

What We Know and Don't Know About Amphibian Declines in the West

Paul Stephen Corn¹

Abstract — The problem of declining amphibian species is thought to be particularly acute in western North America, but there are many gaps in our knowledge. Although several declines have been well-documented, other declines are anecdotal or hypothesized. Most documented declines are of ranid frogs or toads (*Bufo*). Species from montane habitats and those occurring in California have been best studied. Status of many desert species is unknown. Habitat destruction and introduced predators are the most common threats to amphibian populations. Some declines may represent natural variation in population size. Causes have not been determined for several cases where common species have declined over large areas. There are important considerations for ecosystem management, whether changes in amphibian populations are natural or caused by human activities. Causes for declines must be known so that management can be prescribed (or proscribed) to eliminate or minimize these causes. The natural variability of amphibian population numbers and the complexity of metapopulation structure emphasize the necessity of considering multiple temporal and spatial scales in ecosystem management. The decline of amphibian species throughout the world has received considerable recent attention (e.g., Blaustein and Wake 1990, Griffiths and Beebee 1992, Yoffe 1992). Much of this attention derives from a workshop held in February, 1990 on declining amphibians sponsored by the National Research Council Board (NRC) on Biology in Irvine, California (Barinaga 1990, Borchelt 1990). Because of media attention in the aftermath of this conference, it is a popular perception that amphibian declines are a new phenomenon that herpetologists have been slow to recognize (Griffiths and Beebee 1992, Quammen 1993). However, concern about amphibian populations in the United States dates back over 20 years. Beginning in the 1960s, a large, well-documented decline of northern leopard frogs (*Rana pipiens*) occurred in the upper Midwest (Gibbs et al. 1971, Hine, 1981, Rittshof 1975).

Participants in the NRC workshop concluded that declines of amphibians were a global problem. Unfortunately, another conclusion was that much of the information on declines was anecdotal and few causes of declines had been discovered. In the past three years, some progress has been made in documenting the extent of amphibian declines, but many of the causes remain undiscovered.

In North America, amphibian declines have been most numerous in the West and have occurred among species occupying both montane and low-elevation desert habitats. Several species have declined or disappeared from relatively undisturbed habitats, including National Parks and Wilderness Areas (Bradford 1989; Bradford et al., in press; Carey 1993; Corn et al. 1989; Fellers and Drost, in press). Amphibians are key components of many ecosystems, both on small (Seale 1982) and large (Hairston 1987, Petranks et al. 1993) scales, so their disappearance may complicate efforts to manage ecosystems on a sustainable basis.

¹ Paul Stephen Corn is Zoologist, USDI Fish and Wildlife Service, National Ecology Research Center, 4512 McMurtry Avenue, Fort Collins, Colorado 80525-3400

My objective for this review is to summarize the current knowledge of amphibian declines in the western United States (west of the Great Plains). Many declines are now well documented, and the causes for many of these have also been determined. I will describe the unknown-suspected declines that have not been documented and declines for which causes have not been determined. Finally, I will discuss the problems amphibian declines create for ecosystem management.

KNOWN DECLINES

At least 79 species of amphibians inhabit the western United States, including 38 salamanders and 41 anurans (frogs and toads) (Stebbins 1985). Only three of these taxa are listed by the U. S. Fish and Wildlife Service (USFWS) as threatened or endangered. The desert slender salamander (*Batrachoseps aridus*) is endangered in southern California because it is an endemic species restricted to one moist desert canyon (Bury et al. 1980). The Santa Cruz long-toed salamander (*Ambystoma macrodactylum croceum*) is endangered in the Monterey Bay area of central California because most of its breeding ponds have been drained for urban development or agriculture (Ruth 1988). The Wyoming toad (*Bufo hemiophrys baxteri*) is endangered in the Laramie Basin of southern Wyoming (Baxter et al. 1982). The cause or causes of the decline of this species are still unknown. Besides these listed species, moderate to serious declines of several other amphibians have been described in recent years.

No widespread declines of salamanders have been documented. Collins et al. (1988) described the loss of at least 4 of the 17 known populations of the Huachuca tiger salamander (*Ambystoma tigrinum stebbinsi*) in southern Arizona. The size of a population of Arizona tiger salamanders (*A. t. nebulosum*) inhabiting a small group of high-elevation ponds in central Colorado declined from about 1700 in 1982 to 200 in 1987 (Harte and Hoffman 1989), but the same population fluctuated from 2900-3500 salamanders in 1988-1991 (Wissinger and Whiteman 1992).

Most declines have been of anurans. Declines have been verified for several species of toads (genus *Bufo*). Baxter et al. (1982) noted that declines of the Wyoming toad began in the mid-1970s, and within a decade it was considered probably extinct (Lewis et al. 1985). A single population was discovered in 1987 (Anon. 1987). The persistence of the Wyoming toad now relies on a small captive population, because no egg masses have been observed in the wild population since 1991 (Wyoming Dept. Game and Fish, unpublished data). The Amargosa toad (*B. nelsoni*) is also an endemic species, restricted to a few springs in southern Nevada and eastern California. Altig and Dodd (1987) found this species to be absent from most known localities in Nevada.

