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CONSERVATION OF NORTH AMERICAN STREAM AMPHIBIANS

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CENTRAL ISSUES

Concern over the status of amphibians is international in scope (Wake 1991; Houlihan et al. 2000). Although the issue has a long history (Bury 1999), interest in it among both scientists and the public has greatly increased since the formation of the Declining Amphibian Populations Task Force in 1990 by the International Union for the Conservation of Nature (IUCN) Species Survival Commission. There is now considerable evidence that many amphibian species in various parts of the world are in decline (Dodd 1997; Alford and Richards 1999; Corn 2000). Declines appear to be most severe in western North America, Central America, and Australia. The stresses and assaults on amphibian populations are diverse, and some are better understood than others. Experimental evidence for causes of amphibian declines is scarce, and most studies have employed a correlative approach. Factors with the best supporting data include habitat destruction and alteration, disease, introduced predators, and contaminants (Corn 2000; Linder et al., in press). However, the effects of these factors may involve complex interactions and may depend on geography and species.

The recent spate of amphibian declines stimulated concerns that stressors operating globally, such as increasing ultraviolet radiation or global warming, might be responsible (Blaustein and Wake 1990). However, studies increasingly identify different causes in specific cases, and global stressors are not readily apparent (e.g., Carey et al. 2001). The search for common causes of amphibian decline has been elusive and complex because amphibians are an evolutionarily diverse group with complicated life histories and a wide range of habitats. No single factor is likely to affect most species in the same manner. This is no less true for species that breed or dwell in lotic habitats (seeps, streams, and rivers) than the more typical lentic habitats (ponds, lakes).

About one-third of the 265 (or so) species of amphibians north of Mexico can be considered as stream amphibians—those associated with lotic (flowing) water during part of their life history. Most of these species require lotic water for breeding and life as aquatic larvae or adults and the rest are associated with lotic habitats (e.g., are most abundant in adjacent riparian zones). Regarding amphibian decline issues, stream amphibians have received much less attention than lentic-breeding, or even terrestrial species (not including Central American anurans associated with streams, see Chapter 5, this volume). Potentially there are several reasons for this. Fewer recent declines of stream species have been documented, but this may be partly a perceptual problem. Lotic-breeding anurans and salamanders occur at discrete points on the landscape, often in large numbers, and their disappearance is more obvious and easier to document than is the decline of cryptic animals in a continuous riparian habitat. It may also be that declines of stream species have been more gradual and are often associated with long-term habitat alteration (e.g., Welsh 1990).

In the United States, timber harvest in both the Southeast and the Pacific Northwest have altered stream habitats and decreased many amphibian populations. Pollution of rivers and streams in the east is a significant threat to aquatic salamanders. For example, acid precipitation and acid mine drainage are known to damage stream faunas (Gore 1983; Driscoll et al. 2001). In this chapter, we will discuss these and other factors that affect the status and conservation of stream amphibians. First, however, we will survey the diversity, distribution, ecology, and life history of stream amphibians in North America.

MAJOR GROUPS OF STREAM AMPHIBIANS

Stream amphibians in North America occupy the freshwater continuum (Vannote et al. 1980; Welsh et al. 2000) from seeps and headwaters to higher-order streams and large rivers. The largest group of North American stream amphibians (a subgroup of the salamander family Plethodontidae) includes brook (*Eurycea*), dusky (*Desmognathus*), and spring (*Gyrinophilus*) salamanders, and others. These stream salamanders with gilled aquatic larvae and aquatic or semiterrestrial adults are found in headwaters and small to midsized streams. The geographic diversity of this group radiates from the southern Appalachian Mountains, but includes most of the eastern United States and several central and midwestern states. In the Pacific Northwest, several endemic species of salamanders (giant, *Dicamptodon*, torrent, *Rhyacotriton*) and tailed frogs (*Ascaphus*) are also well adapted to life in cascading headwater streams. A few members of the woodland salamanders (*Plethodon*) in the Pacific Northwest do not require lotic water for reproduction but are strongly associated with streamside habitat.

The perennibranchiate *Eurycea* of central Texas comprise a large and poorly understood group of stream and troglobitic salamanders characterized by high levels of

endemism, low population sizes, restricted ranges, irregular hydrology, and proximity to urban areas. This group has unique conservation and management concerns, and include the only federally protected stream salamanders (Barton Springs salamander, *Eurycea sosorum*; Texas blind salamander, *E. rathbuni*; and San Marcos salamander, *E. nana*).

