasses or ferns on the margins of small streams. Stimuli from calls of nearest neighbors increase the calling intensity, creating a chorus, hence making a larger concentration of frogs that is advantageous for mating.

Figure 17. ***Eupsophus emiliopugini*** on a bed of mosses, probably ***Racomitrium*** sp. Photo by Rafael I. Marquez, with permission.

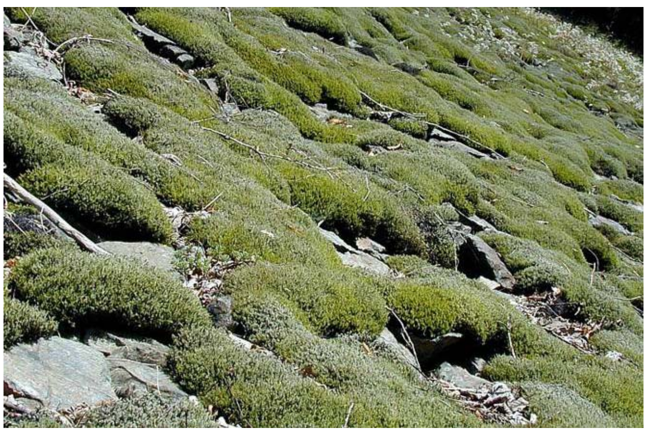

Figure 18. ***Racomitrium lanuginosum*** in Europe. Photo by Michael Lüth, with permission.

Figure 19. ***Racomitrium lanuginosum*** showing spaces where tiny frogs can hide while they call. Photo by Michael Lüth, with permission.

Males of ***Eupsophus calcaratus*** (Figure 20) use cavities within mosses to alter the resonance of their calls (Márquez *et al*. 2005). Hence, the females learn to recognize the resonance characteristics of the mossy burrow-like cavities where the males call. This moss cavity resonance contributes to the recognition by females of the males of their own species in an environment where several species may be calling at the same time.

Figure 20. ***Eupsophus calcaratus***, a frog that uses cavities among mosses to modulate its call resonance. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

It is somewhat of a surprise to find that a Macaya Burrowing Frog (***Eleutherodactylus parapelates***, **Eleutherodactylidae**, formerly in Leptodactylidae) was calling from within a large moss clump at 3 m high in a tree at the Massif de la Hotte of the Haitian Tiburon Peninsula, southwestern Haiti (Hedges & Thomas 1987). Many members of this genus call from mosses on the ground or on trees (*e.g.* ***E. richmondi***, Figure 21). One must interpret general references to the genus ***Eleutherodactylus*** with caution. This genus has recently been divided based on molecular evidence and some members now reside in different families and genera.

Even the larger frogs, in Ranidae, may call from within moss mats. In southwestern Sulawesi, Indonesia, ***Limnonectes*** (=***Rana***) ***arathooni*** calls from 4-10 cm depths within mosses, as well as from leaf litter and rotting roots (Brown & Iskandar 2000).

Figure 21. ***Eleutherodactylus richmondi*** calling from a bed of mosses. Note the really narrow toes that would be of little help in swimming. Photo by Luis J. Villanueva-Rivera, with permission.

Nesting and Reproduction

Some frogs and toads make use of bryophytes as **nesting sites**. Many more species for which the nesting sites are unknown, especially in the tropics, are likely to make use of bryophytes. Altig and McDiarmid (2007) described the arrangement of deposited eggs in amphibians, stating that semiterrestrial eggs need a source of free water without being submerged. Mosses at the edge of a bog or seepy talus often fulfill this need, where some frogs deposit their eggs in wet moss (McDiarmid & Heyer 1994). When the larvae of these species hatch, they do not feed, and they undergo their development right there in the moss bed.

For example, in the Philippines ***Limnonectes* (=*Rana*) *magnus* (Dicroglossidae)**, which is threatened by habitat loss, lays her eggs on rocks and moss (Wells 2007). ***Limnonectes*** (=***Rana***) ***leytensis*** (Swamp Frog, **Dicroglossidae;** Figure 22) also occurs in the Philippines, where it is endemic. The female most frequently deposits her eggs on mosses attached to roots or rocks, although she may also use leaves (Alcala 1962). Males call from the nest and guard the nest until the tadpoles hatch. By placing the eggs near the water, the female provides for the tadpoles to be washed into the water by rain – or to scramble there when disturbed.

Figure 22. The Swamp Frog, ***Limnonectes leytensis***. Photo by Wouter Beukema, with permission.

Frogs that call from mosses often lay their eggs there as well. Figure 23 shows ***Bryophryne cophites*** (**Strabomantidae**) tending her eggs on a bed of moss, perhaps at the same place the male has called to her.

Figure 23. ***Bryophryne cophites*** tending a clutch of eggs laid among mosses. Photos by Alessandro Catenazzi, with permission.

Experimental observations on ***Sooglossus gardineri*** (**Sooglossidae**; Figure 15), an endemic species from the moss forests of Mahe, Seychelles, suggest that wet substrata may be preferred in that species (Nussbaum 1980). In terraria, all observed **amplexus** (mating stage in which a male amphibian grasps a female with his front legs prior to depositing sperm on her eggs; Figure 24) occurred on damp paper towels or mosses. This is one of the tiniest frogs in the world at 9-12 mm long. This small size suggests that it would easily be at home within the epiphytic and ground bryophytes in the mossy forests where it lives. Fortunately, it is relatively widespread in the Seychelles and is not endangered in the way many of these tiny frogs are.

Figure 24. ***Hylarana temporalis*** in amplexus. The smaller frog on top is the male. Photo by Sandilya Theuerkauf, through Wikimedia Commons.

Living in a tree has unique environmental problems for young tadpoles that can't escape or change environmental conditions by swimming. Some species, like tree-dwelling ***Sooglossus seychelles***, have solved the problem by carrying the tadpoles on their backs (Figure 25). Bryophytes in their habitat may help to maintain their moisture.

Figure 25. ***Sooglossus sechellensis*** carrying its tadpoles on its back. Photo by Naomi Doak, with pernission.

Limnonectes* (=*Rana*) *arathooni (Djikoro Wart Frog, **Dicroglossidae)** in Indonesia, where it is endemic (BioDiversity Hotspots), deposits eggs under 4-10 cm of mosses, leaf litter, and rotting roots (Brown & Iskandar 2000). The male guards the eggs until they hatch and calls from within the nest while sitting on top of the eggs. When disturbed, nearly mature larvae can rapidly emerge from the eggs and bounce down rocks, banks, etc to reach the nearby stream water. A further advantage of these streamside nest sites is that the splash of water from the stream keeps them humid, a necessity for these eggs and hatchlings. The height above the water protects the eggs from being washed away during high water periods. ***Limnonectes poilani*** (Figure 26) lives in streams and along their borders in the highlands of central and southern Vietnam and eastern Cambodia. As shown in Figure 26, bryophytes are often common in these habitats.

Figure 26. ***Limnonectes poilani*** **(Dicroglossidae)** on bryophytes in a stream, where its coloration matches that of the rocks. This is a member of a genus that often lays eggs among streamside mosses. Photo by W. Djatmiko, through Wikimedia Commons.

A Cuban species of the widespread bryophyte inhabitant ***Eleutherodactylus*** **(*E. rivularis*;** Figure 27), laid its eggs, a clutch of 42, 4 m from the edge of the Jibacoa River at Las Mercedes (Díaz *et al*. 2001). These eggs where in a hole that had been excavated, presumably by the frog, under a piece of cloth and "moss sheaths."