The Yosemite toad (*B. canorus*), more widely distributed than the previous species, occurs at high elevations in the Sierra Nevada in California. This species apparently has declined over

much of its range. At seven locations in the eastern Sierra Nevada, Kagarise Sherman and Morton (1993) observed averages of 6-70 toads per site per day in 1976 but only 0-5 toads per site per day in 1990. Bradford and Gordon (1992) found this species present at only 17 of 235 sites within 30 randomly selected 15 km² (5.8 mi²) study areas above 2,440 m (8,000 ft). The boreal toad (*B. boreas boreas*) was widely distributed and abundant in the southern Rocky Mountains in Colorado, southeast Wyoming, and northern New Mexico. Corn et al. (1989) failed to find the boreal toad at 49 of 59 (83%) known localities in the Front and Park Ranges of Colorado and the Medicine Bow Mountains in Wyoming. Carey (1993) documented the extinction of several populations of this species in central Colorado. Continued surveys in Colorado have located only a few scattered small populations (Corn, unpublished data). Olson (1992) observed declines of two populations of boreal toads in the Oregon Cascades in 1991 and Blaustein and Olson (1991) described mortality of thousands of boreal toad eggs at a third site nearby in 1990.

All other documented amphibian declines in the West are of frogs of the genus *Rana*. Hayes and Jennings (1986) compiled references, both anecdotal and well-documented, that indicated every ranid frog in the West had undergone either local or regional declines. Leopard frogs (*R. pipiens* Complex) have been hit particularly hard. The Vegas Valley leopard frog (*R. fisheri*) occurred only in the warm springs of the Las Vegas Valley. This species is now extinct (M. R. Jennings 1988b). The relict leopard frog (*R. onca*) occurred along the Virgin River in southern Nevada and southwestern Utah. This species has recently been considered conspecific with the Vegas Valley leopard frog (Pace 1974) and also extinct (M. R. Jennings 1988b). However, R. D. Jennings (1993) found three small populations of relict leopard frogs in Nevada, and he presented a morphological analysis indicating that relict and Vegas Valley leopard frogs were distinct species. Corn and Fogleman (1984) observed extinction of northern leopard frogs from a few ponds in northern Colorado, and more extensive surveys found this species absent from 29 of 33 (88%) known localities in northern Colorado and southern Wyoming (Corn et al. 1989). Northern leopard frogs were also absent from 13 of 28 (46%) known localities in Arizona (Clarkson and Rorabaugh 1989). Chiricahua leopard frogs (*R. chiricahuensis*) were absent from 34 of 36 (94%) of known localities in Arizona (Clarkson and Rorabaugh 1989), and lowland leopard frogs (*R. yavapaiensis*) have been extirpated from the lower Colorado River in Arizona and California and the Imperial Valley in California (Clarkson and Rorabaugh 1989; Jennings and Hayes, in press).

The U. S. Fish and Wildlife Service (USFWS) was petitioned to list the spotted frog (*R. pretiosa*) as threatened in 1989, and USFWS found that listing was warranted but precluded for populations of spotted frogs in western Oregon, western Washington, northern Nevada, southern Idaho, and the Wasatch Front in Utah (USFWS 1993b). Spotted frogs have been rare in western Oregon and Washington for several decades (Dumas 1966, Nussbaum et al. 1983). McAllister et al. (1993) searched

60 locations in western Washington from 1989-1991 and found only a single individual of this species at one site. Turner (1962) failed to find spotted frogs at several known localities in northern Nevada. Spotted frogs are currently restricted to a few disjunct areas along the Wasatch Front in Utah, but Ross et al. (1993) observed 126 adult frogs and 162 egg masses at 19 sites in 1991 and 124 adult frogs and 478 egg masses at 54 sites in 1992. In western Utah, spotted frogs are distributed among a few isolated marshes but are more numerous than in central Utah. Hovingh (1993) observed several hundred egg masses in seven populations in the Tule Valley in periodic observations from 1981-1991, and O. Cuellar (Dept. Biology, Univ. Utah, unpubl. manuscript) found 354 egg masses at Gandy Salt Marsh in Snake Valley in 1992.

The Tarahumara frog (*R. tarahumarae*) occurs mostly in the Sierra Madre Occidental of Mexico, but all five known populations in southeastern Arizona and several other populations in northern Sonora have disappeared (Hale and Jarchow 1987). The California red-legged frog (*R. aurora draytonii*) was once perhaps the most common ranid frog in California, but it has undergone a long-term and severe decline in the San Joaquin Valley (Moyle 1973), Central Valley (Hayes and Jennings 1986), and apparently has been extirpated from drainages in the Mojave and Sonoran Deserts in southern California (Jennings and Hayes, in press). The USFWS was petitioned to list the California red-legged frog as threatened or endangered, and the agency recently determined that such action was warranted (USFWS 1993a).

Mountain yellow-legged frogs (*R. muscosa*) were common in the Sierra Nevada in California, but have been absent from aquatic habitats at middle and lower elevations for several decades (Bradford 1989). This species has recently declined also in remaining high elevation sites. In 1989-1990, Bradford et al. (unpubl. manuscript) resurveyed 27 sites in Sequoia and Kings Canyon National Parks where mountain yellow-legged frogs were observed in 1978-1979, and the species was absent from all but one site. Bradford and Gordon's (1992) survey of 30 randomly selected study areas found this species present at only 12 of 235 sites. Fellers and Drost (in press) searched 16 known localities and 34 other areas of Lassen Volcanic National Park, California in 1991 for Cascades frogs (*R. cascadae*). They found only two individuals at one site. Nussbaum et al. (1983) mentioned a decline of this species in Oregon, but quantitative data for northern populations have not been published.