Several large-bodied salamanders inhabit larger rivers of the eastern United States, including permanently aquatic salamanders in four families (Cryptobranchidae, Proteidae, Amphiumidae, and Sirenidae). A few anurans both in southeastern United States and on the West Coast use lotic waters as breeding habitat. In the Southwest, species of both *Rana* and *Bufo* use small streams, probably because lentic habitats are scarce. Newts (Salamandridae) on the West Coast breed in a variety of waters, including the slower parts of larger streams.

The cool, wet forests of the Pacific Northwest and the Appalachian Mountains are two of the major centers of evolution of living amphibians (Duellman and Sweet 1999), but there are considerable differences in diversity between the two regions. In the Appalachian and Ozark mountains and forests of the East and Southeast, about 47 species from 8 genera of lungless salamanders (Plethodontidae) are the dominant vertebrates of small streams and other lotic waters, such as springs, seeps, and caves (Petranka 1998; Crother 2000). Phylogenetic relationships among genera of aquatic plethodontids are poorly understood (Wake 1993). Speciation within the genus *Plethodon* dates from at least the Pliocene (2 to 10 million years ago; Highton 1995).

In the Pacific Northwest, species in three endemic families breed and live in flowing water: torrent salamanders (Rhyacotritonidae), Pacific giant salamanders (Dicamptodontidae), and tailed frogs (Ascaphidae). Until 20 years ago, *Ascaphus*, *Dicamptodon*, and *Rhyacotriton* were considered monotypic genera. Although molecular techniques have revealed considerable variation within these genera, only 10 species are recognized (Crother 2000; Nielson et al. 2001). This lower species diversity is not the result of a more recent adaptive radiation. Inland lineages of *Ascaphus* and *Dicamptodon* diverged from coastal lineages at the end of the Miocene or beginning of the Pliocene (Nielson et al. 2001), and speciation among the coastal forms of *Dicamptodon* and *Rhyacotriton* occurred during the Pliocene (Good and Wake 1992).

ECOLOGICAL RELATIONSHIPS OF STREAM AMPHIBIANS

Stream amphibians are important components of riparian and aquatic ecosystems. Hairston (1987) estimated that the biomass of aquatic and terrestrial plethodontids in the southern Appalachians was greater than all other vertebrate predators combined. Bury et al. (1991) reported that stream amphibians in the Pacific Northwest were an order of magnitude more abundant than salmonid fish. Estimates of the abundance of stream amphibians are variable, but local densities can be very high. In

North Carolina, Bruce (1995) recorded densities of seal salamanders (*Desmognathus monticola*) of up to 3.5/m², and Allegheny Mountain dusky salamander (*D. ochrophaeus*) densities have been estimated at 7/m² (Tilley 1980) and up to 41/m² on a wet rock face (Huheey and Brandon 1973). Nussbaum and Tait (1977) found densities of southern torrent (*Rhyacotriton variegatus*) and Cascades torrent (*R. cascadae*) salamander larvae to be 12.9/m² and 41.2/m², respectively, in two small streams in Oregon. Welsh and Lind (1992) reported 14/m² for southern torrent salamanders in a northern California stream. Corn and Bury (1989) found the total density of stream species averaged about 3.7/m² in Oregon streams unaffected by logging. These large abundances are ecologically significant. Stream amphibians are often the dominant predators in small streams, and most of these species are, in turn, prey for larger vertebrates (e.g., snakes, birds, shrews, small carnivores). Because the adults in many of these species have semiterrestrial habits, significant energy may be transported from aquatic to terrestrial environments. The effects of the input of terrestrial energy into streams has been a major theme in freshwater ecology, but the reverse pathway has been largely ignored, although there are ecosystems where energy flow out of streams is extremely important (Willson et al. 1998).