Figure 27. ***Eleutherodactylus rivularis*** calling to attract a female. Photo by Ariel Rodríguez, with permission.

Many tropical treefrogs deposit their eggs in mosses. The extent of these occurrences is not well documented, and almost no experimental evidence exists to demonstrate any preference. ***Dendropsophus sarayacuensis*** (formerly *Hyla sarayacuensis*; **Hylidae**) (Shreve's Sarayacu Treefrog; Figure 28) from Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela will lay its eggs on either leaves (Figure 29-Figure 30) or moss-covered trees (Henzi 1987).

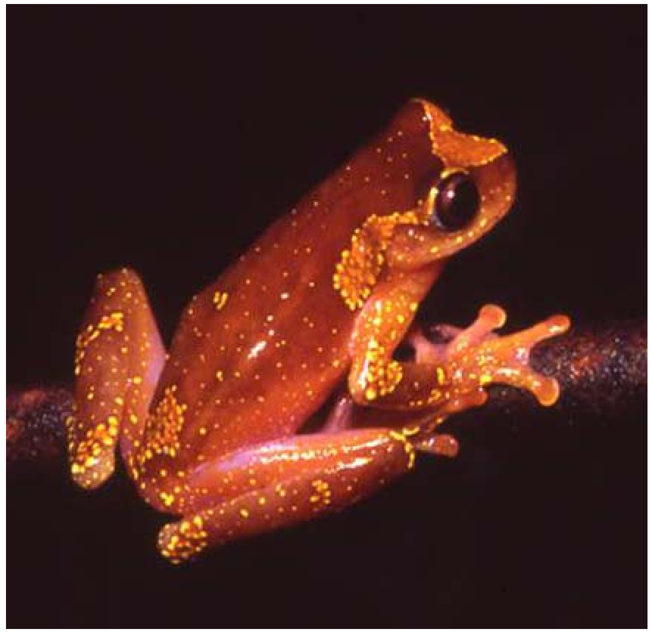

Figure 28. ***Dendropsophus sarayacuensis*** (Shreve's Sarayacu Treefrog) is adapted by its coloration to sitting on a tree branch and looking like lichens or dying leaves that have insect damage. Nevertheless, it also uses mosses as egg-laying substrate. Photo by Andreas Schlüter, through Wikimedia Commons.

Figure 29. Eggs of ***Dendropsophus sarayacuensis*** hanging from the underside of a leaf. Note how easily these masses can break and "drip" the froglets to the ground or water beneath. Photo by Andreas Schlüter, through Wikimedia Commons.

Figure 30. ***Teratohyla*** (formerly *Cochranella*) ***spinosa*** (**Glass Frog**) eggs dripping. Photo by Brian Gratwicke, through Creative Commons.

In North America, the east coast of the USA has several terrestrial species. Among these, we know that the Chorus Frog (***Pseudacris feriarum***; Figure 32) (central Pennsylvania inland south to southern Alabama and Georgia) deposits eggs in February to mid-May at the edge of wet patches (ponds and marshes), often on mosses (Livezey & Wright 1947).

Figure 31. ***Teratohyla*** (formerly *Cochranella*) ***spinosa*** (Glass Frog) on a leaf covered with lichen and liverwort epiphytes. Epiphytes hold moisture and help to keep the frogs moist. Photo by Brian Gratwicke, through Creative Commons.

Figure 32. ***Pseudacris feriarum***, a Chorus Frog that often deposits its eggs on mosses. Photo by John D. Willson, with permission.

The genus ***Mantella*** (Malagasy Poison Frog, Mantellidae) is endemic to Madagascar. It lays clutches of up to 130 eggs that are deposited under moss layers and other hidden places in their captive terrarium, but nesting behavior in the wild may differ (Glaw et al. 2000). ***Mantella laevigata*** (Figure 33) are **oophages** – they eat tadpole eggs, and these may be delivered to them by adult females, providing a type of parental care. Members of the genus ***Mantella*** frequently hybridize with each other, suggesting they aren't quite species yet (see Figure 34 for a member of this group).

Figure 33. ***Mantella aurantiaca*** (golden mantella) on a bed of bryophytes. Photo by Robert Lawton, through Wikimedia Commons.

Overwintering

Many frogs and toads use bryophytes for **cover** from cold and drought, especially in winter or dry weather. It is not uncommon to pick up a moss clump late in the fall and find a hibernating frog or toad under it (personal observation). For some frogs, the bryophytes are a hiding place, and an array of adaptive coloration patterns helps to disguise these amphibians, especially among the tree frogs, as discussed later.

Peatlands may be important temperature mediators for amphibians. Their openness permits warming in the sun, but their branches with air spaces provide a thick insulation from both heat and cold. Toads in north central Alberta, Canada, take advantage of this temperature buffering for hibernation locations (Browne & Paszkowski 2010). In the boreal forest there, 14 out of 21 hibernation sites were in cavities in peat hummocks (Table 1). Other locations were decayed root channels and red squirrel middens (refuse heaps).

Figure 34. ***Mantella expectata***, a species known to hybridize with ***Mantella laevigata***, on a bed of bryophytes. Photo by Paddy Ryan, with permission.

Peatlands in northern areas are known to freeze down to 80 cm. Toads are known to die at temperatures between

-1.5 and -5.2°C (Swanson *et al*. 1996). It is noteworthy that the hibernacula selected by toads in north central Alberta, Canada, rarely or never had temperatures below -5.2°C (Browne & Paszkowski 2010; Table 1). Furthermore, the toads hibernated in communal groups of up to 29 toads, most likely providing further insulation that was not detected by the temperature recorders, although groups of 2-5 were more common. By regularly exchanging positions, they could keep each other from freezing.

The importance of these sites is suggested by their use at distances ranging up to 1020 m from the breeding pond (Browne & Paszkowski 2010). It is likely that the insulation supplied by these peatland sites is crucial for overwintering in these northern sites that mark the limits of tolerance for temperature in ***Anaxyrus***. At the boreal forest site, the toads had a significantly higher selection for black spruce/tamarack stands than for other available habitats, with 79% of the toads hibernating there. Thus it appears that the peat/moss configuration of the forest floor provides the most important overwintering habitat in these northern locations.

Table 1. Site temperature characteristics of paired hibernation and reference sites for Western Toads (***Anaxyrus boreas***). Modified from Browne & Paszkowski 2010.

hibernation or reference	shelter type	depth (cm)	min (C)	consecutive days <0C	<-1.5C	<-5.2C
hibernation	red squirrel tunnel	45	-2.44	176	0.7	0
reference	organic soil under spruce	45	-1.06	154	0	0
hibernation	peat hummock cavities	53	-2.40	149	4.7	0
reference	peat hummock, no cavities	53	-3.37	176	22.2	0
hibernation	burned peat, cavities	47	-8.38	191	10.7	0.6
reference	burned peat, cavities	47	-1.40	163	0	0
hibernation	peat hummock, cavities	62	-9.46	175	41.9	3.2
reference	peat hummock, cavities	62	-6.31	150	21.7	0.7

Undulating Mosses and *Lithobates* (=*Rana*) *sylvaticus* (Wood Frog, Ranidae)

Imagine the mosses around you suddenly heaving and rising! The earliest known report of frogs freezing in winter is that of the Arctic explorer, Samuel Hearne (1769 in Hearne 1911). He reported that he frequently saw Wood Frogs, ***Lithobates sylvaticus*** (Ranidae; formerly placed in *Rana*; Figure 35) that were dug up with the moss when they pitched tents. These seemingly dead frogs could be "brought back to life" by wrapping them in skins and warming them slowly by the fire. For ***Lithobates sylvaticus***, the mosses not only ameliorate the temperature fluctuations, but also greatly reduce the water loss (Churchill & Storey 1993). And, these frogs may very well be frozen, only to start hopping around again in the spring! Despite being the smallest ranid, they are the only frog to be found north of the Arctic Circle (Conant & Collins 1998). Unprotected, the frozen frogs could die in 7-9 days from dehydration, so the moss is an important contributor to their survival.