Data Limitations

Several studies have documented amphibian declines by surveying for presence or absence of a species at known localities where previous occurrence was recorded from museum specimens or from the literature (Altig and Dodd 1987; Bradford et al., unpubl. manuscript; Clarkson and Rorabaugh 1989; Corn et al. 1989; Fellers and Drost, in press; Jennings and Hayes, in press). Surveys for presence or absence have some problems.

Some species, particularly leopard frogs, may be difficult to detect, because adults disperse after the breeding season. Failure to detect a species that is present, of course, overestimates any decline. There are several other caveats that apply to presence/absence data, all of which may overestimate the number of known localities which, in turn, can lead to an overestimate of decline. First, museum records do not always represent breeding populations. Second, some records are from marginal habitat, where breeding may occur but is rarely successful. This is a particular concern for localities at high elevations, but it is extremely difficult in practice to judge which localities are marginal. Finally, museum and literature records are usually combined over several decades, and this ignores natural processes of extinction and recolonization.

There are solutions to these problems. Determination of presence or absence should not be based on single surveys. Multiple surveys of single sites in different seasons are necessary to verify that a species is absent. One method to alleviate the inflation of known localities is to conduct presence/absence surveys for more than one species. The total number of localities searched will usually be greater than the number of known localities for any one species. Presence of a species at many previously unrecorded localities suggests that a widespread decline is unlikely, even though the species may be absent from several known localities. For example, Corn et al. (1989) found tiger salamanders absent from 12 of 22 (55%) known localities but present at 11 new localities, chorus frogs (*Pseudacris triseriata*) absent from 20 of 56 (36%) known localities but present at 19 new localities, and wood frogs (*Rana sylvatica*) absent from 9 of 29 (31%) known localities but present at 9 new localities. I conclude that these species have not declined appreciably in the Rocky Mountains. Conversely, a species that is absent from most known localities and which is not found at many new sites probably has undergone a decline. Corn et al. (1989) found boreal toads absent from 83% of known localities and at only 2 new localities and northern leopard frogs absent from 88% of known localities and at no new localities. I conclude that both of these species have undergone serious declines.

SUGGESTED DECLINES

The foothill yellow-legged frog (*Rana boylei*) inhabits rocky streams at middle elevations in California and Oregon. Moyle (1973) felt that this species had declined in the San Joaquin Valley and the adjacent foothills of the Sierra Nevada, and Hayes and Jennings (1988) and Jennings (1988a) described a general decline in California. No data have yet been published, however, on numbers of populations that have disappeared or rates of decline.

Several species of amphibians inhabit or are associated with small streams in the forests of the Pacific Northwest (Bury 1988): tailed frog (*Ascaphus truei*), giant salamanders (four species of *Dicamptodon*), torrent salamanders (four species of

Rhyacotriton), and woodland salamanders (at least three species of *Plethodon*). Logging and associated road building destroy or alter amphibian habitat, especially through sedimentation in low-gradient streams (Bury and Corn 1988). Amphibian populations may be eliminated or severely depressed for several decades (Corn and Bury 1989). Because approximately 90% of the low- and mid-elevation forests west of the Cascades have been logged (Morrison 1989), and much of that in the last 40 years (Harris 1984), it is a reasonable hypothesis that populations of stream-dwelling amphibians have declined over much of the landscape (Welsh 1990). Raphael (1988) predicted declines of three species of terrestrial salamanders in northern California, based on continued harvest of old-growth Douglas-fir (*Pseudotsuga menziesii*) forest: Petranka et al. (1993) recently made a similar prediction for terrestrial salamanders in the Appalachian Mountains of the southeastern United States. There have been no studies, however, documenting changes in the regional distribution and abundance of stream amphibians.

CAUSES OF DECLINES

A variety of explanations have been offered for amphibian declines in the West, but few of these have been tested rigorously. One certain reason for the lack of experimentation is the lack of experimental subjects. Most amphibian declines have been observed after the fact, so causes for declines have been based more on correlative than experimental evidence. Causes for declines fall into two broad categories: human-induced (anthropogenic) or natural (usually climatic) factors. Most anthropogenic causes are attributable to habitat destruction or alteration.

Habitat Destruction and Alteration

Several amphibian declines are clearly attributable to conversion of wetland habitat to urban or agricultural use or by water development projects. The transformation of the Las Vegas Valley from a spring-fed wetland to a large city and the Colorado and Virgin Rivers to Lake Mead have caused the extinction of the Vegas Valley leopard frog and the near-extinction of the relict leopard frog (Jennings 1988b; Jennings and Hayes, in press). The large reservoirs and channelization of the lower Colorado River in Arizona and California and agricultural development of the Imperial Valley in California have eliminated appropriate habitat for the lowland leopard frog (Jennings and Hayes, in press). Similar changes are blamed for much of the disappearance of California red-legged frogs from desert drainages in southern California (Jennings and Hayes, in press). Moyle (1973) considered habitat alteration to be a factor in declines of California red-legged frogs and foothill yellow-legged frogs in the San Joaquin Valley. Jennings (1988a) considered alteration of riparian vegetation by livestock grazing

to be an important factor in the decline of ranid frogs in California. The role of logging in the possible decline of amphibians in the Pacific Northwest was discussed previously.

