ABSTRACT

The status of thirty-two amphibian taxa currently found in the Sierra Nevada region of California was reviewed. Of this number, thirty are native species or subspecies, one is an introduced species (bullfrog [Rana catesbeiana]), and one is of uncertain origin (tiger salamander [Ambystoma tigrinum]). Of the thirty definite native species or subspecies, nine are frogs and toads and twenty-one are salamanders. Fourteen (47%) of these taxa are native to the Sierra Nevada, and of this total, twelve taxa (86%) are in need of some form of protection, including six taxa (43%) that are either extinct or threatened with extinction in the near future. The most imperiled amphibians are the true toads (Bufo spp.) and true frogs (Rana spp.)-which make up 23% of the fauna-because of their widespread declines in the region over the past twenty-five years. For the salamanders, nine (43%) species or subspecies are at risk. As a whole, amphibians occurring in aquatic habitats are at greatest risk, because these habitats are being threatened by alteration of their physical or biotic structure by several types of human use of water and adjacent land. The uses that most severely affect aquatic habitats and their contained species are overgrazing by livestock; stream channelization; construction of hydroelectric, recreational, or water storage reservoirs of significant size; removal of ground and surface water near or beyond recharge or volume capacities; placer mining; and the introduction of a suite of exotic species (especially fishes) with which the native aquatic amphibian fauna frequently cannot coexist. The most imperiled aquatic habitats in the Sierra Nevada that harbor one or more of the taxa recommended for listing are springs, seeps, and bogs; rain (or vernal) pools; marshes; and small headwater streams. In the Sierra Nevada, taxa occurring in terrestrial habitats are generally less imperiled, because most terrestrial habitats in the region have a much greater total area than all aquatic habitats combined. Yet, aside from outright destruction and development, several widespread activities and land uses continue to alter the structure and vegetation of most terrestrial habitats in a manner unfavorable to the survival of their contained taxa. Among such uses the most significant are the impacts of off-road vehicles, overgrazing by livestock, timber harvest, mining, and urbanization.

INTRODUCTION

Over the past four years, there has been a heightened concern about the decline of a number of amphibian species in various parts of the world (see reviews in Blaustein 1994). In the Sierra Nevada region covered in this chapter (figure 31.1), such concern is borne out by the fact that all species of native true toads (Bufo spp.) and true frogs (Rana spp.) inhabiting the area have disappeared from significant portions of their ranges during the past twenty-five years, despite having large portions of habitat protected in wilderness areas and national parks (Jennings 1995). Because of the present uncertainty regarding the status of the amphibians of the Sierra Nevada region, this study was conducted to provide a benchmark or snapshot of the current status of each amphibian taxon. Although the information presented comes from data gathered from other studies, recommendations are made for taxa in need of active management by resource agencies.

METHODS

Much of the information contained in this chapter comes from Jennings and Hayes 1994, which reviews the status of the entire herpetofauna of California. An effort was made to include information on the status of taxa not already covered

Sierra Nevada Ecosystem Project: Final report to Congress, vol. II, Assessments and scientific basis for management options. Davis: University of California, Centers for Water and Wildland Resources, 1996.

FIGURE 31.1

Geographic area of the Sierra Nevada as defined by the SNEP Team. Amphibians found only within the shaded area are covered in the text.



in that report, especially if it relates to amphibian populations in the Sierra Nevada. Distribution maps were compiled with the aid of verified museum records and field reconnaissance in specific regions of California to help assess the presence or absence of taxa within their known range. Historical assessments of the past distributions of each taxon were made from a combination of verified museum specimens and the field notes of current and former naturalists. A full description of the methodology used is provided in Jennings and Hayes 1994.

Data from the aforementioned sources were organized into generalized accounts for mole salamanders (Ambystomatidae), lungless salamanders (Plethodontidae), newts (Salamandridae), tree frogs (Hylidae), spadefoot toads (Pelobatidae), true toads (Bufonidae), and true frogs (Ranidae). Current distribution maps are provided for each taxon present within the study region.

For determining the status of each amphibian taxon in the Sierra Nevada, I followed Jennings and Hayes 1994 and assigned one of four categories:

- 1. Taxa for which endangered status is justified (i.e., those animals that are in serious danger of becoming extinct throughout all or a significant portion of their range due to one or more causes, including loss of habitat, change in habitat, overexploitation, predation, competition, or disease)
- 2. Taxa for which threatened status is justified (i.e., those animals that are not currently threatened with extinction but that are likely to become an endangered species in the foreseeable future in the absence of special protection and management efforts required by state and governmental agencies)
- 3. Taxa for which special concern status is justified (i.e., those animals that may become listed as threatened or endangered in the near future due to habitat modification or destruction, overcollecting, or disease or that are threatened in any way by introduced species)
- 4. Taxa for which no status is justified (i.e., those animals that are currently common throughout their range. Most amphibians fall under this category.)

I based my determination of whether endangered or threatened status was justified on the state-level definitions published in the California Fish and Game Code (California Administrative Code, title 14, sec. 670.5). For determining special concern status, I followed the criteria indicated in Williams 1986 and Moyle et al. 1989.

RESULTS

Of the thirty-two taxa reviewed, thirty are native species (or subspecies), one is an introduced species, and one species is of uncertain origin (table 31.1). Of the thirty definite species or subspecies, nine are frogs and toads, and twenty-one are salamanders. Fourteen (47%) of these taxa are endemic to the Sierra Nevada. At present, fourteen of the native species or subspecies (47%) do not have declining populations, although

five of these taxa (17%) have very localized distributions and as such are vulnerable to localized disturbances. Of the remaining sixteen species or subspecies, one species (3%) is apparently extinct, five species (17%) are formally listed (or proposed for listing) as threatened or endangered, five species (17%) clearly merit such listing, and five species (17%) are declining and so are of special concern (table 31.1). Of the fourteen endemics, only the Sierra Nevada salamander (Ensatina eschscholtzii platensis) and the Sierra newt (Taricha torosa sierrae) can be regarded as secure; the rest (86%) fit into one of the other three categories, including six taxa (43%) that are extinct or threatened with extinction in the near future. Of the twenty-one species or subspecies of salamanders, nine taxa (43%) are at risk, while eight (89%) of the nine frogs and toads are at risk. Accounts of all taxa follow.