Figure 35. Wood Frog, ***Lithobates*** (=*Rana*) ***sylvaticus***, among woodland **Polytrichaceae**. Photo by Michael Zahniser, through Wikimedia Commons.

It is not surprising that peatlands are one of the habitats providing a winter home for Wood Frogs. (Wikipedia 2008). Richard Andrus relays "a curious thing I've seen with Wood Frogs in our area (Adirondacks, New York, USA). These critters are explosive breeders in vernal pools for which the eggs and tadpoles are susceptible to predation. So they have a need to find pools that won't support larger frogs and fish. Several years ago I was at a floating mat bog in late April just as the ice was melting. There was ice and snow in the spruce forest around the pond but the mat itself had melted. When we reached the open mat we saw literally 1000's of Wood Frogs all over the mat, in the water, and pouring out of the forest. The reason for this huge number was apparently that the *p*H of the water (ca 4.0) was too low for fish and Green Frog tadpoles (***Lithobates clamitans***; Figure 36) but not too low for Wood Frogs (***Lithobates sylvaticus***; Figure 35). So this was a huge 'safety zone' for them to breed without these predators. They were coming from the north side as its southern exposure caused this to warm up first. On a hunch, the very next week I went out to another floating ***Sphagnum*** (Figure 37) mat I knew of and saw exactly the same thing repeated!! So apparently at least this species can escape egg and tadpole predation by using ***Sphagnum***-acidified ponds."

Figure 36. ***Lithobates clamitans*** (Green Frog) sitting on mosses. Photo by Matthew Niemiller, with permission.

Figure 37. ***Sphagnum lindbergii*** and ***S. balticum*** in Alaska. Photo by Matthew Johnson, for fair use.

Cold Water – *Rana temporaria* (Common Frog, Ranidae)

Despite their **ectothermic** (cold-blooded) nature, many frogs are able to survive winters that take them to below freezing (Koskela & Pasanen 1974). ***Rana temporaria*** (the European Common Frog; Ranidae; Figure 38-Figure 39) is not freeze-tolerant (Voituron *et al.* 2009a). Instead, as is common in northern Finland, ***Rana temporaria*** spends its winters under water to avoid freezing (Koskela & Pasanen 1974). From the time these frogs enter their winter habitat until they leave in April (mature individuals) or May (immature frogs), they disappear into the bottom muds or under bottom moss carpets, stones, or other hiding places. They are not in hibernation, and they can become active if disturbed, but they do not feed. When the air temperature exceeds 5ºC, the adult frogs emerge to land, with the juveniles emerging 1-3 weeks later. Following mating, a large mass of eggs with up to 2000 individuals is produced (Peatlands 2009). The eggs hatch into tadpoles within a week. In Northern Ireland the species is declining due to loss of peatlands and other wetlands. Hence, the species has been legally protected from capture for sale.

Figure 38. European Common Frog (grass frog, brown frog), ***Rana temporaria*** (Ranidae). Photo through Czech Wikipedia GNU Free Documentation License.

Figure 39. European Common Frogs, ***Rana temporaria***, amid their eggs at Cambourne, Cambridgeshire. Photo by Brian Eversham, with permission.

Freeze Tolerance – *Rana arvalis*

In contrast to ***Rana temporaria***, ***Rana arvalis*** (Moor Frog, **Ranidae**; Figure 40) is **freeze-tolerant** (Voituron *et al.* 2009a). It spends the winter not in the water, but in the soil under litter or mosses. The juveniles can survive freezing temperatures for about 72 hours at body temperatures of -3°C (Voituron *et al.* 2009b). In nature, they prepare for this when the temperature drops to the range of 4 to -1°C. In this temperature range, glucose increases 14-fold in the liver and 4-fold in the muscles. **Aerobic** metabolism (using oxygen) persists at a low level, decreasing with temperature, thus preventing the toxic conditions that would arise from **lactate** accumulation. Voituron *et al.* (2009b) suggest that their terrestrial habitat beneath mosses and litter layers provides a temperature regime that shortens the time they spend frozen. Allowance for temperatures to -3°C would permit them to live without freezing under the insulation of snow with the added insulation of the litter, including mosses.

Figure 40. ***Rana arvalis*** (Moor Frog) on a bed of mosses. Photo by Petr Balej, with permission.

Despite this cold tolerance, ***Rana arvalis*** (Figure 40) seems to be rare in the Czech Republic (Šandera *et al.*

2008). It requires nearby water with emergent vegetation where it can attach its eggs (Martin Šandera, pers. comm. 20 February 2011). Its breeding period is a short one week, and that is the time it is best to observe it. After that, even if found, it is difficult to identify.

Under Woodland Bryophytes - *Pelophylax* (Ranidae)

Other frogs **hibernate** in woodlands. ***Pelophylax lessonae*** (Pool Frog; Figure 41) and ***P. ridibundus*** (Edible Frog; Figure 42-Figure 43), both formerly placed in *Rana*, leave the ponds to prepare for winter (Holenweg & Reyer 2000). ***Pelophylax esculentus*** (Figure 44) is a hybrid of ***Pelophylax lessonae*** (Figure 41) and ***Pelophylax ridibundus*** (Marsh Frog, also formerly included in *Rana*), (Figure 42-Figure 43), but it is no longer recognized as a separate species by Frost (2011). In the woodlands, members of this frog group hibernate 3-7 cm below the surface, often under mosses, fallen leaves, or soil. Interestingly, they change hibernation sites during the winter, sometimes more than once. They seem able to find warmer spots – the hibernation sites had warmer temperatures than other spots that were sampled.

Figure 41. The Pool Frog (***Pelophylax lessonae***) from Europe. Photo by M. Betley, through Wikimedia Commons.

Figure 42. Marsh Frog, ***Pelophylax ridibundus***. Photo by Christian Fischer, through Creative Commons.

Figure 43. Marsh Frog, ***Pelophylax ridibundus***, with secreted white mucous that is most likely poisonous or distasteful to some of its would-be predators. Photo by Piet Spaans, through Creative Commons.

Figure 44. The Edible Frog, ***Pelophylax esculentus*** group. Photo by Leo Bogert, through Wikimedia Commons.

Bryophytes for Food and Food Locations

Strangely enough, Ting (1950) found that ***Sphagnum*** (Figure 37) mixed with egg yolk could serve as a food source when rearing various species of tadpoles. It has the added advantage of reducing the bacterial growth. Hartmann (1971) discovered that certain mosses produced **neurohormones** that stimulate frog hearts much like the action of **acetylcholine** (and have the same RF value). However, there is no conclusive evidence that mosses serve as an intended food source for adult frogs in nature.

Tadpoles may, however, consume at least some bryophytes in nature. We generally think of tadpoles as being algal and detrital feeders. However, at least in the terrestrial habitat, bryophytes may form part of the diet (Wickramasinghe *et al*. 2007). The semi-terrestrial tadpoles of ***Nannophrys ceylonensis*** (Ceylon Streamlined Frog, **Dicroglossidae**; Figure 45) in Sri Lanka, like most tadpoles, shift from a scraping food strategy as larvae to catching live prey as adults. During their larval stage, algae are an important part of their diet, with the majority of diatoms being ***Selenastrum*** (Figure 46). Surprisingly, in the population studied by Wickramasinghe *et al*., ***Barbula*** sp. (*sensu lato*; Figure 47) accounted for most of the moss consumption. As the body size increases, the consumption of mosses decreases significantly, as does the consumption of diatoms. At the same time the mosses and diatoms diminish in the diet, so does the gut size. (Longer guts are needed to absorb nutrients from food organisms with cell walls, like algae and mosses.)