Introduced Predators

Introduction of exotic species of predators, for which native species may have poor defenses, is a special case of habitat alteration. The bullfrog (*R. catesbeiana*), a large ranid from eastern North America, has become established throughout the West (Bury and Whelan 1984). Predation or competition by bullfrogs has been blamed for declines of relict leopard frogs (Cowles and Bogert 1936), spotted frogs (Dumas 1966), northern leopard frogs (Hammerson 1982), and California red-legged and foothill yellow-legged frogs (Moyle 1973). Hayes and Jennings (1986) pointed out that there was little experimental evidence to support this hypothesis, and suggested that predation by introduced warm water fish, mainly centrarchids (*Micropterus* spp. and *Lepomis* spp.) and catfish (*Ictalurus* spp.), and habitat alteration were equally likely to explain declines of ranids in California. Jennings and Hayes (in press) observed that other introduced potential predators, including mosquitofish (*Gambusia affinis*) and red swamp crayfish (*Procambarus clarkii*), as well as bullfrogs, were present at most historical native frog localities in southern California.

Introduction of salmonid fish (*Oncorhynchus* spp., *Salmo* spp., *Salvelinus*, spp.) into historically fishless waters is thought to be responsible for the decline of the mountain yellow-legged frog in the Sierra Nevada. Bradford (1989) sampled 67 lakes and documented that frogs and fish did not coexist in any of them. Bradford et al. (in press) found that presence of fish has fragmented remaining populations of mountain yellow-legged frogs in Sequoia and Kings Canyon National Parks. This fragmentation may be contributing to the continuing decline of this species (Bradford et al., unpubl. manuscript).

Human exploitation might also be considered to be a form of predation. Although bullfrogs are a game species in most states, there is no evidence that other native frog species are sought in large numbers. There were large harvests of California red-legged frogs for food from 1888-1935 (Jennings and Hayes 1985), but there is no real evidence that this contributed to the current scarcity of this species.

Pollutants

Hale and Jarchow (1987) speculated that deposition of heavy metals from copper smelters in Arizona and Mexico was responsible for the disappearance of the Tarahumara frog, but evidence to support this hypothesis was lacking. Harte and Hoffman (1989) concluded that episodic acidification during snowmelt in Colorado may have caused mortality of tiger salamander embryos. Wissinger and Whiteman (1992) did not

observe acid conditions in the same populations of salamanders, and found that salamanders did not breed during the initial stages of snowmelt. Anthropogenic episodic acidification occurs during initial snowmelt when acid anions (sulfate and nitrate deposited throughout the winter) are flushed out, lowering the buffering capacity of surface waters (Vertucci 1988). This is usually before there is open water in breeding ponds and before breeding begins for most amphibians (Vertucci and Corn 1993).

Chronic acidification (the permanent lowering of buffering capacity) is probably a minor occurrence in the Rocky Mountains that is not responsible for amphibian declines. Acid deposition is relatively low, and no amphibian species breed exclusively in habitats with the lowest buffering capacity (Corn and Vertucci 1992). Similarly, Bradford et al. (1992) argued that acid precipitation was not responsible for declines of mountain yellow-legged frogs and Yosemite toads in California.

Disease

Mass mortality of amphibians from disease is not uncommon and may be a natural feature of the biology of a species, or it may be induced by an anthropogenic agent. Redleg disease or other bacterial infections have killed larval tiger salamanders in Arizona (Collins et al. 1988) and Utah (Worthylake and Hovingh 1989), mountain yellow-legged frogs (Bradford 1991) and Yosemite toads (Kagarise Sherman and Morton 1993) in California, boreal toads in Colorado (Carey 1993), and Wyoming toads (Wyoming Dept. Game and Fish, unpublished data). Redleg affects amphibians whose immune systems have been weakened by stress, and Carey (1993) hypothesized that a regional anthropogenic stress was responsible for the declines of boreal toads in Colorado. This hypothesis explains the apparent synchronous decline over a large area, but the stressor has yet to be identified. The only potential anthropogenic stressor discussed by Carey (1993) was acid precipitation, but there are no data to support this hypothesis.

Kagarise Sherman and Morton (1993) suggested that stress from handling and observation may have contributed to redleg disease in Yosemite toads. They observed the greatest mortality in 1978-1979 when observations of breeding toads were most intense, including the use of drift fences and pitfall traps.

Climate

Weather is one of the most significant natural killers of amphibians. Many amphibians breed in temporary ponds that may or may not persist long enough for tadpoles to transform. Temperature extremes or fluctuations in water level during breeding may kill large numbers of embryos. Such short-term events are unlikely to have caused large declines of western amphibians. Many species are long-lived and occasional mass

mortality of embryos or tadpoles can be tolerated (Olson 1992). However, several species of southwestern anurans inhabit streams in canyons, and short-term events such as flash floods (spates) can cause catastrophic mortality of adults. Flooding has been suggested as contributing to declines of California red-legged frogs (Hayes and Jennings, in press) and foothill yellow-legged frogs (Sweet 1983) in southern California, and Chiricahua leopard frogs in New Mexico (R. D. Jennings, Western New Mexico State Univ., Silver City, NM, pers. comm.). Metter (1968) described catastrophic mortality in tailed frog populations after flash floods in Idaho and Oregon. The streams were altered substantially, most tadpoles were washed away, and many adult frogs that survived suffered amputated limbs.

Excessive precipitation does not have to be concentrated in a brief period. Bradford (1983) documented mass mortality of mountain yellow-legged frogs in the Sierra Nevada. Overwintering frogs died from oxygen depletion in shallow lakes when heavy precipitation resulted in ice cover that was thicker and more persistent than normal.