Mole Salamanders (Ambystomatidae)

Mole salamanders are represented by three species in the Sierra Nevada: the California tiger salamander (Ambystoma californiense), the southern long-toed salamander (A. macrodactylum sigillatum), and the tiger salamander (A. tigrinum ssp.) (figure 31.2). The tiger salamander population in the eastern Sierra is of uncertain origin and may be the result of animals originally brought in for live fish bait at reservoirs such as Lake Crowley (Jennings and Hayes 1994).

All of these salamanders are long-lived (up to twenty years or more) (Bowler 1977; M. Allaback, Biosearch Wildlife Surveys, letter to the author, October 12, 1995). They have a threeto six-month aquatic larval stage, followed by metamorphosis into a terrestrial juvenile stage. After one or more years as juveniles, the salamanders then mature into the terrestrial adult form. They breed in temporary ponds at low to middle elevations (southern long-toed salamanders also breed at high elevations) and often use the same breeding ponds year after year. Juveniles and adults spend most of the year underground in small mammal burrows except during the winter months, when sufficient rainfall allows for surface activity and breeding. The California tiger salamander is a low-elevation species that is currently threatened by the destruction of its breeding ponds and the introduction of predatory fish (especially mosquito fish [Gambusia affinis]), Louisiana red swamp crayfish (Procambarus clarkii), and bullfrogs (Rana catesbeiana) into its habitat. It is considered threatened (Jennings and Hayes 1994) and has been found warranted for listing under the Endangered Species Act (ESA) (Sorenson 1994).

The southern long-toed salamander is currently recognized as a subspecies of the widely distributed long-toed salamander (A. macrodactylum) in northwestern North America (Stebbins 1985). Its Sierran populations are currently believed to be stable, although they are depleted in some areas due to the introduction of trout (Oncorhynchus spp.) and charr (Salvelinus spp.) into high-elevation lakes formerly used by salamanders for breeding purposes (e.g., see Liss and Larson 1991).

TABLE 31.1

Native amphibians of the Sierra Nevada (based largely on Stebbins 1985). Status levels based on Jennings and Hayes (1994).

Taxon	Drainage		Status	
California tiger salamander, <i>Ambystoma californiense</i> Southern long-toed salamander, <i>Ambystoma macrodactylum sigillatum</i>	Sacramento–San Joaquin Rivers Eagle Lake, Lahontan, Sacramento–San Joaquin Rivers	Lowlands, foothills High elevations	Threatened Stable or expanding	
Tiger salamander, Ambystoma tigrinum ssp.	Owens Valley	High elevations	Stable or expanding; introduced?	
Lungless Salamanders Arboreal salamander, Aneides lugubris California slender salamander, Batrachoseps attenuatus Black-bellied slender salamander, Batrachoseps nigriventris Pacific slender salamander, Batrachoseps relictus Relictual slender salamander, Batrachoseps relictus Kern Canyon slender salamander, Batrachoseps simatus Tehachapi slender salamander, Batrachoseps stebbinsi Breckenridge Mountain slender salamander, Batrachoseps sp. Fairview slender salamander, Batrachoseps sp. Kern Plateau slender salamander, Batrachoseps sp. Hell Hollow slender salamander, Batrachoseps sp. Yellow-blotched salamander, Ensatina eschscholtzii croceater Sierra Nevada salamander, Ensatina eschscholtzii vanthoptica Limestone salamander, Ensatina eschscholtzii xanthoptica	Sacramento–San Joaquin Rivers Sacramento–San Joaquin Rivers Sacramento–San Joaquin Rivers, Tulare Lake Sacramento–San Joaquin Rivers, Tulare Lake Sacramento–San Joaquin Rivers, Tulare Lake Tulare Lake Tulare Lake Tulare Lake Owens Valley, Tulare Lake Sacramento–San Joaquin Rivers Tulare Lake	Foothills Lowlands, foothills Foothills Foothills Foothills Foothills High elevations Foothills High elevations Foothills Foothills Foothills Foothills Foothills	Stable or expanding Stable or expanding Stable or expanding Special concern Threatened ^a Endangered ^b Stable or expanding Stable or expanding	
Mount Lyell salamander, <i>Hydromantes platycephalus</i>	Lahontan, Owens Valley, Sacramento–San Joaquin Rivers, Tulare Lake	High elevations	Special concern	
Neute	Owens valley	Fightelevations	Special concern	
Northern rough-skinned newt, <i>Taricha granulosa granulosa</i> Sierra newt, <i>Taricha torosa sierra</i> e	Sacramento–San Joaquin Rivers Sacramento–San Joaquin Rivers, Tulare Lake	Foothills Foothills	Stable or expanding Stable or expanding	
Frogs and Toads True Toads				
California toad, <i>Bufo boreas halophilus</i> Yosemite toad, <i>Bufo canorus</i>	All drainages Lahontan, Owens Valley, Sacramento–San Joaquin Rivers	Lowlands, foothills, high elevations High elevations	Stable or expanding Endangered	
<i>Tree Frogs</i> Pacific tree frog, <i>Hyla regilla</i>	All drainages	Lowlands, foothills, high elevations	Stable or expanding	
<i>True Frogs</i> California red-legged frog, <i>Rana aurora draytonii</i> Foothill yellow-legged frog, <i>Rana boylii</i> Cascade frog, <i>Rana cascadae</i> Bullfrog, <i>Rana catesbeiana</i> Mountain yellow-legged frog, <i>Rana muscosa</i>	Sacramento–San Joaquin Rivers, Tulare Lake Sacramento–San Joaquin Rivers, Tulare Lake Sacramento–San Joaquin Rivers All drainages Lahontan, Owens Valley, Sacramento–San Joaquin Rivers, Tulare Lake	Lowlands, foothills Foothills Foothills, high elevations Lowlands, foothills High elevations	Endangered Threatened Endangered Stable or expanding; introduced Threatened	
Northern leopard frog, Rana pipiens	Lahontan, Owens Valley, Sacramento-San Joaquin Rivers	High elevations	Threatened	
Spadefoot Toads Western spadefoot, Scaphiopus hammondii	Sacramento–San Joaquin Rivers, Tulare Lake	Lowlands, foothills	Special concern	

^aCurrently listed as threatened by the State of California (Jennings 1987). ^bProbably extinct.