Figure 45. ***Nannophrys ceylonensis*** among the small plants of the moss ***Fissidens*** on the rock. Photo by Peter Janzen, with permission.

Figure 46. ***Selenastrum***, an alga that provides food for larval ***Nannophrys ceylonensis***. Photo by Yuuji Tsukii, with permission.

Figure 47. ***Barbula convoluta*** from Europe, member of a genus that can provide food for frogs. Photo by Michael Lüth, with permission.

Stebbins (1955) found the Tailed Frog ***Ascaphus truei*** (Figure 48) (Leiopelmatidae) in company of the Olympic Salamander ***Rhyacotriton olympicus*** under moss-covered rocks along the Pacific coast. Since the seepage where they were found was nearly completely hidden by the mosses, it is not clear that presence of the moss on the rocks was an important habitat consideration or simply that both frogs and mosses preferred the same conditions. But it seems that the two amphibians prefer the same food (Bury 1970). More specifically, young frogs eat a diet similar to that of the salamander. ***Ascaphus truei*** shifts from having mostly **Collembola** in the diet when young to eating more amphipods at older stages. But even when both are eating the same foods, the abundance of food items among the mosses prevents competition. ***Ascaphus truei*** climbs on rocks that are covered with mosses and algae, and Noble and Putnam (1931) suggested that these moss-covered rocks might provide a richer food source than locations within the rapid flow of the stream. Bury (1970) indicated that this habitat of ***Ascaphus truei*** was consistent throughout their range, where they lived in association with "small, water-washed or moss-covered rocks" in running water or along its borders.

Figure 48. Coastal Tailed Frog, ***Ascaphus truei***. Photo by James Bettaso, with permission.

Occasional Usage – A Place to Travel

In Panama, aerial frogs like the Banded Horned Treefrogs, ***Hemiphractus fasciatus*** (formerly ***Cerathyla panamensis*; Hemiphractidae**) (Figure 49-Figure 53) may make indirect or intermittent use of bryophytes. This frog lives among **bromeliads** – those basket-shaped plants that capture water and live in trees (Stejneger 1917). The female ***Hemiphractus fasciatus*** carries her eggs and her young on her back (Myers 1966; Figure 49-Figure 50), suggesting that desiccation could become a problem. The bromeliads are abundant on both trees and the ground, and mosses are frequently present around them. It is difficult to imagine that these frogs do not take advantage of the cover, camouflage, and moisture of the mosses as they move from place to place. At the very least, one might expect to find these frogs when looking for bryophytic treasure on tropical tree branches. However, it appears that this species does not need to hide from many kinds of predators.

Instead, it rears up, arches its body, and throws up its head (Figure 51). The yellowish-orange tongue and large mouth present an imposing image (Figure 53). If a would-be predator makes contact, the frog has further defense by clamping two sharp tooth-like projections (Figure 53) into the attacker and hanging on with a strong grip (Figure 52), a painful experience that Myers knew all too well. The frog had to be pried loose!

Figure 49. ***Hemiphractus fasciatus*** female carrying eggs on her back. Photo by Edgardo J. Griffith, El Valle Amphibian Conservation Center (EVACC), Director, with permission.

Figure 50. ***Hemiphractus fasciatus*** female with juvenile frogs on its back. Eggs are retained in patches until the larvae develop into young adults, then remain for some time with the mother after hatching (Myers 1966). This behavior permits the adult to carry the young to locations with sufficient moisture. Photo by Brian Gratwicke, through Wikimedia Commons.

Figure 51. ***Hemiphractus fasciatus*** rearing up in a defensive position. Photo by Brian Gratwicke, through Creative Commons.

Figure 52. ***Hemiphractus fasciatus*** eating an earthworm. Note the two sharp teeth just to the right of the worm on the lower jaw. Photo by Edgardo J. Griffith, El Valle Amphibian Conservation Center (EVACC), Director, with permission.

Figure 53. ***Hemiphractus fasciatus*** with open mouth, showing yellow tongue and two sharp front teeth (in front lower jaw). Photo by Marcos Guerra, through fair use copyright.

Adaptations to Bryophyte Habitats

It is interesting that so many species of anurans exist sympatrically (same geographic area) in "mossy" habitats such as the mountain tops of tropical areas. Hofer *et al.* (2004) paraphrased Gause's Rule by stating that "If interspecific competition is a strong structuring force of communities, ecologically similar species should tend to have spatial ranges at local scale that do not overlap." They used collected data to test the hypothesis and were surprised to find that whereas lizards and birds exhibited adjustments that reduced the potential for interspecific competition, the frogs did the opposite – there was a greater than chance co-occurrence of ecologically similar frog species. They suggested that resource requirements such as breeding sites may be more important for frogs than competition.

With this in mind, we can see that bryophytes can play a role in providing breeding sites that maintain moisture and provide cover that contributes to keeping the eggs safe. They furthermore provide moist respites for travelling anurans, and for many species can provide hiding places. Given this usage of bryophytes to define part of the anuran niche, we should expect adaptations to have evolved that make this bryological life somewhat easier.

An Altered Life Cycle

Alcala (1962) divided the tadpoles of anurans into three environmental categories. Stream dwellers have depressed bodies, strong tail muscles, and reduced body and tail fins (Figure 54); pond tadpoles have subspherical bodies, weak tail muscles, and high body and tail fins (Figure 55). Both of these aquatic larvae come from small eggs laid in large clutches. Larvae with direct development (out of water) have altered larval structures, including abdominal sacs instead of gills, and derive from large eggs in small clutches. A fourth category is those anurans that have no tadpoles at all, but that hatch directly into froglets.

Figure 54. ***Atelopus limosus***, showing the flattened body of a stream tadpole. Photo by Brian Gratwicke, through Creative Commons.

Figure 55. ***Paracrinia haswelli*** (**Haswell's Frog**) tadpole showing the high body and tail fins typical of pond tadpoles. Photo through Wikimedia Commons.

In the study area of Negros, Philippine Islands, more than 50% of the eggs are laid out of water (Alcala 1962). Among those in the study, some eggs were attached to mosses growing on rocks above a pool in a mountain stream, including ***Platymantis dorsalis*** (=*Cornufer meyeri*; **Ceratobatrachidae**; Figure 56) whose adults live on the montane forest floor, sometimes under moss mats.

Figure 56. ***Platymantis dorsalis***, a frog that seeks refuge under moss mats on the forest floor. Photo by Amir Hamidy, with permission.

Food Capture

Terrestrial adults require different adaptations to capture their food than do the aquatic larvae of their ancestors. One of these adaptations is an extremely fast tongue (O'Reilly & Nishikawa 1995). The anuran tongue is attached at the front, permitting a rapid and extended unfolding.

Escaping Predators and Flying Moss Frogs

When hiding among the mosses is not an option for avoiding predators, then a fast getaway might work. ***Ecnomiohyla rabborum*** (**Rabb's Fringe-limbed Treefrog**, **Hylidae**) is only known from the cloud forest in the mountains near El Valle de Anton, Panama, in the narrow elevational range of 900-1150 m asl (Mendelson *et al*. 2008; Mendelson 2009), where it lives in the canopy. Its large feet (Figure 57) permit it to glide downward from its arboreal habitat, effecting a rapid escape route. It lays its eggs in tree holes, just above the water line. Males remain near the eggs and defend them (Frost 2011). Although I could find no documentation that this species uses mosses, its habitat in the canopy of the cloud forest almost assures that it does.