Drought may also cause amphibian declines over large areas. Corn and Fogleman (1984) described extinction of several populations of northern leopard frogs in Colorado when breeding ponds dried after a severe winter drought in 1976-1977. Kagarise Sherman and Morton (1993) felt that low snowfall in several years since 1971 has contributed to the decline of the Yosemite toad by causing ponds to dry before tadpoles complete metamorphosis.

Carey (1993) listed cold weather as a potential stressor that could cause suppression of the immune system leading to redleg disease. Cold weather was associated with mortality of Tarahumara frogs (Hale and Jarchow 1988), mountain yellow-legged frogs (Bradford 1991), Yosemite toads (Kagarise Sherman and Morton 1993), boreal toads (Carey 1993), and Wyoming toads (Wyoming Dept. Game and Fish, unpublished).

Population Dynamics

It has been suggested that many changes in amphibian abundance that have been termed declines may be fluctuations that are within the natural range of variation in population size. Pechmann et al. (1991) monitored numbers of amphibians breeding at a pond in South Carolina and found that some species could be rare or absent for several years and then reach high abundance in one or two good years. Harte and Hoffman (1989) and Wissinger and Whiteman (1992) may have observed a similar phenomenon in the decline and recovery of tiger salamanders in Colorado. Amphibian populations can be extremely variable from year to year (Berven and Grudzien 1990, Pechmann et al. 1991), but stochastic variation is an unlikely cause when most populations in a large area decline or go extinct at the same time (for example, boreal and Wyoming toads).

Unknown

As yet, there are no satisfactory hypotheses to explain declines of boreal toads in Colorado, Wyoming toads, and mountain yellow-legged frogs in the Sierra Nevada. Boreal toads and mountain yellow-legged frogs were widely distributed and abundant, and the lack of a ready answer for their decline is alarming, even if the declines represent natural fluctuations in the populations of both species. Variable environments periodically turn hostile and produce periods of intense selection pressure, or "ecological crunches" (Wiens 1977), with associated declines in population size. If populations are too small, random demographic variation can create an extinction vortex (Gilpin and Soulé 1986) that makes extinction a common event.

IMPLICATIONS FOR ECOSYSTEM MANAGEMENT

Bury et al. (1980) reviewed the status of amphibians in the United States thought to be declining or in danger of declining. They listed 15 species from the West, including 9 salamanders of the family Plethodontidae, all of which were endemic or isolated species with small ranges. Most species were listed because they were highly susceptible to habitat destruction, and few actual declines were documented. There are now at least 15 species of amphibians with documented declines, including 7 species of anurans with large distributions (boreal toad, Yosemite toad, northern leopard frog, lowland leopard frog, Chiricahua leopard frog, California red-legged frog, and mountain yellow-legged frog). Declines of common, widely distributed species are much more of a problem for ecosystem management than is conservation of narrowly distributed endemics, for which complete protection of small areas of suitable habitat is the most appropriate action.

Any attempt at ecosystem management must take into account temporal and spatial variation in ecosystem processes (Landres 1992). This is especially true of amphibians, not only because of temporal variation in population size, but because amphibian populations are structured in a variety of ways. The term metapopulation describes a group of populations, linked by migration, that undergo a dynamic process of extinction and recolonization (Hanski and Gilpin 1991). A variety of metapopulation models have been developed that describe real populations with varying degrees of success (Harrison 1991). Different amphibian species may have very different metapopulation structures. In Virginia, wood frogs inhabiting small ponds within a radius of 1 km are essentially a single genetic population (Berven and Grudzien 1990). Ponds outside this radius are connected by occasional migration by juvenile frogs. This is very similar to the situation for pool frogs (*R. lessonae*) in Sweden, where populations more than 1 km from other populations have a higher probability of extinction (Sjögren 1991). However, red-spotted newts (*Notophthalmus*

viridescens) that share the same ponds in Virginia with wood frogs are dominated by a single large, stable population that sends migrants to peripheral sites that suffer high rates of extinction (Gill 1978). Active management would be very different for wood frogs and newts, and specific recommendations for each species might be different. This is a potential conflict because both species occupy the same ponds.

Predation by introduced fish is a significant problem for amphibians and also native fish (Rinne and Minckley 1991) in the West. However, sport fishing is a huge industry supported by the public and administered by Federal land management and State game and fish agencies. If ecosystem management includes preserving native species (Samson 1992), non-native fish must be removed from large areas of the West. Such an action, although probably feasible, would generate much controversy and strong private and public opposition. To implement ecosystem management fully, there are many other equally difficult challenges and hard choices to be made.

In summary, there is much we know and don't know about amphibian declines in the West. We know that ranid frogs in the Southwest and California have suffered large declines, and several species of toads have declined throughout the West. We don't know the extent of declines of stream-dwelling amphibians in the Pacific Northwest, and we have little knowledge of the status of most desert species, such as spadefoot toads (*Spea* spp.). Habitat destruction and introduction of alien predators have probably caused most declines of ranid frogs. We do not know the causes of other declines, including boreal and Wyoming toads. Including amphibians in plans for ecosystem management may cause conflicts with other management objectives and desired conditions.

ACKNOWLEDGMENTS

I thank Bill Block for inviting me to participate in this symposium. R. B. Bury and N. J. Scott, Jr. read and commented on the manuscript.