FIGURE 31.2

Historic and current distribution of (A) California tiger salamander (Ambystoma californiense), (B) southern long-toed salamander (Ambystoma macrodactylum sigillatum), (C) tiger salamander (Ambystoma tigrinum ssp.), (D) arboreal salamander (Aneides lugubris), and (E) relictual slender salamander (Batrachoseps relictus) in the Sierra Nevada.

Larson 1991).

Lungless Salamanders (Plethodontidae)

Lungless salamanders are represented by seventeen taxa (made up of fifteen species) in the Sierra Nevada (table 31.1; figures 31.2–31.7). They are among the most terrestrial of all amphibians in the Sierra Nevada because they do not require

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Historic and current distribution of (A) California slender salamander (*Batrachoseps attenuatus*), (B) Pacific slender salamander (*Batrachoseps pacificus*), and (C) Tehachapi slender salamander (*Batrachoseps stebbinsi*) in the Sierra Nevada.



der talus slopes, or in natural rock caves (Stebbins 1951; Gorman 1956). Many species show parental care of eggs (Stebbins 1985). Development is direct. Because most of these salamanders are small in size and of ancient origin, they have undergone a high degree of isolation in the Sierra Nevada so much so that twelve of the seventeen (71%) taxa are endemic to the region. Such endemism has only recently been recognized, and at least five species are in the process of be-



FIGURE 31.4

Historic and current distribution of (A) Kern Canyon slender salamander (*Batrachoseps simatus*), (B) Fairview slender salamander (*Batrachoseps* sp.), (C) Hell Hollow slender salamander (*Batrachoseps* sp.), and (D) northern rough-skinned newt (*Taricha granulosa* granulosa) in the Sierra Nevada.

ing formally described after genetic studies demonstrated their uniqueness (R. Hansen, editor, Herpetological Review, letter to the author, December 1, 1988; D. Wake, director, Museum of Zoology, University of California, Berkeley, letter to the author, July 19, 1994, conversation with the author, June 19, 1995). As a whole, lungless salamanders are generally restricted to small home ranges characterized by small patches of suitable habitat. Since much of the surrounding region is

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Historic and current distribution of (A) blackbellied slender salamander (*Batrachoseps nigriventris*), (B) limestone salamander (*Hydromantes brunus*), (C) Mount Lyell salamander (*Hydromantes platycephalus*), and (D) Owens Valley web-toed salamander (*Hydromantes* sp.) in the Sierra Nevada.



often composed of dry (or otherwise unsuitable) habitats, these salamanders are often vulnerable to activities that disrupt the hydrology of riparian canyons, the forest floor, and other mesic habitats (Jennings and Hayes 1994). Such negative activities include road building, mining, dam construction, and logging. Thus, at least seven species—the relictual slender salamander (Batrachoseps relictus) (special concern), the Kern Canyon slender salamander (B. simatus) (threatened),



FIGURE 31.6

Historic and current distribution of (A) Breckenridge Mountain slender salamander (*Batrachoseps* sp.), (B) Kern Plateau slender salamander (*Batrachoseps* sp.), and (C) Sierra newt (*Taricha torosa sierrae*) in the Sierra Nevada.

the Tehachapi slender salamander (B. stebbinsi) (threatened), the yellow-blotched salamander (Ensatina eschscholtzii croceater) (special concern), the limestone salamander (Hydromantes brunus) (threatened), the Mount Lyell salamander (H. platycephalus) (special concern), and the Owens Valley webtoed salamander (Hydromantes sp.) (special concern)—are at risk because of these hydrology-disrupting activities in their habitats (e.g., see Steinhart 1990 and Jennings and Hayes 1994),

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Historic and current distribution of (A) yellowblotched salamander *(Ensatina eschscholtzii croceater),* (B) Sierra Nevada salamander *(Ensatina eschscholtzii platensis),* and (C) yellow-eyed salamander *(Ensatina eschscholtzii xanthoptica)* in the Sierra Nevada.



and the Breckenridge Mountain slender salamander (Batrachoseps sp.) apparently became extinct after a Forest Service road was rerouted above the seep that was its only known habitat (R. Hansen, conversation with the author, October 8, 1988). Without appropriate management actions by the responsible agencies or landowners, the same factors that have caused the decline of these seven species can also affect the five other endemic species with restricted distributions that so far have not had major disturbances within their known habitats.

Newts (Salamandridae)

Newts are represented by two species in the Sierra Nevada: the northern rough-skinned newt (Taricha granulosa granulosa) (figure 31.4) and the Sierra newt (T. torosa sierrae) (figure 31.6). Both newts have a life cycle like that of mole salamanders except that they also breed in streams as well as temporary pools, and adults are often found on the surface throughout much of the year. Both newts are secure within their current ranges, probably because the adults breed in small, often temporary streams at low to middle elevations (Stebbins 1951; observations by the author, 1988-95). They also seem better adapted to fluctuating conditions in streams than other aquatic salamanders. However, there is some recent evidence to indicate that aquatic newt larvae are highly susceptible to predation by introduced fishes (Liss and Larson 1991). Additionally, introduced bullfrogs are known to successfully consume juvenile and adult newts when given the opportunity (observations by the author). Recent ongoing genetic studies by students at the University of California, Berkeley, indicate that there are at least two taxa (probably species) within the subspecies currently recognized as T. t. sierrae (D. Wake, conversation with the author, June 19, 1995). Thus, further evaluation may be needed regarding these new endemic species with restricted distributions.