Figure 57. ***Ecnomiohyla rabborum*** (**Rabb's Fringe-limbed Treefrog**, Hylidae), illustrating the large, very webbed feet used for gliding in the Costa Rican forest. Photo by Brian Gratwicke, through Creative Commons.

I thought I had finished adding new species to this chapter when I ran into "moss frogs." None of the names I had seen used this terminology except for the "mossy frogs" that mimicked mosses. But these were a whole new group of frogs, the genus ***Arthroleptella*** (**Moss Frogs, Pyxicephalidae**; southern Africa) and the family **Rhacophoridae** (Old World Tropics) (Wikipedia 2015a). Well – not quite all were new. ***Theloderma***, the genus of the Vietnamese Mossy Frog, is in the **Rhacophoridae** and will be discussed below.

Of interest is that some members of the genus ***Rhacophorus*** are known as **Flying Frogs** or **Parachuting Frogs**. ***Rhacophorus malabaricus*** (**Malabar Flying Frog**, **Rhacophoridae**; Figure 58-Figure 59) lives in the Western Ghats of India with an altitudinal range of 300-1200 m asl (Biju *et al*. 2004).

Rhacophorus malabaricus lives in tropical moist evergreen and deciduous forests as well as secondary forests and agricultural forests such as coffee plantations (Wikipedia 2011b). It spends its time in the lower canopy or understory and breeds in overhanging vegetation where tadpoles can drop from the foam nests into ponds and pools.

Rhacophorus malabaricus frogs are known as flying frogs because of their ability to glide from their arboreal habitat to the ground. Using their leg and toe spread (Figure 60) and unique morphology, they are able to minimize their descent (falling/gliding) speed and maximize their descent time (Emerson & Koehl 1990). Rather than relying on increasing horizontal travelling distance, their particular maneuverability permits them to actually decrease horizontal distance during descent. These gliding pathways can carry them 9-12 m, about 115 times their length (Wikipedia 2011b). Webbing between the toes further increases their gliding ability.

Figure 58. ***Rhacophorus malabaricus*** showing its narrow legs. Photo by L. Shyamal, through Wikimedia Commons.

Rhacophorus arboreus (**Japanese Green Treefrog**; **Kinugasa Flying Frog**; Figure 61-Figure 62) lives in Honshu, Japan, from sea level to 2000 m asl (Chantasirivisal 2011). It is a comparatively large treefrog; adult males are smaller (42-60 mm) than females (59-82 mm). During breeding season, they live in ponds and rice fields. Otherwise, they live in trees and leaf litter. They hibernate through the winter under moss or shallow soil. Unlike the moss frogs of ***Arthroleptella***, ***Rhacophorus arboreus*** females deposit eggs in a foam nest on vegetation near standing water where the larvae can easily enter the water. To protect the eggs, the female excretes an albumin-based fluid from her cloaca. She creates the foam by beating her hind legs, forming a nest to protect the 300-800 eggs. The male then fertilizes the eggs and the foam hardens, protecting the eggs from water loss and predators.

Figure 59. ***Rhacophorus malabaricus*** showing its ability to flatten against its substrate. Photo by L. Shyamal, through Wikimedia Commons.

Figure 60. ***Rhacophorus malabaricus*** in amplexus. Note the webbing between the toes that helps it to glide and maneuver to the ground. Photo by Sandilya Theuerkauf, through Wikipedia Commons

Figure 61. ***Rhacophorus arboreus*** (**Japanese Green Tree Frog; Kinugasa Flying Frog**). Photo by Peter Janzen, with permission.

Figure 62. ***Rhacophorus arboreus*** (**Japanese Green Tree Frog**) in its arboreal home. Photo © Danté B. Fenolio <www.anotheca.com>, with permission.

Arthroleptella bicolor (**Bainskloof Moss Frog**, **Pyxicephalidae**) lives in fynbos and heathland of Western Cape Province, South Africa at 300-2000 m asl (IUCN 2011). This species breeds in wet mossy areas usually near water, where it lays 8-10 eggs in terrestrial mosses or similar vegetation. Nevertheless, its eggs do not hatch into tadpoles, but develop directly into froglets.

Arthroleptella drewesii (**Drewe's Moss Frog, Pyxicephalidae**; Figure 63) is endemic to Table Mountain and other mountains, up to 1,000 m asl, in the Cape Peninsula of South Africa (IUCN 2011). It lives in fynbos and heathland, as well as forest. It lays its 5-12 unpigmented eggs in moss or similar vegetation in wet mossy areas similar to those of ***A. bicolor***. As in ***A. bicolor***, the eggs hatch directly into froglets.

Arthroleptella lightfooti (**Lightfoot's Moss Frog** or **Cape Chirping Frog**, **Pyxicephalidae**) is endemic to Table Mountain and to the other mountains of the Cape Peninsula, South Africa, where it occurs from sea level up to 1000 m asl (Frost 2011). Like the other ***Arthroleptella*** species thus far, it lives in fynbos, heathland, and forest (IUCN 2011). It lays its 5-12 eggs in mosses or similar vegetation in wet mossy areas, and likewise chooses locations near wet areas and streams (Rose 1929; Livezey & Wright 1947; Frost 2011). It, too, has direct development into froglets. Metamorphosis to adults occurs there on the mosses (Livezey & Wright 1947).

Figure 63. ***Arthroleptella drewesii*** on a bed of moss. Photo by Robert C. Drewes, with permission.

Arthroleptella villiersi (**De Villiers' Moss Frog, Pyxicephalidae**) is endemic to the western cape of South Africa, from sea level up to 1,000 m asl (IUCN 2011). It lives in lowland and montane fynbos and heathland, where it breeds in wet mossy areas similar to those of the other ***Arthroleptella*** species mentioned here. It lays its 10 eggs in moss and similar vegetation.

Anhydrophryne hewitti (**Hewitt's Moss Frog, Pyxicephalidae**; Figure 64) lives in forest and dense vegetation in the Drakensberg and midlands of Kwa-Zulu Natal, South Africa (IUCN 2011). Its breeding habitat is in wet mossy areas of riverine bush and forest near waterfalls and rapids. The 14-40 eggs are laid in moss and leaf-litter on edges of streams. Despite its preference for streamside habitats, the eggs develop directly without a larval stage.

Figure 64. ***Anhydrophryne rattrayi***, here blending with the leaf litter, shows the small size of these frogs. Another member of its genus, *A. hewitti*, lays its eggs in wet mossy areas along streams. Photo by Robert C. Drewes, with permission.

But most frogs don't glide. Some can hop quite high. I had a pet **Green Frog** (***Lithobates clamitans***) I soon named Mr. Wanderlust. He lived in my garden room on the main floor of the house, but he would often escape. I found him hopping across the TV room at the other end of the house several times, at the top of the stairs on the second story several times, and once I found him on top of the open door! I watched him jump one time as I saw him on the floor beside me at my desk. Then suddenly, he was on the desk beside me! But despite our usual vision of hopping frogs, many of them spend more time creeping and climbing (Figure 65). That is how Mr. Wanderlust escaped under the hanging screen to get free from the garden room.

Figure 65. ***Lithobates clamitans*** attempting to climb a soil bank. Photo by Sheryl Pollock, with permission.