Stream salamanders have provided material for extensive studies of community and behavioral ecology. In the east, community interactions are complex in dusky salamanders (*Desmognathus*), with at least 11 unique combinations of *Desmognathus* species occurring in streams in the Appalachians (Hairston 1987). *Desmognathus* are often distributed along a moisture gradient with the smallest-sized species (e.g., Allegheny Mountain and northern, *Desmognathus fuscus*, dusky salamanders) in more upland areas, slightly larger salamanders (e.g., seal salamanders) in water margins and shallow water, and the largest species, the black-bellied salamander (*D. quadrimaculatus*), in the deepest and fastest water. Southerland (1986) found that excluding seal salamanders from a community changed the substrate use by other species. This partitioning of habitat may result from inter- and intraspecific resource competition, predation, or both. Competition alone is inadequate to explain distribution of *Desmognathus* species, because the distribution of species does not correlate well with body size (Hairston 1980). For example, small body size necessarily increases evaporative water loss, but the smallest species is the most terrestrial. Camp and Lee (1996) found few salamanders in the stomach contents of the large-sized black-bellied salamander, suggesting that predation might not be the driving force behind salamander distribution. Despite strong habitat preference among species, access to both terrestrial and aquatic habitats may be important for homeostasis.

Stream species separate ecologically not only on a moisture gradient perpendicular to the water, but occurrence and abundance of amphibians change along the stream continuum from the uppermost ends of watersheds (seeps and headwater streams) downstream to larger waters with more open canopies.

In the Pacific Northwest, several species are adapted to cascading streams in ma-

ture forest with closed canopies that maintain the cool temperatures required for embryonic and larval development. Rocky seeps and the margins of headwater streams are occupied by one species of *Aneides* (H. H. Welsh, U.S. Forest Service, Redwood Sciences Laboratory, Arcata, CA, unpublished data), one of three species of *Plethodon*, and one of the four *Rhyacomitron*. Torrent salamanders also occur on the bottoms of headwater streams, along with one of the two species of *Ascaphus* and one or two species of *Dicamptodon*. Pacific giant (*D. tenebrosus*) and Cope's giant (*D. copei*) salamanders are sympatric near Mount Rainier and along the Columbia River in Washington and Oregon, but congeners of stream amphibians in the Northwest otherwise have allopatric distributions. *Ascaphus* occur in headwaters and higher-order streams (generally less than 2-m wide), but on occasion are found in larger waters, perhaps being swept downstream in seasonal flooding. *Dicamptodon* occur from headwaters to larger streams, including warmer streams in more open forests. *Dicamptodon* and *Ascaphus* co-occur with trout and salmon in some larger waters. In large streams and rivers, backwaters and pools with slow water are breeding habitat for foothill yellow-legged frogs (*Rana boylei*), red-legged frogs (*R. aurora*), western toads (*Bufo boreas*), and Pacific newts (*Taricha* spp.). Foothill yellow-legged frogs are restricted to these habitats, but the other species can be considered riparian associates and breed in lotic sites, when available.

In the Southeast, there is higher species diversity, with greater sympatry among closely related species. Competition and predation have led to greater subdivision on the perpendicular moisture gradient, but there are similarities to the Pacific Northwest along the stream continuum. There is no eastern analog to tailed frogs, but dusky (*Desmognathus*) and brook (*Eurycea*) salamanders occur in seeps and headwaters and are replaced by larger plethodontids (species of *Gyrinophilus* and *Pseudotriton*) in larger, forested streams. Large, open streams and rivers with a rocky substrate are home to hellbenders (*Cryptobranchus alleganiensis*), and slower portions of larger waters are home to varied large aquatic salamanders (*Siren*, *Amphiuma*) and river frogs (*Rana heckscheri*). The causes of habitat segregation of salamanders across the moisture gradient have received considerable attention, but the reasons for separation of amphibians along the stream continuum are poorly documented. Predation is probably a major factor. Several species are restricted to headwaters with cold, cascading waters and few or no fishes. Progressing downstream, the canopy is increasingly open, stream temperature rises, volume of water increases, and velocity slows. Predaceous fish dominate these habitats and the amphibians that occur there tend to be large predators (*Cryptobranchus*, *Dicamptodon*).

The Edwards Plateau and Balcones Escarpment region of Texas is home to several endemic species of *Eurycea* that occupy springs and lotic waters in caves (Hillis et al. 2001; Petranksa 1998). These include the federally protected San Marcos, Texas (*Eurycea neotenes*), and Texas blind salamanders, the only stream salamanders listed as threatened or endangered. These species occupy habitats that are often inaccessible, which has resulted in a dearth of knowledge about their ecology, natural history, and

systematics. Several species have only recently been recognized (Hillis et al. 2001). Many of these species have highly restricted distributions consisting of a few springs at a single location (Petranka 1998).