True Toads (Bufonidae)

True toads are represented by two species in the Sierra Nevada: the California toad (Bufo boreas halophilus) and the Yosemite toad (B. canorus) (figure 31.8). Both species require standing water (either in slow-moving streams or in ponds) for reproduction. The aquatic larval period for the true toads is short, usually only about two months (Storer 1925). After metamorphosis, the juveniles disperse into riparian habitats or other areas to mature (Stebbins 1951). Adults may live for ten years or more (Bowler 1977; Kagarise Sherman and Morton 1993).

The California toad is a subspecies of the widely distributed western toad (Bufo boreas), a species that has undergone a substantial range reduction in the Rocky Mountain region and the Pacific Northwest during the past two decades (Carey 1993). In California, populations of the California toad seem to have been reduced as a result of urbanization, changing farming practices, and the use of pesticides, but the levels noted are not critical, as larvae, juveniles, and adults continue to be found in all known habitats (observations by the author, 1988–95). The Yosemite toad, on the other hand, is endemic to isolated high-mountain meadows in the central part of the Sierra Nevada. Its populations are declining so rapidly that the toad merits being listed as endangered (Jennings and Hayes 1994). For example, both Drost and Fellers (1994) and Jennings and Hayes (1994) found this species to have disappeared from about half of its known historic localities. The causes for this decline are apparently similar to those for the decline of native true frogs (discussed later).

Tree Frogs (Hylidae)

Tree frogs are represented by a single species, the Pacific tree frog (Hyla regilla), in the Sierra Nevada (figure 31.9). Like all frogs and toads, it has an aquatic larval stage that metamorphoses into a terrestrial juvenile. Pacific tree frogs reach maturity within one to two years after metamorphosis and are often found in terrestrial situations that may be more than 0.8 km (0.5 mi) from the nearest water source (Storer 1925; observations by the author, 1988–95). This tree frog is widely distributed throughout the American West and is found in good numbers at most Sierra Nevada localities (Bradford 1989; observations by the author, 1988-95). Bradford (1989) attributed this to the ability of Pacific tree frogs to breed in shallow water habitats or temporary ponds that are free of fish predators. However, Drost and Fellers (1994) note that while Pacific tree frogs are still widely distributed in the central Sierra Nevada, their numbers seem to be reduced at high elevations compared with historic observations. This reduction may be due to natural population fluctuations, as North American tree frogs (Hylidae) are known to undergo population fluctuations as much as thirtyfold or more (see Pechmann et al. 1991).

True Frogs (Ranidae)

True frogs are represented by six species in the Sierra Nevada: the foothill yellow-legged frog (Rana boylii) (figure 31.10), the northern leopard frog (R. pipiens) (figure 31.10), the bullfrog (R. catesbeiana) (figure 31.11), the California red-legged frog (R. aurora draytonii) (figure 31.12), the mountain yellow-legged frog (R. muscosa) (figure 31.12), and the Cascade frog (R. cascadae) (figure 31.13). The bullfrog is an introduced species originating in the United States east of the Rocky Mountains. It was first released in the Sierra Nevada about 1915 (Storer 1922) and has become well established in most perennial streams and ponds below 1,829 m (6,000 ft). Although currently considered a game species by the California Department of Fish and Game, it has been implicated in the decline of a number of native frog species (Moyle 1973; Hayes and Jennings 1986), and its game status is now under review by the California Fish and Game Commission (J. Brode, senior fisheries biologist, Inland Fisheries Division, California Department of Fish and Game, letter to the author, March 29, 1995).

All native true frogs have life histories like those of true toads and tree frogs. Their aquatic larval stage normally requires three to six months of development, and terrestrial juveniles require two to three years to reach adulthood (Zweifel 1955; Jennings and Hayes 1985), except for the mountain yel-



Historic and current distribution of (A) California toad (Bufo boreas halophilus) and (B) Yosemite toad (Bufo canorus) in the Sierra Nevada.



toads and tree frogs. Their aquatic larval stage normally requires three to six months of development, and terrestrial juveniles require two to three years to reach adulthood (Zweifel 1955; Jennings and Hayes 1985), except for the mountain yellow-legged frog, which has a considerably longer larval period of one to two and a half years (Bradford 1983). Such a long larval stage for the mountain yellow-legged frog makes it extremely vulnerable to predation by introduced aquatic



FIGURE 31.9

Historic and current distribution of the Pacific tree frog *(Hyla regilla)* in the Sierra Nevada.

predators such as trout, charr, and crayfish (Bradford 1989; Bradford et al. 1993).

The true frogs have shown the most dramatic declines of all groups of amphibians in the Sierra Nevada. They have

disappeared from significant portions of their historic range over the past twenty-five years (Jennings 1995). In the Sierra Nevada, the California red-legged frog has disappeared from 99% of its historic range and has been proposed for listing as

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Historic and current distribution of (A) foothill yellow-legged frog (*Rana boylii*) and (B) northern leopard frog (*Rana pipiens*) in the Sierra Nevada.



in 1987–88 foothill yellow-legged frogs were absent from all locations in the San Joaquin valley foothills where in 1970 they had been widespread and abundant (Moyle 1973; P. B. Moyle, Department of Wildlife, Fisheries, and Conservation Biology, University of California, Davis, conversation with the author, November 20, 1995). Currently, the foothill yellow-legged frog, Cascade frog, mountain yellow-legged frog, and northern leopard frog seem to have disappeared from



FIGURE 31.11

Current distribution of the introduced bullfrog (*Rana catesbeiana*) in the Sierra Nevada.

about 45%, 50%, 50%, and 95% of their historic ranges in California and from about 66%, 99%, 50%, and 99% of their historic ranges in the Sierra Nevada, respectively (Jennings and Hayes 1994). All of these frogs can now be considered to be

threatened in the Sierra Nevada, except for the Cascade frog, which is considered to be endangered in this same region (Jennings and Hayes 1994).

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Historic and current distribution of (A) California red-legged frog (*Rana aurora draytonii*) and (B) mountain yellow-legged frog (*Rana muscosa*) in the Sierra Nevada.