LITERATURE CITED

- Altig, Ronald, and C. Kenneth Dodd, Jr. 1987. The status of the Amargosa toad (*Bufo nelsoni*) in the Amargosa River drainage of Nevada. *Southwestern Naturalist* 32:276-278.
- Anonymous. 1987. Rediscovery of the Wyoming toad. *Endangered Species Technical Bulletin* 12(11-12): 7.
- Barinaga, Marcia. 1990. Where have all the froggies gone? *Science* 247:1033-1034.
- Baxter, George T., Mark R. Stromberg, and C. Kenneth Dodd, Jr. 1982. The status of the Wyoming toad, *Bufo hemiophrys baxteri*. *Environmental Conservation* 9:348, 338.
- Berven, Keith A., and Thaddeus A. Grudzien. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution* 44:2047-2056.

- Blaustein, Andrew R. and Deanna H. Olson. 1991. Declining amphibians. *Science* 253:1467.
- Blaustein, Andrew R. and David B. Wake. 1990. Declining amphibian populations: a global phenomenon? *Trends in Ecology and Evolution* 5:203.
- Borchelt, Rick. 1990. Frogs, toads, and other amphibians in distress. *National Research Council News Report* 40(4):2-5.
- Bradford, David F. 1983. Winterkill, oxygen relations, and energy metabolism of a submerged dormant amphibian, *Rana muscosa*. *Ecology* 64:1171-1183.
- Bradford, David F. 1989. Allopatric distribution of native frogs and introduced fishes in high Sierra Nevada lakes of California: implications of the negative impact of fish introductions. *Copeia* 1989:775-778.
- Bradford, David F. 1991. Mass mortality and extinction in a high-elevation population of *Rana muscosa*. *Journal of Herpetology* 25:174-177.
- Bradford, David F. and Malcolm S. Gordon. 1992. Aquatic amphibians in the Sierra Nevada: current status and potential effects of acidic deposition on populations. Draft final report to California Air Resources Board. Contract No. A932-139. 85 p. + appendices.
- Bradford, David F., Christina Swanson, and Malcolm S. Gordon. 1992. Effects of low pH and aluminum on two declining species of amphibians in the Sierra Nevada, California. *Journal of Herpetology* 26:369-377.
- Bradford, David F., David M. Graber, and Farinaz Tabatabai. *In press*. Isolation of remaining populations of the native frog, *Rana muscosa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. *Conservation Biology*.
- Bury, R. Bruce. 1988. Habitat relationships and ecological importance of amphibians and reptiles. p. 61-76. *In* Kenneth J. Raedeke, ed., *Streamside management: riparian wildlife and forestry interactions*. Proceedings of a symposium [University of Washington, Seattle, February 11-13, 1987] 277 p. Contribution 59. Institute of Forest Resources, University of Washington.
- Bury, R. Bruce and Paul Stephen Corn. 1988. Responses of aquatic and streamside amphibians to timber harvest: a review. p. 165-181. *In* Kenneth J. Raedeke, ed., *Streamside management: riparian wildlife and forestry interactions*. Proceedings of a symposium [University of Washington, Seattle, February 11-13, 1987] 277 p. Contribution 59. Institute of Forest Resources, University of Washington.
- Bury, R. Bruce and Jill A. Whelan. 1984. Ecology and management of the bullfrog. Resource Publication 155. U. S. Fish and Wildlife Service, Washington, D. C. 23 p.
- Bury, R. Bruce, C. Kenneth Dodd, Jr., and Gary M. Fellers. 1980. Conservation of the Amphibia of the United States. Resource Publication 134. U.S. Fish and Wildlife Service, Washington, D. C. 34 p.
- Carey, Cynthia. 1993. Hypothesis concerning the causes of the disappearance of boreal toads from the mountains of Colorado. *Conservation Biology* 7:355-362.
- Clarkson, Robert W. and James C. Rorabaugh. 1989. Status of leopard frogs (*Rana pipiens* complex: Ranidae) in Arizona and southwestern California. *Southwestern Naturalist* 34:531-538.
- Collins, James P., Thomas R. Jones, and Howard J. Berna. 1988. Conserving genetically distinctive populations: the case of the Huachuca tiger salamander (*Ambystoma tigrinum stebbinsi* Lowe). p. 45-53. *In* Robert C. Szaro, Kieth E. Severson, and David R. Patton, tech. coords., *Management of amphibians, reptiles, and small mammals in North America*. Proceedings of a symposium [Flagstaff, Arizona, July 19-21, 1988] 458 p. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado, General Technical Report RM-166.
- Corn, Paul Stephen and R. Bruce Bury. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. *Forest Ecology and Management* 29:39-57.
- Corn, Paul Stephen and James C. Fogleman. 1984. Extinction of montane populations of the northern leopard frog (*Rana pipiens*) in Colorado. *Journal of Herpetology* 18:147-152.
- Corn, Paul Stephen and Frank A. Vertucci. 1992. Descriptive risk assessment of the effects of acidic deposition on Rocky Mountain amphibians. *Journal of Herpetology* 26:361-369.
- Corn, Paul Stephen, William Stolzenburg, and R. Bruce Bury. 1989. Acid precipitation studies in Colorado and Wyoming: interim report of surveys of montane amphibians and water chemistry. Biological Report 80(40.26). U.S. Fish and Wildlife Service, Washington, D.C. 56 p.
- Cowles, R. B. and C. M. Bogert. 1936. The herpetology of the Boulder Dam region (Nev., Ariz., Utah). *Herpetologica* 1:35-42.
- Dumas, Philip C. 1966. Studies of the *Rana* species complex in the Pacific Northwest. *Copeia* 1966:60-74.
- Fellers, Gary M. and Charles A. Drost. *In press*. Disappearance of the Cascades frog, *Rana cascadae*, at the southern end of its range. *Biological Conservation*.
- Gibbs, Erich L., George W. Nace, and Marvin B. Emmons. 1971. The live frog is almost dead. *Bioscience* 21:1027-1034.
- Gill, Douglas E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecological Monographs* 48:145-166.
- Gilpin, Michael E. and Michael E. Soulé. 1986. Minimum viable populations: processes of species extinction. p. 19-34. *In* Michael E. Soulé, ed., *Conservation biology*. The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.
- Griffiths, Richard, and Trevor Beebe. 1992. Decline and fall of the amphibians. *New Scientist* 134(1827):25-29.
- Hairston, Nelson G., Sr. 1987. Community ecology and salamander guilds. New York: Cambridge University Press. 230 p.