Camouflage and Mimicry

When you make a good dinner, it is helpful to be invisible. A number of species of frogs have disruptive coloration that would make them less conspicuous than a solid color. Greens and browns are common colors among frogs, again providing good camouflage for moss dwellers. But some have disruptive skin surfaces with warts and other extensions, making them blend with the mosses even more.

Importance of Being Still

One reason we know so little about the moss-dwelling frogs is that they do camouflage so well. Cooper *et al*. (2008) noted that camouflaged frogs should limit their movement to avoid detection by disrupting their crypsis. They experimented with ***Craugastor fitzingeri*** (formerly *Eleutherodactylus fitzingeri*; **Craugastoridae**; Figure 66-Figure 67) and demonstrated that when the frogs were motionless, four humans were able to detect only 60% of them in a 2 m diameter circle within 60 seconds. Over 90% of the individuals of five species of ***Craugastor*** remained motionless until the potential predator reached them.

Disruptive Coloration - *Boophis*

Vallan *et al*. (1998) reported on a new tree frog in the genus ***Boophis*** (**Bright-eyed Frogs**, **Mantellidae**; Figure 68) from Madagascar. This frog was especially adapted to blending with tree bark covered with lichens – it has tubercles and fringes and flattens against the branch when it is disturbed. It can change colors from whitish to brown, thus making it also camouflaged on some bryophytes. This mimicry makes it very different in appearance from other members of the genus, such as ***B. viridis*** (**Green Bright-eyed Frog**; Figure 69).

Figure 66. ***Craugastor fitzingeri*** on mosses. Photo by Brian P. Folt, with permission.

Figure 67. ***Craugastor fitzingeri***, with colors that blend with the soil. This one seems to be eyeing an ant, a potential food source. Sitting quietly not only protects it from being preyed upon, but also permits it to lie in wait for food organisms without being noticed. Photo by William Leonard, with permission.

Figure 68. ***Boophis lichenoides*** showing small tubercles, fringes and mottled (disruptive) coloration that help it to be inconspicuous among lichens on bark. Photo by Franco Andreone, through Creative Commons.

Figure 69. ***Boophis viridis*** (**Green Bright-eyed Frog**), a greenish member of the genus that looks very different from the lichen mimic, ***B. lichenoides***. Photo by Franco Andreone, through Creative Commons.

Ceratophrys ornata, A Bryophyte Mimic

Some frogs and toads really play it safe with both disruptive coloration and tubercles, making them look like the light and dark patches of a bryophyte clump. Such is the case for ***Ceratophrys ornata*** (up to 16.5 cm long), the Argentine Horned Frog, but it appears that this frog typically spends its time in grassland (except in captivity). In fact, moss in a terrarium can cause impaction if the frogs eat it. These frogs are unusual in having teeth and a strong jaw – strong enough to inflict pain on animals that attack them. The mouth is extremely large, and they feed on rodents, small reptiles, large spiders, and insects. Gut analysis of thirty-four specimens from Uruguay included 78.5% anurans, 11.7% passerine birds, 7.7% rodents, and 0.3% snakes, leaving only 1.8% as "other" (Basso 1990). They use a "lie-in-wait" strategy that is facilitated by their similarity to the bryophyte (or other) background. There are several color forms, ranging from mostly green to mostly brown. The larvae are also unusual – these are the only vertebrates to make calls in the larval state.

Figure 70. ***Ceratophrys ornata*** in a bed of moss. Photo through Flickr Creative Commons.

Figure 71. ***Ceratophrys ornata*** squatted among bryophytes. Photo by John White, from Wikimedia Commons.

Tubercles - *Theloderma corticale* (Vietnamese Mossy Frog, Rhacophoridae)

The **Vietnamese Mossy Frog, *Theloderma corticale*** (Figure 72-Figure 73), is one of many moss mimics among the amphibians, and perhaps the most famous. Literally translated from medical terminology, its generic name means nipple skin. Although it resembles a toad, it is not one. This strange animal can mimics both mosses and bird droppings, sometimes in the same animal! (Indraneil Das, pers. comm. 8 January 2012).

Figure 72. **Vietnamese Mossy Frogs**, ***Theloderma corticale***. Photo by Milan Kořínek, with permission.

It is an inhabitant of the karst zones of northern Vietnam, where it lives in flooded caves and other deep holes on the banks of mountain streams (Ryboltovsky 1999). Its skin is a mottled black and green that resembles a "bunch of moss." Numerous spines and tubercles add to the disruptive pattern that makes it quite invisible among the dense moss and lichen cover (Figure 73).

These frogs remain quiet in the daytime and hunt at night (Figure 73). When frightened, they will roll into a ball and play dead (Figure 74) (Wikipedia 2015b). They also avoid detection by being ventriloquists – throwing their voice to another location so they cannot be found while calling. This rare frog is now being bred as a terrarium pet. It appears that the starter pair has been rescued from an area that is rapidly becoming unsuitable as a home. Despite its broad habitat range, it is threatened by habitat loss (Animal Photo Album 2007).

Figure 73. ***Theloderma corticale*** (**Vietnamese Mossy Frog**) camouflaged among bryophytes. Photo by Brian Gratwicke, through Creative Commons.

Figure 74. ***Theloderma corticale*** (**Vietnamese Mossy Frog**) on its back, feigning death. Photo © Chris Mattison <http://www.agefotostock.com/age/ingles/home01b.asp>, with permission.

Green and Wet - *Centrolene geckoideum* (Pacific Giant Glass Frog, Centrolenidae)

The Pacific Giant Glass Frog, ***Centrolene geckoideum*** (Figure 75), lives in tropical and South American cloud forests of Ecuador and Colombia (Glass Frogs: Centrolenidae), especially near waterfalls or rapids, where traversing mossy substrata must surely be a necessity in some locales. This is the largest of the glass frogs and its coloration of dark green to lime green, and skin covered with tubercles, most likely helps it to be inconspicuous among wet bryophytes and rocks. Clearing of forests for farming and chemical sprays from agriculture have reduced numbers so that this is listed as an IUCN vulnerable species (IUCN 2011).

Figure 75. ***Centrolene geckoideum***, the Pacific Giant Glass Frog, from near Tandayapa, Province of Pichincha, Ecuador. Note the tubercles and greenish color that helpsto camouflage this frog among bryophytes and lichens. Photo by William Duellman, courtesy of Biodiversity Institute, University of Kansas, with permission.

Changing Colors - *Platymantis* spp. (Ground Frogs, Ceratobatrachidae)

Platymantis macrosceles (Figure 76), endemic to Papua New Guinea, where it lives in montane forests, is not known for its arboreal behavior. However, when Foufopoulos and Brown (2004) found them in New Britain, two of them were perched on moss-covered branches of shrubs about 1 m above the ground and 2 m from a small stream. Their tubercles, combined with brown spots on green backs, made them all but invisible on their mossy perch. Interestingly, when removed from the mosses, they lost their patterned colors and became a yellowish green color (Figure 76; Johannes Foufopoulos pers. comm. 10 February 2009).

Figure 76. ***Platymantis macrosceles***, after losing its color when removed from its mossy perch. Photo by Johannes Foufopoulos, with permission.

Platymantis mamusiorum (**Ceratobatrachidae**; Figure 77), another little-known frog from the Nakanai Mountains of New Britain, Papua New Guinea, lives in montane rainforests where the ground and logs are thickly covered with moss (Foufopoulos & Brown 2004). It spends resting time on bushes and low branches up to about 1 m from the ground, but its cryptic coloration permits it to remain unseen against a mossy background. It is not as well camouflaged as the former species, lacking the brown spots and tubercles (Johannes Foufopoulos pers. comm. 10 February 2009).