Spadefoot Toads (Pelobatidae)

Spadefoot toads are represented by a single species, the western spadefoot (Scaphiopus hammondii) in the Sierra Nevada (figure 31.13). It is a lowland species that has adapted to dry environments by breeding in temporary ponds and slowmoving streams (Stebbins 1985). Adults and juveniles burrow into suitable substrates near breeding sites or use small mammal burrows to avoid desiccation throughout most of



FIGURE 31.13

Historic and current distribution of (A) Cascade frog (*Rana cascadae*) and (B) western spadefoot (*Scaphiopus hammondii*) in the Sierra Nevada.

the year (Storer 1925). Adults are active on the surface only during short periods of time (such as the winter months) when conditions are suitable. The species is largely endemic to California and is found along the western edge of the Sierra Nevada foothills. Because of habitat loss due to agriculture and urbanization, this organism is considered a species of special concern (Jennings and Hayes 1994).

CAUSES OF AMPHIBIAN DECLINES

The reasons for the precipitous declines in certain amphibians (especially native frogs) are complex. Certainly the disappearance of all of the middle- to low-elevation species is due largely to habitat alteration from agriculture, urbanization, water development, placer mining, livestock grazing, drought, and the introduction of a wide variety of non-native predatory fishes, crayfish, and bullfrogs (Jennings 1995). However, in many localities none of these activities have occurred, vet amphibians such as native salamanders and frogs have still disappeared within the past twenty-five years (Jennings and Hayes 1994). The widespread disappearance of native frogs from middle- to high-elevation areas is even more perplexing. Some of these population extinctions can be explained by the widespread introduction of predatory fishes (especially trout and charr) in the Sierra Nevada over the past one hundred years (Bradford et al. 1993; Fellers and Drost 1993), as well as extensive livestock grazing and increased levels of recreation in sensitive breeding areas (Jennings and Hayes 1994). However, in literally hundreds of localities both introduced trout and native salamanders and frogs seemingly cooccurred together for at least fifty years, based on old fish planting records and common observations of trout and frogs in the same aquatic habitats in the 1960s and early 1970s (observations by the author, 1960-95). Apparently, a number of different factors are contributing to the declines in these amphibian species. Declines such as these are often the result of long-term, cumulative effects of multiple factors, where natural low points in amphibian population cycles synergize with widespread environmental alterations to create extinction events (e.g., many of the Yosemite toad populations in the Sierra Nevada underwent dramatic population crashes when they were unable to reproduce at historical breeding sites during extended periods of drought in the Sierra Nevada, 1986-90 [Kagarise Sherman and Morton 1993]). Amphibians seem to be in worse condition than most other organisms because they are uniquely vulnerable to these cumulative environmental effects. This is because species are either highly localized in their distribution (as is the case with lungless salamanders) or because they fit into the classic models of metapopulation dynamics (as is true of true frogs and true toads). Some of the best metapopulation studies come from work on true frogs in Scandinavia, where researchers find localized frog populations undergoing continuous cycles of extinction and recolonization from nearby sources (see Harrison 1991). Such recolonization events for native frog populations in the Sierra Nevada are now impossible for many areas because of the widespread extinction of many local source frog populations and the presence of introduced predators in most formerly suitable habitats (Bradford et al. 1993).

Whatever the problems are that are causing the decline among amphibians, there is no doubt that many stressors are

now present in the environment that negatively affect amphibians such as native frogs, possibly predisposing them to native or introduced pathogens. These stressors could have contributed to the precipitous declines in many frog populations during the 1970s. Possible stressors include air pollution, increased levels of ultraviolet light radiation, acid precipitation, and pesticides (each of these is discussed in more detail later in this chapter). It is important to note that all of these stressors are linked to human needs, especially as a result of ever-increasing population growth in the Sierra Nevada and the rest of California.

The following is an annotated list of the possible causes of amphibian declines in the Sierra Nevada. More details can be found in Jennings and Hayes 1994 and the references cited therein.

Natural Causes

Amphibian populations naturally undergo wide fluctuations in abundance in response to environmental conditions, especially droughts, floods, and epizootic diseases (Pechmann et al. 1991; Pechmann and Wilbur 1994). Local or even regional extirpations are apparently common, but populations are maintained over wide areas through dynamic recolonization events. For example, some populations of foothill yellowlegged frogs disappeared from a number of streams in the southern Sierra Nevada after the extreme floods of 1968 and 1969 (personal observations by the author, 1970-95). Another example is provided by Bradford (1991), who observed the extinction of a population of mountain yellow-legged frogs when a flock of Brewer's blackbirds (Euphagus cyanocephalus), not normally regarded as significant frog predators, devoured the entire cohort of metamorphosing frogs that emerged from the breeding pond. Such extinction events (and subsequent recolonizations) have presumably governed amphibian populations in the Sierra Nevada since the Pleistocene. However, in recent years the natural ability of amphibian populations to recover from local extirpation events has been greatly reduced as the result of human-induced environmental changes.

Alteration of Terrestrial Habitats

All Sierra Nevada amphibians have a terrestrial stage to their life cycle. This is most pronounced in the lungless salamanders, which spend their entire lives without needing open-water environments. Thus, any activity that severely alters the terrestrial environment, such as urbanization, agriculture, livestock grazing, timber harvest, mining, or road building, is likely to result in the reduction and occasional extirpation of amphibian populations. For example, the release of domestic livestock in high-mountain meadows utilized by Yosemite toads (for reproduction) has resulted in the pollution of breeding ponds as well as the trampling of toad larvae and juveniles (Jennings and Hayes 1994). Except for unusual circumstances, such as the construction of the road that modified the only known habitat for the Breckenridge Mountain slender salamander (Jennings and Hayes 1994), single actions do not eliminate species. Nonetheless, changes to terrestrial habitats are often cumulative (as is the case with long-term livestock grazing, which tends to eliminate certain plants that provide important cover for many amphibian species) and may occur too frequently for population recovery following events that reduce resident amphibian populations.