- Hale, Stephen F. and James L. Jarchow. 1987. The status of the Tarahumara frog (*Rana tarahumarae*) in the United States and Mexico: Part II. Unpublished Report. Arizona Game and Fish Department, Phoenix, Arizona and U. S. Fish and Wildlife Service, Albuquerque, New Mexico. 80 p.
- Hammerson, Geoffrey A. 1982. Bullfrogs eliminating leopard frogs in Colorado? *Herpetological Review* 13:115-116.
- Hanski, Ilkka and Michael Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42:3-16.
- Harris, Larry D. 1984. The fragmented forest. Island biogeography theory and the preservation of biotic diversity. Chicago: University of Chicago Press. 211 p.
- Harrison, Susan. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* 42:73-88.
- Harte, John and Erika Hoffman. 1989. Possible effects of acidic deposition on a Rocky Mountain population of the tiger salamander *Ambystoma tigrinum*. *Conservation Biology* 3:149-158.
- Hayes, Marc P. and Mark R. Jennings. 1986. Decline of ranid frog species in western North America: are bullfrogs (*Rana catesbeiana*) responsible? *Journal of Herpetology* 20:490-509.
- Hayes, Marc P. and Mark R. Jennings. 1988. Habitat correlates of distribution of the California red-legged frog (*Rana aurora draytonii*) and the foothill yellow-legged frog (*Rana boylei*): implications for management. p. 144-158. In Robert C. Szaro, Kieth E. Severson, and David R. Patton, tech. coords., Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium [Flagstaff, Arizona, July 19-21, 1988] 458 p. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado, General Technical Report RM-166.
- Hine, Ruth L., Betty L. Les, and Bruce F. Hellmich. 1981. Leopard frog populations and mortality in Wisconsin, 1974-1976. Technical Bulletin 122. Wisconsin Department of Natural Resources, Madison, Wisconsin. 39 p.
- Hovingh, Peter. 1993. Aquatic habitats, life history observations, and zoogeographic considerations of the spotted frog (*Rana pretiosa*) in Tule Valley, Utah. *Great Basin Naturalist* 53:168-179.
- Jennings, Mark R. 1988a. Natural history and decline of native ranids in California. p. 61-72. In Harold F. De Lisle, Philip R. Brown, Bonnie Kaufman, and Brian M. McGurty, eds., Conference on California herpetology. Proceedings [Los Angeles, California, October 10-11, 1987] 143 p. Southwestern Herpetologists Society, Van Nuys, California. Special Publication 4.
- Jennings, Mark R. 1988b. *Rana onca*. Catalogue of American Amphibians and Reptiles 417.1-2.
- Jennings, Mark R. and Marc P. Hayes. 1985. Pre-1900 overharvest of California red-legged frogs (*Rana aurora draytonii*): the inducement for bullfrog (*Rana catesbeiana*) introduction. *Herpetologica* 41:94-103.
- Jennings, Mark R. and Marc P. Hayes. *In press*. Decline of native ranids in the desert Southwest. In Philip R. Brown and John W. Wright, eds., Conference on the herpetology of North American deserts. Proceedings. Southwestern Herpetologists Society, Van Nuys, California. Special Publication.
- Jennings, Randy D. 1993. Rediscovery of *Rana onca* in southern Nevada and a taxonomic reevaluation of some southwestern leopard frogs. Paper presented at the annual meeting of the American Society of Ichthyologists and Herpetologists and Herpetologists' League, Austin Texas, 27 May - 2 June, 1993.
- Kagarise Sherman, Cynthia and Martin L. Morton. 1993. Population declines of Yosemite toads in the eastern Sierra Nevada of California. *Journal of Herpetology* 27:186-198.
- Landres, Peter B. 1992. Temporal scale perspectives in managing biological diversity. Transactions of the North American Wildlife and Natural Resources Conference 57:292-307.
- Lewis, Daniel L., George T. Baxter, Kevin M. Johnson, and Michael D. Stone. 1985. Possible extinction of the Wyoming toad, *Bufo hemiophrys baxteri*. *Journal of Herpetology* 19:166-168.
- McAllister, Kelly R., William P. Leonard, and Robert M. Storm. 1993. Spotted frog (*Rana pretiosa*) surveys in the Puget Trough of Washington, 1989-1991. *Northwestern Naturalist*, *in press*.
- Metter, Dean E. 1968. The influence of floods on population structure of *Ascaphus truei*. *Journal of Herpetology* 1:105-106.
- Morrison, Peter H. 1988. Old growth in the Pacific Northwest: a status report. Washington, DC: The Wilderness Society. 46 p.
- Moyle, Peter B. 1973. Effects of introduced bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. *Copeia* 1973:18-22.
- Nussbaum, Ronald A., Edmund D. Brodie, Jr., and Robert M. Storm. 1983. Amphibians and reptiles of the Pacific Northwest. University Press of Idaho, Moscow, Idaho. 332 p.
- Olson, Deanna H. 1992. Ecological susceptibility of amphibians to population declines. p. 55-62. In Richard R. Harris, Don E. Erman, tech. coords., and Hannah M. Kerner, ed., Symposium on biodiversity of northwestern California. Proceedings [Santa Rosa, California, October 28-30, 1991] 283 + XXV p. University of California, Wildland Resources Center Report 29.
- Pace, Ann E. 1974. Systematics and biological studies of the leopard frogs (*Rana pipiens* complex) of the United States. Miscellaneous Publication 148. Museum of Zoology, University of Michigan, Ann Arbor. 140 p.
- Pechmann, Joseph H. K., David E. Scott, Raymond D. Semlitsch, Janalee P. Caldwell, Laurie J. Vitt, and J. Whitfield Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253:892-895.