THREATS TO STREAM AMPHIBIANS

Stream species are subject to the same threats as other amphibians, mainly habitat alteration, pollution, introduced predators, disease, and the future effects of climate change. However, the effects of only a few of these threats on stream amphibians have been studied in any detail. Here, we examine the effects of habitat alteration by timber harvest, pollution from acidification, and briefly discuss other factors that have been identified.

Timber Harvest

Because the majority of stream amphibians occur in forested landscapes, timber harvest and related road building is the primary agent of habitat alteration. The effects of logging on stream species have been studied most intensively in the Pacific Northwest.

Headwater streams are required habitat for several species of stream amphibians endemic to the Pacific Northwest because these taxa require cool temperatures and permanent waters. Removal of canopy or streamside vegetation by logging or up-slope activities such as road development creates immediate changes in stream habitats. The initial impact of clearcut logging increases insolation and raises stream temperatures, thereby increasing microbial respiration, primary production, invertebrate consumers, and populations of invertebrate and vertebrate predators. Stream amphibians may be susceptible physiologically to increased temperatures. For example, tailed frog larvae prefer temperatures below 22°C (deVlaming and Bury 1970), and the abundance of southern torrent salamanders is limited by water temperature (Welsh and Lind 1996).

Logging may also result in long-term alteration of the stream habitat. Streams in natural forests are rocky (gravels, cobble, and boulders), which provide vital cover for stream amphibians. The presence of large, downed wood in streams also provides energy input to the stream ecosystem. Streams in logged areas suffer increased sedimentation, which degrades amphibian habitat by reducing availability of cover sites (Corn and Bury 1989; Welsh and Ollivier 1998; Dupuis and Steventon 1999). However, this effect is influenced by topography and geology. Increasing stream gradient results in greater flushing of sediments, which may mitigate inputs from logging. Hall et al. (1978) studied headwater streams in the Cascade Mountains in central Oregon and found that when the stream gradient was more than 9%, there was a higher density of Pacific giant salamanders in streams traversing clearcuts than in streams in old-growth forest. The nature of the bedrock underlying drainages also is impor-

tant in determining the severity of sedimentation. Wilkins and Peterson (2000) surveyed stream amphibians on heavily logged private forests in southwestern Washington. As have other researchers, they found greater abundance of all species as the gradient increased. But they also found that amphibians were less abundant (*Dicamptodon* spp.) or absent (tailed frogs) in drainages underlain by sedimentary rock than in drainages underlain by basalt. Elsewhere, in streams unaffected by logging in Olympic National Park in Washington (Adams and Bury 2002) and Prairie Creek Redwoods State Park in California (Welsh and Ollivier 1998), amphibians were abundant in streams with sedimentary bedrock.

Stream amphibian populations in the Pacific Northwest are reduced in landscapes dominated by logging (Corn and Bury 1989; Welsh and Lind 1996; Dupuis and Steventon 1999). Because most forests that support amphibians have been logged in the last 50 years, Corn (1994) hypothesized that regional populations of stream amphibians are much lower than before European settlement. Whether this has resulted in local extinctions of any species is unknown, but there is concern for the status of tailed frogs and species of torrent salamanders. Comparisons of the abundance of tailed frogs and the southern torrent salamander in Redwood National Park and in commercial timberlands revealed significant reduction or elimination of both species in streams in logged areas (Welsh et al. 2000). Although a petition to list the southern torrent salamander as a Federal threatened species was denied because of lack of evidence, the torrent salamanders are the northwestern species most sensitive to the effects of logging. These salamanders are likely to be extirpated from some streams in logged areas, and recovery of populations may take decades (Bury and Corn 1988b; B. Bury and D. Major, U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, OR, unpublished).

In the eastern United States, timber harvest is also a major factor altering forest habitats. Petraska (1993) estimated that clearcuts in western North Carolina reduced forest salamanders in mature stands by as much as 75 to 80%, including at least five species with aquatic larvae that use forest streams. Ash and Bruce (1994) criticized the magnitude of these conclusions, but the disappearance of salamanders from clearcuts was undisputed. Ford et al. (2002) found that abundance and diversity of salamanders, including stream species, were positively related to stand age, stand size, and amount of nearby habitat in cove hardwood stands in the southern Appalachians, suggesting that salamanders in this habitat are vulnerable to logging.