Alteration of Riparian Habitats

Since most Sierra Nevada amphibians spend significant portions of their life cycles either in or moving through riparian habitats, these areas are important to their overall survival. For instance, foothill yellow-legged frogs and California redlegged frogs seem to require riparian areas that are well developed structurally (for cover and estivation as well as the production of food resources) but that also contain open areas for basking (Hayes and Jennings 1988). Thus, the degradation of riparian areas can lead to habitat fragmentation, loss of corridors necessary for recolonization, and the ultimate loss of local amphibian populations. Specific examples of factors contributing to this degradation are livestock grazing, road building, reservoir construction, and recreation (Jennings and Hayes 1994). The most obvious reasons for the demise of native amphibians due to these factors are (1) increased dehydration and increased predation due to the loss of vegetative cover; (2) changes in the structure and composition of the flora (thus affecting important food resources); and (3) the crushing or removal of small or cryptic individuals due to trampling, vehicles, or the results of human activities. Specific examples include (1) increased dehydration rates for slender salamanders in habitats where the riparian cover was removed (see Ray 1958); (2) the loss of riparian willows (Salix spp.), which resulted in increased predation on California redlegged frogs by raccoons (Procyon lotor) (Miller 1994); (3) the loss of important food resources that are critical for the growth and survival of juvenile frogs and toads, due to the removal of vegetation upon which invertebrates feed (Jennings and Hayes 1994); and (4) the crushing of individuals by livestock grazing in alpine meadows, which resulted in trampled larval and juvenile Yosemite toads (D. Martin, Martin, Canorus Ltd., letter to the author, May 12, 1991), or by motorcycle use in riparian zones, which crushed juvenile and adult foothill yellow-legged frogs and garter snakes (personal observations by the author, 1986–90).

Alteration of Aquatic Habitats

As is widely stated in the literature (e.g., see Moyle 1976), aquatic habitats of the Sierra Nevada have been greatly altered through dams, diversions, channelizations, siltation, livestock grazing, timber harvest, placer mining, and many other factors. The same factors that have made these habitats less suitable for native fishes have also made them less suitable for native amphibians. Reservoirs, found on most larger Sierra Nevada streams, disrupt native aquatic amphibians because most of these organisms cannot live in, or move through, the exposed shorelines, nor can they successfully reproduce in such fluctuating environments containing introduced predatory fish, crayfish, and bullfrogs. For example, mountain yellow-legged frogs seem unable to successfully produce a cohort of young in artificial reservoirs (with predatory fish) unless shallow side channels or disjunct pools are present that are separated from the main body of water (thus excluding the fish) (D. Bradford, U.S. Environmental Protection Agency, conversation with the author, February 4, 1992). Additionally, there are a number of observations of native adult frogs (R. a. draytonii, R. cascadae, and R. muscosa) being consumed by large introduced trout after the frogs were accidentally scared into the water by humans (Drost and Fellers 1994; L. Simons, graduate student, Department of Evolution and Ecology, University of California, Davis, letter to the author, September 9, 1994; observations by the author, 1989–90).

Besides the above, alteration of the natural hydrological regime often creates habitat conditions unfavorable to native amphibians, and the dams and their associated structures may create serious barriers to movements by dispersing juveniles and migrating adults. For example, open pipelines and canals have been found to catch and kill migrating adult California tiger salamanders that fall into them (Sorenson 1994). An additional example is the placement of reservoirs at middle to lower elevations in the Sierra Nevada, which has resulted in the creation of many year-round cold-water streams below dams. These reservoirs (along with unseasonal releases of water) resulted in unsuitable breeding habitats for foothill vellow-legged frogs and the scouring out of their egg masses downstream during the spring (Jennings and Hayes 1994). Thus, it is rare to find open-water-dependent native amphibians immediately below reservoirs, especially large reservoirs.

Introduction of Aquatic Predators

Hayes and Jennings (1986), Bradford (1989), Bradford et al. (1993), and Jennings and Hayes (1994), along with many others, have noted the generally negative correlation between the presence of introduced predators (especially fishes and bullfrogs) and the abundance of native amphibians in streams and lakes of California. Introduced bullfrogs, fishes, and crayfishes seem to be a particular problem for many species (such as California tiger salamanders and mountain yellow-legged frogs), probably because these organisms did not coevolve with a suite of aquatic predators (Hayes and Jennings 1986). Limited field and laboratory observations on how bullfrogs, fishes, and crayfishes feed on native amphibians indicate that although all life stages of the latter are eaten, it is the larvae of mole salamanders, newts, and true frogs and toads that are most susceptible (observations by the author, 1989–91). This is because most native amphibian larvae have traits that predispose them to introduced predators-especially sight predators such as trout or tactile predators such as crayfish during periods of darkness (e.g., the larvae lack toxic skin secretions, lie on top of the benthos at night, have poor swimming escape tactics) (Hayes and Jennings 1986). Mountain yellow-legged frogs are probably the most obvious example of a species that is predisposed to predation because they have such a long larval period (one to two and a half years) that there is a relatively good chance of being exposed at some point to introduced aquatic predators if the latter are present. Overall, there is strong evidence that introduced fishes continue to limit the distribution and abundance of certain native amphibians in parts of the Sierra Nevada (Bradford et al. 1993; Jennings and Hayes 1994).

Disease

The presence of a wide variety of pathogens (some of which are native and others introduced) in salamanders and frogs has long been noted as a cause of local amphibian declines (Bradford 1991). The role of disease in the decline of certain frog and toad species in the American West has recently received more attention (see Carey 1993 and Scott 1993). Some of the more plausible hypotheses are that stressors, such as increased levels of UV-B radiation or air pollutants, cause a weakening of the immune system, which could cause an increased susceptibility to natural diseases (Blaustein and Wake 1995). Another hypothesis, supported by limited observations, is that diseases carried by planted trout may attack and kill amphibian eggs and larvae (Blaustein et al. 1994b). The overall importance of diseases as a cause of death among native amphibians is hard to assess, but it is probably the most important source of mortality for individuals stressed by other factors (Scott 1993).

Acid Precipitation

The widespread acidification of mountain streams and lakes in the Northeast, Rocky Mountains, and Europe has been associated with amphibian declines (Haines 1981). While unbuffered waters of the Sierra Nevada are subject to acidification from air pollution (Nikolaidis et al. 1991), Bradford et al. (1994) could not find any evidence that anthropogenic acidification is a major problem there, except for highly localized spots that receive acid runoff from a point source (such as a mine). However, the potentially negative effects of acidification were demonstrated by an examination of naturally acidic lakes in the Sierra Nevada. No lake with a pH value less than 6 supported amphibian populations (Bradford et al. 1994).