- Petranka, James W., Matthew E. Eldridge, and Katherine E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. *Conservation Biology* 7:363-370.
- Quammen, David. 1993. Frog in the night-time. The strange case of vanishing amphibians. *Outside* 18(5):39-40, 42, 44, 46-48.
- Raphael, Martin G. 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in Douglas-fir forests of northwestern California. p. 23-31. In Robert C. Szaro, Kieth E. Severson, and David R. Patton, tech. coords., *Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium* [Flagstaff, Arizona, July 19-21, 1988] 458 p. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado, General Technical Report RM-166.
- Rinne, John N. and W. L. Minckley. 1991. Native fishes of arid lands: a dwindling resource of the desert Southwest. General Technical Report RM-206. U. S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. 45 p.
- Rittschof, Daniel. 1975. Some aspects of the natural history and ecology of the leopard frog, *Rana pipiens*. Ph.D. Dissertation, University of Michigan, Ann Arbor. 212 p.
- Ross, David A., Dennis L. Shirley, Patricia A. White, and Leo D. Lentsch. 1993. Distribution of the spotted frog along the Wasatch Front in Utah, 1991-1992. Publication 93-4. Utah Division of Wildlife Resources, Salt Lake City, Utah. 24 p.
- Ruth, S.B. 1988. The life history and current status of the Santa Cruz long-toed salamander, *Ambystoma macrodactylum croceum*. p. 89-110. In Harold F. De Lisle, Philip R. Brown, Bonnie Kaufman, and Brian M. McGurty, eds., *Conference on California herpetology. Proceedings* [Los Angeles, California, October 10-11, 1987] 143 p. Southwestern Herpetologists Society, Van Nuys, California. Special Publication 4.
- Samson, Fred B. 1992. Conserving biological diversity in sustainable ecological systems. *Transactions of the North American Wildlife and Natural Resources Conference* 57:308-320.
- Seale, Dianne B. 1980. Influence of amphibian larvae on primary production, nutrient influx, and competition in a pond ecosystem. *Ecology* 61:1531-1550.
- Sjögren, Per. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biological Journal of the Linnean Society* 42:135-147.
- Stebbins, Robert C. 1985. A field guide to western reptiles and amphibians. Second edition, revised. Houghton Mifflin Company, Boston. 336 p.
- Sweet, Samuel S. 1983. Mechanics of a natural extinction event: *Rana boylei* in southern California. Paper presented at the annual meeting of the Society for the Study of Amphibians and Reptiles and Herpetologists' League, Salt Lake City, Utah, August 7-12, 1983.
- Turner, Frederick B. 1962. An analysis of geographic variation and distribution of *Rana pretiosa*. *American Philosophical Society Yearbook* 1962:325-328.
- U. S. Fish and Wildlife Service. 1993a. Endangered and threatened wildlife and plants: finding on petition to list the California red-legged frog. *Federal Register* 58:38553.
- U. S. Fish and Wildlife Service. 1993b. Endangered and threatened wildlife and plants: finding on petition to list the spotted frog. *Federal Register* 58:27260-27263.
- Vertucci, Frank A. 1988. Methods of detecting and quantifying lake acidification. p. 596-610. In I. G. Poppoff, C. R. Goldman, S. L. Loeb, and L. B. Leopold, eds., *Proceedings International Mountain Watershed Symposium*. Tahoe Resource Conservation District, South Lake Tahoe, CA.
- Vertucci, Frank A. and P. Stephen Corn. 1993. Episodic acidification is not responsible for amphibian declines in the Rocky Mountains, USA. *Bulletin of the Ecological Society of America* 74(2) Supplement:470.
- Welsh, Hartwell H., Jr. 1990. Relictual amphibians and old-growth forests. *Conservation Biology* 4:309-319.
- Wiens, John A. 1977. On competition and variable environments. *American Scientist* 65:590-597.
- Wissinger, Scott A. and Howard Whiteman. 1992. Fluctuation in a Rocky Mountain population of salamanders: anthropogenic acidification or natural variation? *Journal of Herpetology* 26:377-391.
- Worthylake, Kathleen Muriel and Peter Hovingh. 1989. Mass mortality of salamanders (*Ambystoma tigrinum*) by bacteria (*Acinetobacter*) in an oligotrophic seepage mountain lake. *Great Basin Naturalist* 49:364-372.
- Yoffe, Emily. 1992. Silence of the frogs. *New York Times Magazine*, December 13, 1992:36-39, 64, 66, 76.