Figure 77. A ground frog, ***Platymantis mamusiorum*** showing cryptic coloration on a bryophyte-covered perch. Photo by Johannes Foufopoulos, with permission.

Colors Matter

As seen by the foregoing discussion, cryptic and disruptive coloration permit frogs to sit quietly without being seen. But it is not just blending with one particular substrate that provides an advantage. Having multiple color forms within a species increases chances for the species to survive. Forsman and Hagman (2009) demonstrated this in their studies of 194 species of Australian frogs. The polymorphic color patterns afforded larger ranges, more survival habitats, less negative population trends, and less vulnerability to extinction compared to species with non-variable color patterns. Among these, we can assume, is the ability for some color forms to utilize bryophyte habitats to their advantage where they are available. is a good example of multiple color morphs.

Oophaga pumilio has many color morphs (Pröhl & Ostrowski 2011; Figure 78-Figure 81) with estimates of 15-30 different forms (Summers *et al*. 2003). The green morphs typically remain within the moss mats and spend less time foraging compared to the brightly colored morphs that are more active (Pröhl & Ostrowski 2010). This dual strategy in a highly poisonous frog permits two different kinds of adaptations to operate in the same population. The brightly colored morphs advertise their poisonous nature through their warning coloration, whereas the green morphs are less conspicuous to us, to predators, and apparently also to potential mates.

Figure 78. Orange color morph of the Strawberry Poison Dart Frog, ***Oophaga pumilio***. Photo by Peter Janzen, with permission.

Figure 79. White color morph of the Strawberry Poison Dart Frog, ***Oophaga pumilio***. Photo by Peter Janzen, with permission.

Figure 80. Yellow color morph of the Strawberry Poison Dart Frog, ***Oophaga pumilio***. Photo by Peter Janzen, with permission.

Figure 81. Blue color morph of the Strawberry Poison Dart Frog, ***Oophaga pumilio***. Photo by Peter Janzen, with permission.

Does Size Matter?

Although some large frogs and toads make use of mosses for nesting and moisture retention, those that live within the mosses terrestrially are typically quite small. Bryophytes, particularly mosses, provide them with small spaces where they can navigate without being seen by hungry predators. But it appears that bryophytes might have had a role in their evolution and size characteristics.

The tiny ***Noblella pygmaea*** (**Noble's Pygmy Frog, Strabomantidae**; Figure 82) was found for the first time in southern Peru, where it occupied two habitat types, one along the montane ridge and the other in the elfin forest where moss cover was abundant (Lehr & Catenazzi 2009). This frog is the smallest in the Andes (females 12.5 mm, males 10 mm) and one of the smallest in the world. (Note that members of **Leptodactylidae** and related families have many small members and will be discussed later). Having a small size, while beneficial for hiding in mosses, is detrimental for venturing away from the moss during the drying heat of day. As size decreases, the surface area to volume ratio increases, providing relatively more surface area for losing water.

To understand the role of size and other parameters in the evolution of Neotropical amphibians, Gonzalez-Voyer *et al*. (2011) examined the correlates of species richness with habitat parameters and body morphology. They found that a greater age of the clade did not increase richness. Rather, ecological and morphological traits seemed most important. One of these traits that correlated well with greater terrestrialization and ability to live at high altitudes was the presence of greater vascularization in the ventral skin. This, presumably, may aid in moistening the body by ventral contact with moist substrates such as bryophytes.

Figure 82. Adult ***Noblella pygmaea*** on what appears to be a liverwort. Photo by Alessandro Catenazzi, with permission.

Since being small can also be a problem for eggs, having only two eggs permits ***Noblella pygmaea*** to make larger eggs with less relative surface area to suffer drying out (Figure 83) (Gonzalez-Voyer *et al*. 2011). The moss cover should help to protect both eggs and adults against water loss as well as provide camouflage, but the preferred egg-laying locations of many of these small species, including ***Noblella pygmaea***, are not known.

Figure 83. Adult ***Noblella pygmaea*** with its two eggs. Photo by Alessandro Catenazzi, with permission.

Although Gonzalez-Voyer *et al.* (2011) found no correlation between latitude and richness, Wiens (2007) and Moore and Donoghue (2007) found greater diversification rates in amphibians in lower latitudes. Amphibians seem to have evolved in contrast to **Bergmann's** (1847) **rule** (species of larger size are found in colder environments; usually applied to endotherms), having greater body size farther from the poles and small size at high elevations in the tropics (Feder *et al*. 1982; Adams & Church 2007; Lehr & Catenazzi 2009). Geist (1987) disagreed with Bergmann's rule and instead claimed that in mammals body size initially increases with latitude, but at latitudes of 53-65°N it reverses, with the result being small body sizes at the lowest and highest latitudes.

But does this relationship apply to ectotherms like anurans? Ashton (2002) found a distinct body size relationship with latitude and elevation in salamanders, with 13 of 18 species being larger in higher latitudes and elevations. But anurans seemed less likely to conform, with only 10 of 16 species showing these trends.

Part of the disagreement lies in what is being compared. The within species comparison of Ashton (2002) is not the same as comparing among species and genera. Blackburn and Hawkins (2004) quote Bergmann as saying that "on the whole. . . larger **species** live farther north and the smaller ones farther south."

For terrestrial frogs, Gonzalez-Voyer *et al*. (2011) found that larger body size correlated only marginally with latitude and elevation. In fact, they suggested that small-bodied species may diversify more than larger ones in the Neotropics, at least in the Andes, because they are able to partition the niches on a finer scale (see also Lomolino 1985; Purvis *et al*. 2003).

The first explanation that comes to mind regarding Bergmann's rule is that a larger body is less susceptible to losing heat due to a smaller surface area to volume ratio. While this is a reasonable explanation for endotherms, there does not seem to be any reason to assume this for ectotherms. In fact, Ashton (2002) found no clear relationship between body size of salamanders and environmental temperature.

One explanation for the ability of small frogs to survive at high altitudes is their ability to make a physiological activity shift in response to lower temperatures (Navas 1996, 2006; Lehr & Catenazzi 2009).

This ability permits them to occupy the "mosaic" of small patches where the habitat is suitable and a food source is available (Hutchinson & MacArthur 1959). These terrestrial frogs have the advantage that they do not need to migrate to water to lay their eggs, and generally their home range is small, sparing them of the dangers of moving among a patchwork of unfavorable habitats. Such small patches would be unsuitable for larger frogs with greater food demands and need for moisture.

Let us consider the genus ***Pristimantis***, a genus that includes arboreal bryophyte dwellers, in this discussion. ***Pristimantis*** (Figure 84) represents the clade with the greatest number of terrestrial species (Gonzalez-Voyer *et al*. 2011). Lynch and Duellman (1997) reported a correlation between small body size and arboreal species richness in this genus. Concomitantly, prey size correlates with body size, a phenomenon which Duellman (2005) suggested might indicate competitive release through resource partitioning, subsequently explaining high local diversity that can reach as high as 139 species in 6.5 km^2 in the Amazon (Bass *et al*. 2010).

One explanation for the successful niche partitioning is that large amphibians retain water more easily and maintain body heat at a more constant temperature (Shoemaker 1992). The presence of many body sizes permits greater niche partitioning, with each size group locating where moisture and temperature are optimal. In this regard, the variety of bryophyte growth forms available can provide a wide range of niches with different moisture and insulating abilities. Conversely, the divergent niches offered create divergent selection pressures that, coupled with the geographic isolation afforded by ridge and valley topography, provide suitable conditions for speciation (Lynch 1986; Lynch & Duellman 1997).