Acidification

Most research on the effects of acid conditions on amphibians has examined pond-breeding species. Although amphibians, particularly their embryos, are vulnerable to acidification, the effect on populations is uncertain. There is no convincing evidence that the decline of any species can be attributed to acidification (Rowe and Freda

2000). Still, acid conditions, either directly or through interactions with other ions and toxic metals, have multiple negative effects on amphibians, including direct mortality, increased rates of deformity, and reduced rates of growth and development (Rowe and Freda 2000). A significant percentage of stream habitats in the eastern United States have been acidified or are vulnerable to acidification (Herlihy et al. 1993), indicating a potentially serious threat to conservation of stream amphibians.

Acidification is not considered a threat to western amphibians, but streams in the east are subject to acidification from a variety of sources. The mid-Atlantic states, particularly the northern Appalachian Mountains, receive some of the highest amounts of atmospheric deposition of sulfate and nitrate ions (Driscoll et al. 2001). Streams are also acidified when Anakeesta rock formations are exposed to air by mining, road construction, or landslides, resulting in oxidation and leaching of toxic amounts of sulfuric acid and various metals (Kucken et al. 1994). Another pathway for stream acidification is defoliation of forests by insect pests, such as gypsy moth caterpillars (*Lymantria dispar*), which results in inputs of excess nitrogen into surface waters (Eshleman et al. 1998). Vulnerability of streams to acidification is largely based on geology. Streams in watersheds with carbonate (limestone) or crystalline (basalt or granite) bedrock have high acid neutralizing capacity (ANC). Watersheds underlain by siliclastic (noncarbonate sedimentary) bedrock have streams with low ANC and are vulnerable to acidification (Herlihy et al. 1993) that is chronic (permanent reduction in ANC and pH) or episodic (reductions in ANC and pH following storms or snowmelt).

Acidification from mine drainage and exposure of Anakeesta rock has occurred in several thousand kilometers of streams in the Appalachians, with severe effects on salamanders and other organisms (Gore 1983; Kucken et al. 1994). The effects on salamanders of acidification from atmospheric deposition are more difficult to demonstrate. Chronic and episodic acidification has affected a large percentage of Appalachian streams in areas with sensitive geology, and native fish diversity has been significantly reduced (Heard et al. 1997; Bulger et al. 2000). Although few studies have been done on stream salamanders, we would expect that larvae might suffer mortality from acidic episodes, but the semiterrestrial adults could move out of the stream to avoid temporary acid conditions. Responses of salamanders to acidification, particularly episodic acidification, are likely to be complex.

Introduced Species

Nonnative species, as either predators or competitors, can threaten the survival of stream amphibians. The top predators in small streams are often salamanders, which may be unable to deal with the introduction of predaceous fish, either native or nonnative. Brook trout (*Salvelinus fontinalis*) have negative effects on survival and growth of spring salamanders (*Gyrnophilus porphyriticus*) and northern two-lined salamanders (*Eurycea bistriata*), and significantly reduce diversity of salamanders in Appala-

chian streams (Rescariis 1997). The streamside salamander (*Ambystoma barbouri*) is one of the few species of *Ambystoma* to breed in flowing water, using pools in intermittent streams that are free of fish. Salamander larvae often become prey when they drift downstream into pools or reaches containing predatory green sunfish (*Lepomis cyanellus*). Surviving larvae alter their behavior, remaining more under rocks in shallow water than in deeper open water (Sih et al. 1992).

Crayfish (*Procambarus clarkii*) native to the southeastern United States have been introduced widely in the West. These aggressive predators are suspected of contributing to declines of ranid frogs in the Southwest. Gamradt et al. (1997) observed that *P. clarkii* attacked adult California newts (*Taricha torosa*) in experimental cages and, when crayfish colonized a stream in southern California, newts reproduction failed. The American bullfrog (*Rana catesbeiana*), another eastern species that has been widely introduced in the West, has long been implicated in declines of native western frogs. Kupferberg (1997) documented that reaches of the Eel River drainage in northern California invaded by bullfrogs have a significantly reduced abundance of foothill yellow-legged frogs. Competition experiments resulted in reduced survival and growth of foothill yellow-legged frog tadpoles in the presence of bullfrog tadpoles.

Other Threats

Water pollution is a major problem for large salamanders in eastern rivers (Petranka 1998). The eastern hellbender (*Cryptobranchus alleganiensis*) is scarce or absent in drainages that have received acid mine drainage, industrial effluents, or inadequately treated urban sewage (Gates et al. 1985). Davidson et al. (in press) analyzed a number of factors involved with declines of amphibians in California. The disappearance of foothill yellow-legged frogs and other species from previously documented locations was correlated with the amount of agricultural land upwind of the sites. This suggests that aerial transport of agricultural chemicals may be a factor in these declines.