Pesticides

Like acid precipitation, pesticides have been suspected of affecting amphibian abundance, especially agricultural pesticides drifting upward from the San Joaquin valley. Previously, DDT was found in significant quantities in mountain yellowlegged frogs throughout the Sierra Nevada (Cory et al. 1970). More recently, the finding that pesticides mimic estrogen in vertebrates has been proposed as a hypothesis for amphibian declines (see the discussion in Stebbins and Cohen 1995). Pesticide deposition has increased in recent years in the San Joaquin foothills because of the rise of mega-agriculture on the valley floor (T. Cahill, Crocker Nuclear Laboratory, University of California, Davis, conversation with the author, April 26, 1995). However, none of these pesticide hypotheses have been tested, and their overall effects on Sierra Nevada amphibians are unknown.

Automobile Emissions

Recent studies by the Crocker Nuclear Laboratory, Air Quality Group, University of California, Davis, have noticed that the pattern of recent frog extinctions in the southern Sierra Nevada corresponds with the pattern of highest concentrations of air pollutants from automobile exhaust (T. Cahill, conversation with the author, April 26, 1995). It is possible that the increased nitrification (or other changes) in streams and lakes by these chemicals may be affecting frog reproduction and survival. Air pollution seems to be seriously weakening the coniferous trees of the Sierra Nevada (California Air Resources Board 1987) and may be having negative effects on other parts of the ecosystem as well.

Ultraviolet Light

As the ozone layer of the upper atmosphere thins due to some forms of air pollution, the earth has been bombarded by increased ultraviolet (UV) radiation. For amphibians that sun themselves (and amphibian eggs that develop in unshaded, shallow water habitats), exposure to increased levels of UV-B radiation may increase mortality rates, especially for those species that are unable to repair DNA damaged by UV-B radiation (see Blaustein et al. 1994a and Blaustein et al. 1995). The hypothesis that UV radiation is related to amphibian declines is favored by some herpetologists (see especially Blaustein and Wake 1995) because it could help explain (1) global amphibian declines, (2) the coincidence of rapid declines of several different species in many areas in recent years, and (3) the severe declines at high elevations (Wake 1991). However, this hypothesis has come under increasing attack by a number of scientists because "of its apparent lack of scientific rigor with regard to observed field situations" (e.g., see Roush 1995; but see also Blaustein 1995; Formanowicz 1995; Halliday 1995; and Reznick 1995). As Drost and Fellers (1994) state, "The evidence for an influence from ultraviolet radiation remains speculative and circumstantial, but until compelling evidence is brought forth for some other cause, this hypothesis must be considered an important possibility" (Drost and Fellers 1994, 31). Closer examination of the subject reveals three facts that make the hypothesis suspect. The first is that observed die-offs of native frogs and toads in the American West occur among adults and juveniles (e.g., see Carey 1993 and Scott 1993), not among developing embryos, as shown in Blaustein et al. 1994a. Second, UV-B would negatively affect all organisms sensitive to this factor. However, there have been no documented die-offs of likely sensitive plants and insects due to "increased" UV-B in the Sierra Nevada. Finally, measurements by the Crocker Nuclear Laboratory, Air Quality Group, University of California, Davis, indicate that UV levels at high elevations in the Sierra Nevada have increased by no more than 5% over the past several decades (T. Cahill, conversation with the author, April 26, 1995). Thus, it is unlikely that increased UV-B levels are a major cause of amphibian declines in the Sierra Nevada.

CONCLUSIONS

It is apparent that a significant percentage of the native amphibian species inhabiting the Sierra Nevada have shown dramatic declines in abundance, distribution, and diversity in recent years. A total of 53% of the thirty native taxa now require some sort of protection. That these declines have something to do with the life history traits of the taxa and the disruption of aquatic environments is made evident by examining the status of reptiles in the Sierra Nevada (Jennings and Hayes 1994). Of the twenty-six Sierra Nevada species (twenty-four of which are terrestrial) within the study region-excluding another twenty desert species that occur on the periphery of the mountains-twenty (77%) are secure, four (15%) are listed or merit listing, and two (8%) are of special concern. Only one of the four threatened species is in serious decline-the western pond turtle (Clemmys marmorata), a highly aquatic species.

It is certain that amphibian declines and extinctions have been caused by a number of interacting factors, with each taxon being affected in different ways (table 31.2). Such factors can range from global to local, but the most important ones in the Sierra Nevada appear to be the alteration of terrestrial and aquatic habitat, habitat fragmentation, and the introduction of aquatic predators (table 31.2). Fortunately, there are still some watersheds where native amphibians thrive in sufficient numbers to ensure survival for the time being. In the foothills, these locations tend to be small streams that have a heavy riparian canopy, that are free of introduced predators, and that have been relatively undisturbed by livestock grazing, timber harvest, water development, and placer mining. At high elevations, such habitats tend to be in clusters of fishless lakes and streams in remote areas. These observations suggest that localized restoration of amphibian habitats, such as the creation of fishless basins (or watersheds) in wilderness areas, is possible. It is essential that the watersheds listed in table 31.3 (which have especially high values for amphibian conservation) be considered for protecting important amphibian resources. Further, it is also important to note that native amphibians (especially true frogs) in the Sierra Nevada can no longer exist as metapopulations but rather must be seen as fragmented, individual populations that are highly vulnerable to extirpation. This fragmentation and likely extinction (without hope of recolonization) is certain to lead to local, then regional, then Sierra-wide extinctions of selected amphibian species if current trends continue.

Finally, it should be noted that there is a hopeful sign for the potential recovery of certain lower-elevation species if the habitat is restored and introduced aquatic predators are reduced or eliminated. For example, the South Fork of the Yuba River was badly sluiced by placer gold mining activities from the 1850s to the 1870s. With the recovery of the riparian zone, this stream currently has a good population of foothill yellow-legged frogs in suitable patches of habitat. There are a number of other large Sierran streams that fit this category (especially in the northern half of the Sierra Nevada), and efforts should be made to restore riparian and aquatic habitats and protect any sensitive native amphibians that are extant.