Figure 84. ***Pristimantis bacchus*** on a bed of mosses. Photo by Esteban Alzte, through Creative Commons.

One peculiar habit noted for small frogs in marshy areas of Suryamaninagar, Tripura, India, is that they form small groups as rain approaches, effectively becoming a large animal, but after it stops they separate from each other (Acharya 2011). One could hypothesize that this behavior may help to prevent overcooling during the rain, so it would be interesting to know if the same behavior would occur if they were able to sit within the cover of bryophytes.

The Frog or the Egg?

When frogs invaded bryophytes, whether on the ground or in the trees, did they invade because they were small, or did they become smaller as they adapted more and more to terrestrial living and bryophytic habitats? Did the tiny frogs invade first, or did they begin using bryophytes as egg-laying sites, taking advantage of UV protection, moisture, and protection from larger predators? If the latter, did birth among the mosses direct more and more of them to seek shelter there later in life, creating greater survival for those that did, and driving selection toward those with that behavior and miniature size? Did bryophytes drive anuran evolution in the tropics, or were they just convenient co-evolvers in time? In any event, being small permits a wider range of uses of bryophytes by anurans.

Enter the Bryophytes – and *Eleutherodactylus* (Eleutherodactylidae)

The genus ***Eleutherodactylus*** has many species of very small frogs associated with mosses. Their subtle coloring, often with disruptive patterns, makes them inconspicuous in a variety of habitats, including bryophytes. This is clearly demonstrated for ***E. cuneatus*** in Figure 85. So far, we do not know much about the moss interactions of this species. Is it pre-adaptive to becoming a moss-dweller when its environment becomes too dry for open exposure? Or is its coloration already an adaptation to the multiple habitats it must cross during its daily activities?

Figure 85. Some frogs, like this Cuban endemic ***Eleutherodactylus cuneatus***, blend in well with the mosses they cross by having a disruptive pattern of light and dark browns. This same coloration would serve it well as it crosses forest soil and patchy, decomposing leaf litter. Nevertheless, it is on the IUCN red list. Is it rare because it is disappearing, or only because we seldom see it due to its coloration? Photo by Ansel Fong, with permission.

Being tiny is one adaptation that permits some members of this genus to inhabit mosses. The smallest frogs known in the world are in this genus, measuring only 8.5 mm long (Wikipedia 2011a). The tiny ***Eleutherodactylus coqui*** (Figure 86) has invaded Hawaii, where it competes with native species (Kreaser *et al*. 2007). Frogs of this small size are likely invaders in the moss trade, where they can travel unnoticed among the imported moss species. But of even greater concern is the trafficking of these tiny frogs in the plant trade.

Figure 86. ***Eleutherodactylus coqui*** on a tree bole, surrounded by bryophyte and algae growth. Photo by Alan Cressler, with permission.

One species of *Eleutherodactylus* appears in greenhouses so commonly through plant transport that it has been named the **Greenhouse Frog** (***Eleutherodactylus planirostris***; Figure 87) (Frost 2011). The natural distribution of this species is in Cuba, and the Isla de Juventud (0-720 m asl), Cayman Islands, and Caicos Islands. But they have been introduced into Florida, southern Louisiana, southern Georgia, Oahu, and the island of Hawaii, USA, and to Guam, Jamaica, Honduras, and Veracruz, Mexico. This terrestrial species lives in both mesic and xeric habitats, including forests, caves, beaches, nurseries, gardens, and urban areas (Hedges *et al*. 2004). In the Cayman Islands it has naturalized in bromeliads. No surprise, it is categorized as least concern by the IUCN.

Figure 87. ***Eleutherodactylus planirostris*** on moss. Photo by Brian Gratwicke, through Creative Commons.

When you are as small as these ***Eleutherodactylus*** species, even thin mats of bryophytes can help maintain moisture. Note in Figure 88 the wet leafy liverworts that are epiphyllous on the leaf, maintaining a moist location for this tiny ***Eleutherodactylus gryllus*** (**Cricket Robber Frog**; Figure 88-Figure 89). A native of interior uplands in Puerto Rico from 300-1182 m asl, it is known from only a few localities and is considered endangered (IUCN 2011). Mosses provide daytime retreats in its forest home. It calls from perches in trees and shrubs (Figure 88). Eggs still require water and are laid in basins of bromeliads, but Father Alejandro Sánchez found them under bryophytes (Figure 90). These develop young froglets, with no tadpole stage.

Figure 88. ***Eleutherodactylus gryllus*** (**Cricket Robber Frog**) calling from a leaf covered with epiphylls. Photo by Luis J. Villanueva-Rivera, USDA, with permission.

Figure 89. ***Eleutherodactylus*** sp. calling from a plant. Photo by Brian Gratwicke, through Creative Commons.

Figure 90. Eggs of ***Eleutherodactylus*** sp. under layer of moss on a tree trunk, El Yunque National Forest, Puerto Rico. Photo by Father Alejandro Sánchez, with permission.

Most of these species don't bear any coloration patterns that distinguish them as bryophyte dwellers. However, ***Pristimantis galdi*** (formerly *Eleutherodactylus galdi*) (Espada's Robber Frog; Figure 91) has both color patterns and tubercles to render it invisible in the right setting; *i.e.*, it is a moss mimic. This species lives in both secondary and old-growth humid evergreen forests in Peru and the Cordillera of Ecuador from 1000 to 1740 m asl (Frost 2011; Rodríguez *et al*. 2004). It seems to prefer leaves at 1-2 m above the ground (Lynch & Duellman 1980). Its habitat is threatened by livestock farming, agriculture, and logging, classifying it at near threatened (Rodríguez *et al*. 2004).

Figure 91. ***Pristimantis galdi***, showing its tubercles from an arboreal branch. Photo © 2007 German Chavez, with permission for educational use.

Summary

Bryophytes and amphibians are both transitional organisms that have adapted to land. Their life cycles are characterized by two phases that have different requirements. Frogs need to maintain moist skin, so bryophytes can provide them with a suitable habitat. Mosses provide moist safe sites from the drying sun during the day and serve as mating and calling sites for many species. *Sphagnum* can offer a moisture refugium for migrating amphibians. The same moisture advantage is offered to eggs. The male Leyte Wart Frogs (***Limnonectes leytensis***) stay under the mosses with their eggs; tadpoles can later be washed into the nearby water by rain. In winter, the bryophytes can provide insulation for hibernating anurans that can become frozen up to 60%, as well as reducing the risk of desiccation. And some bryophytes can serve as food and even sources of oxygen. ***Sphagnum***, mixed with egg yolk, can even serve as food for rearing several species of tadpoles. At the very least, mosses provide refuge for a number of invertebrates that are suitable food for the anurans. For some species, using mosses as cover during overwintering may save their lives. In summer, some frogs may even return day after day to the same spot among the mosses.

Some Anura seem to be well adapted for the bryophyte habitat. Small size is an advantage for living among the stems or climbing across epiphytes on branches. Many have disruptive coloration of browns and greens. And some have protuberances that further disrupt the shiny surface, serving as additional camouflage. Some even change their color to blend with their substrate. Altered life cycles are adaptations to land in general, with such modifications as parental care of eggs, carrying eggs on their backs, having large but few eggs, and burying the eggs in mossy nests. Because of these anuran traits, bryophytes offer them **safe sites** against not only environmental conditions, but also against predation.

One means of escape for Moss Frogs and others is "flying." This is actually gliding, and some of these frogs have modified muscle placement that permits them to maneuver to a selected landing spot. Others simply hop or crawl.

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