Alteration in the hydrology of free-flowing rivers caused by construction of dams and other water projects may have serious effects on stream amphibians. For example, Lind et al. (1996) found that habitat for foothill yellow-legged frogs was reduced by 95% for 40 miles below a dam on the Trinity River in California. In some years, water releases designed to benefit endangered salmon were ill timed for frogs and resulted in the washing away of egg masses and young larvae. In the Edwards Plateau of Texas, alteration of groundwater hydrology may have devastating effects on endemic *Eurycea*. This unique assemblage of salamanders occurs in a region undergoing rapid population growth and associated urban development that may put several species at risk of extinction. In 1951, a streambed excavation discovered a new stream species (blanco blind salamander, *Eurycea robusta*). Only four individuals were found and the species has not been detected since (Potter and Sweet 1981).

Global climate change has been suggested as the cause of declines of anurans in

Central America (Pounds et al. 1999) and episodic mortality of western toad (*Bufo boreas*) eggs in Oregon (Kiesecker et al. 2001a), but it has not yet been implicated as affecting the status of stream species in North America. However, amphibians are vulnerable to the effects of climate change because of their dependence on water for breeding and the relationships between temperature and amphibian growth and development (Ovaska 1997). The future effects of climate change may be severe. During the twenty-first century, climate models based on increasing atmospheric carbon-dioxide concentrations predict warming over the United States of between 2.8 and 5°C, reduced snow cover, reduced soil moisture, and more frequent extreme precipitation events (MacCracken et al. 2001). Decreased soil moisture and increased summer temperatures could affect stream amphibians in many ways (Donnelly and Crump 1998). It is likely that terrestrial habitat and prey populations will be reduced. Reduced stream flow during summer will reduce aquatic habitat and duration of remaining pools, especially in headwater streams that are primary habitat for many amphibians. Conversely, increased frequency of storm events will increase flooding, which is a major cause of catastrophic mortality among stream species (Kupferberg 1996).

The pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*) has been associated with declines of frogs throughout the world and may be at least the proximate cause of amphibian declines that lack another plausible explanation (Berger et al. 1998; Bosch et al. 2001; Muths et al., in press). The chytrid fungus has not yet been reported in stream species in North America, but it is potentially a serious threat.

Fire has considerable potential to cause habitat change, but the effects of fire on amphibians are only recently receiving attention. Direct mortality of aquatic and wetland-associated life stages of amphibians may be low where wet areas (e.g., riparian zones) provide suitable refugia from fire (Vogl 1973), but terrestrial life stages in uplands may experience much higher mortality associated with the direct and indirect (e.g., prey availability, shelter, microclimate) effects of fire (Russell et al. 1999). Further, physical and biological changes in adjacent uplands may influence biota in riparian zones through changes in hydrology and water chemistry in the streams.

POTENTIAL SOLUTIONS AND CONSERVATION STRATEGIES

Adopting a Landscape Perspective

To effectively conserve stream amphibians, we need to identify threats to amphibians and offer potential solutions with a landscape perspective that address the diversity and interactions of organisms along the stream continuum. Most requirements for riparian protection have only included fish-bearing, larger streams while ignoring seeps, intermittent streams, and permanent headwater streams that are home to sig-

nificant amphibian populations. These "feeder" sites intimately affect downstream water chemistry, hydrology, and biota. Research and management must address conservation issues at all levels of the stream continuum.

Some current logging regulations include prescriptions to protect headwaters and adjacent riparian buffer zones. In California, Diller and Wallace (1996) predicted that these regulations would be sufficient to protect populations of the southern torrent salamander in logged landscapes. Welsh and Lind (1996) criticized this conclusion, suggesting that the regulations are not sufficient to protect the microclimatic conditions required for survival of headwater amphibians, particularly at inland locations that are warmer and drier than the coastal sites studied by Diller and Wallace (see also Welsh et al. 2000). Thornburgh et al. (2000) provided further analysis of the California regulations, which are among the most restrictive of state forest practices, concluding that they are inadequate to protect headwater riparian habitats, particularly because they are biased toward larger, fish-bearing streams and that there is no long-term protection from sedimentation resulting from perturbations (e.g., failure of logging roads). Wilkins and Peterson (2000) suggested that streams in drainages with unconsolidated, erodible bedrock (e.g., more recent marine deposits) are poor habitat for stream amphibians and could receive lower priority for protection. On the contrary, streams with this lithology in unlogged forests harbor abundant amphibian populations, indicating that such streams are highly vulnerable to sedimentation from logging activities and may require higher levels of protection (Adams and Bury 2002; Welsh and Ollivier 1998).