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TABLE 31.2

Relative importance of various factors in the decline of Sierra Nevada amphibians.

Species	Natural Causes	Terrestrial Alteration	Fragmen- tation	Riparian Changes	Aquatic Changes	Introduced Predators	Acid Rain	Pesticides/ Pollutants	UV Radiation	Disease
Salamanders Mole Salamanders California tiner salamander	1	3	2	3	1	2	0	1	2	1
Lunglaga Calamandara		Ū.	-	Ū		-	Ũ	•		
Policitual alandar aalamandar	2	2	2	1	1	0	0	0	0	0
Kern Canvon slonder salamander	2	3	2	1	1	0	0	0	0	0
Tehachani slender salamander	0	3	2	0	0	0	0	0	0	0
Breckenridge Mountain slender salamander	1	3	3	3	0	0	0	0	0	0
Yellow-blotched salamander	0	2	1	1	0	0	0	0	0	0
Limestone salamander	0	2	2	1	0	0	0	0	0	0
Mount Lyell salamander	0	1	1	0	0	0	0	0	0	0
Owens Valley web-toed salamander	0	2	1	2	0	0	0	0	0	0
Frogs and Toads True Toads										
Yosemite toad	2	1	2	1	1	2	1	1	?	?
True Frogs										
California red-legged frog	2	2	3	2	1	3	0	1	0	1
Footnill yellow-legged frog	2	1	2	2	1	3	0	1	0	2
Cascade frog	1	0	2	1	0	2	0	0	0	2
Nountain yellow-legged frog	1	0	2	1	0	3	1	1	<i>?</i>	2
Northern leopard frog	I	I	I	I	I	I	0	0	0	2
Spadefoot Toads Western spadefoot	1	3	1	2	1	2	0	1	0	0
Totals	14	30	29	22	7	18	2	6	0	10

0 indicates the factor was of no importance. 1 indicates the factor was a minor contributor. 2 indicates the factor was an important contributor. 3 indicates the factor was a major contributor. ? indicates the importance of the factor is unknown.

TABLE 31.3

Watersheds with especially high values for amphibian conservation that should be protected.

County	Watershed	Species
Alpine	North Fork Mokelumne River (all tributaries)	Yosemite toad, mountain yellow-legged frog
Alpine	North Fork Stanislaus River (above Union Reservoir)	Yosemite toad, mountain yellow-legged frog
Amador	North Fork Mokelumne River (all tributaries)	Mountain yellow-legged frog
Butte	Big Chico Creek	Foothill yellow-legged frog
El Dorado	Alder Creek	Mountain yellow-legged frog
El Dorado	Camp Creek	Foothill yellow-legged frog
El Dorado	Caples Creek	Mountain yellow-legged frog
El Dorado	Silver Fork American River (all tributaries)	Mountain yellow-legged frog
Fresno	Big Creek	Yosemite toad
Fresno	Jose Creek	Foothill yellow-legged frog
Fresno	North Fork Kings River (all tributaries)	Slender salamander complex, Yosemite toad, mountain yellow-legged frog
Fresno	Piute Creek	Mountain yellow-legged frog
Fresno	South Fork Kings River (all tributaries)	Slender salamander complex, mountain yellow-legged frog
Fresno	South Fork San Joaquin River (all tributaries)	Slender salamander complex, Yosemite toad, mountain yellow-legged frog
Inyo	All eastern Sierra tributaries	Slender salamander complex, Owens Valley web-toed salamander, Yosemite
		toad, mountain yellow-legged frog, northern leopard frog
Kern	Breckenridge Mountain (all tributaries)	Slender salamander complex, yellow-blotched salamander, mountain yellow- legged frog
Kern	Caliente Creek	Slender salamander complex, yellow-blotched salamander
Kern/Tulare	Middle Kern River (all tributaries)	Slender salamander complex, yellow-blotched salamander
Kern/Tulare	South Fork Kern River (all tributaries)	Slender salamander complex
Mariposa	Bull Creek	Foothill yellow-legged frog
Mariposa	Middle and Upper Merced River (all tributaries)	Slender salamander complex, limestone salamander, Mount Lyell salamander, Yosemite toad, mountain yellow-legged frog
Mono	All eastern Sierra tributaries	Slender salamander complex, Owens Valley web-toed salamander, Yosemite toad, mountain yellow-legged frog, northern leopard frog
Plumas	Boulder Creek	Mountain yellow-legged frog
Plumas	Butt Creek	Cascade frog, mountain yellow-legged frog
Plumas	Canyon Creek	California red-legged frog
Plumas	Middle Fork Feather River (all tributaries)	Mountain yellow-legged frog
Plumas	North Fork Feather River (all tributaries)	Mountain yellow-legged frog
Tehama	Antelope Creek	Cascade frog, foothill yellow-legged frog
Tehama	Deer Creek	Cascade frog, foothill yellow-legged frog
Tehama	Mill Creek	Cascade frog, foothill yellow-legged frog
Tulare	Blossom Lakes	Mountain yellow-legged frog, Mount Lyell salamander
Tulare	Marble Fork Kaweah River (all tributaries)	Mountain yellow-legged frog, Mount Lyell salamander
Tulare	Upper Kern River (all tributaries)	Mountain yellow-legged frog, slender salamander complex
Tuolumne	Cherry Creek	Mountain yellow-legged frog
Tuolumne	Clavey River	Foothill yellow-legged frog, mountain yellow-legged frog
Tuolumne	Coyote Creek	Foothill yellow-legged frog
Tuolumne	Middle Fork Stanislaus River (all tributaries)	Yosemite toad, Mount Lyell salamander, foothill yellow-legged frog, mountain yellow-legged frog
Tuolumne	Rose Creek	Foothill yellow-legged frog
Tuolumne	South Fork Stanislaus River (all tributaries)	Yosemite toad, Mount Lyell salamander, foothill yellow-legged frog, mountain yellow-legged frog

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