Stream conservation efforts must also address the diverse life histories of stream amphibians. In many cases, we lack data about the movement patterns, dispersal abilities, and landscape-level needs of stream amphibians necessary for effective conservation. For example, current protection of tailed frog streams is based on the habitat needs of larvae (MoF and MELP 1995). However, because forest harvest or other human alterations may remove potential dispersal corridors, research on the overland movement patterns of adult stream amphibians is needed. Although we know a considerable amount about the life history of a few species (e.g., desmognathine salamanders), basic life history data are lacking for most stream amphibians. Demographic modeling could be used to predict the responses of stream amphibians to habitat alteration or climate change, but in many cases the necessary data are not yet available. For most stream amphibians, we have only rudimentary knowledge of their reproductive ecology (even clutch sizes), diet, growth rates, physiological tolerances, and, in particular, habitat requirements.

Clean Air Act and Reductions in Sulfate Deposition

The Clean Air Act of 1970 and Amendments (CAAA) have resulted in significant reductions of sulfate emissions from coal-fired power plants (Driscoll et al. 2001). However, deposition of sulfate and nitrate anions during the past 150 years caused signi-

ficant depletion of base cations in forest soils, which now limits the buffering capacity of the soil. This means that even modest inputs of acid anions today can result in acidification of surface waters, and recovery of aquatic and terrestrial systems will require several decades, even if additional proposed reductions in power plant emissions occur (Driscoll et al. 2001). Bulger et al. (2000) predicted that sulfate deposition needs to be reduced by more than 70% to result in recovery of acidified trout streams in Virginia. A further complication is that nitrate deposition has significant sources other than power plants (e.g., automobile emissions) and has not been significantly reduced since implementation of the CAAA (Driscoll et al. 2001). High nitrate deposition will prevent or limit ecosystem recovery, even if emissions from power plants continue to be reduced. As with logging issues, the emphasis on acidification damage and recovery has been on larger, fish-bearing streams. The threats to stream amphibians from acidification remain more a hypothesis than a proven fact, and research is still needed.

Changing Forestry Practices

Historic clearcut logging over large areas has likely fragmented local populations of stream amphibians, and continued timber harvest at these sites may further deplete remaining populations. However, the response of amphibians to logging is complex; it can be mitigated somewhat by the retention of the microhabitats and dispersal routes required by amphibians. For upland species or life stages, this means retaining coarse woody debris and some canopy, as well as reducing the amount of soil disturbance. For larvae and stream life, the primary prescriptions are to retain a buffer strip or riparian reserve of uncut trees along streams, to reduce or eliminate entry by machinery into riparian zones, and to reduce the number of stream crossings by new logging roads (deMaynadier and Hunter 1995; Dupuis and Steventon 1999). We must yet determine the effectiveness and cost efficiency of buffer zones along streams and of leaving uncut timber upstream to protect aquatic organisms.

Fire

Almost nothing is known about the responses of amphibians to fire and fire management, including fire retarding chemicals and site preparation techniques. Because several amphibian species in the mountainous regions of the western United States are declining, understanding the effects of fire on amphibians and amphibian habitats is increasingly important. Several studies are starting on the topic, but are few compared to the vast landscape occupied by stream amphibians. Amphibian populations should respond positively to increased productivity (periphyton growth) when canopies are open, but they are also sensitive to changes in water velocity, temperature, chemistry, substrate size, and sedimentation that result from perturbations and loss of forest canopies.

Special Habitats

Ultimately, conservation of stream amphibians depends on conservation of habitat. Conservation efforts should emphasize specialized habitats: seeps, headwater streams, and riparian zones. These habitats are relatively small, patchily distributed on the landscape, and extremely vulnerable to disruption. For example, the recently discovered diversity of *Eurycea* in springs and caves in Texas may be threatened by greater demands on groundwater supplies from a growing human population. The effect of altered hydrology on stream amphibians is another topic that needs research. Information necessary to improve the protection of specialized habitats can help ensure the conservation of a large proportion of stream species.