

lakes in the
SJ, Kings,
Haweah +
Kern River
watersheds.

Isolation of Remaining Populations of the Native Frog, *Rana muscosa*, by Introduced Fishes in Sequoia and Kings Canyon National Parks, California

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Abstract: *Rana muscosa* (mountain yellow-legged frog) was eliminated by introduced fishes early in this century in many of the lakes and streams in Sequoia and Kings Canyon National Parks, California. In waters not inhabited by fish, however, *R. muscosa* has disappeared from many sites within the parks during the past 30 years, and it appears to have gone extinct in some drainage systems. Fragmentation of populations may have caused or contributed to these recent extinctions, because *R. muscosa* populations are significantly more isolated from one another by fish at present than in prestocking conditions. A total of 312 lake-sites in 95 drainage basins were surveyed for amphibians and fish in 1989–1990. For the 109 sites containing *R. muscosa*, we delineated networks of sites connected to one another via fishless streams, and we compared these present fishless networks ("present networks") to those expected for the same sites assuming that fish had not been introduced to the parks ("former networks"). Most present networks consist of only one site (mean = 1.4), whereas the former networks average 5.2 sites. This difference represents approximately a 10-fold

Aislamiento de las poblaciones remanentes de la rana nativa, *Rana muscosa*, por peces introducidos en los Parques Nacionales del Cañon de los Reyes y Sequoia, California

Resumen: *Rana muscosa* fue eliminada en muchos de los lagos y cursos de agua de los Parques Nacionales del Cañon de los Reyes y Sequoia, California, por peces introducidos al comienzo de este siglo. Sin embargo, en aguas no habitadas por peces, *R. muscosa* ha desaparecido de muchos sitios dentro de los parques durante los pasados 30 años, y parece haberse extinguido en algunos sistemas de drenaje. La fragmentación de la población puede haber causado o contribuido a estas extinciones recientes porque en la actualidad, las poblaciones de *R. muscosa* están significativamente más aisladas unas de otras (a causa de los peces) que durante las condiciones anteriores a la siembra. En 1989–90 se realizó una evaluación de los anfibios y peces en un total de 312 sitios en lagos y 95 cuencas de drenaje. Para los 109 sitios que contenían *R. muscosa*, delineamos redes de sitios conectados entre sí a través de ríos sin peces, y comparamos estas redes sin peces actuales ("redes actuales") con aquellas predcidas para los mismos sitios bajo la suposición de que los peces no habían sido introducidos en los parques ("redes anteriores"). La mayoría de las redes actuales consisten de un único sitio (media = 1.4), mientras que las redes ante-

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difference in connectivity of populations, which is defined as the mean number of potential dispersal links (fishless streams) per network. Connectivity averages only 0.43 in present networks, in contrast to 4.15 in former ones.

riores promedian 5.2 sitios. Esta diferencia representa aproximadamente una diferencia de 10 veces en la conectividad de las poblaciones, la cual es definida como el número promedio de los lazos potenciales de dispersión (i.e., cursos sin peces) por red. En las redes presentes, la conectividad promedio solamente 0.43, lo que contrasta con el 4.15 de las anteriores.

Introduction

During the past three decades, populations of many species of amphibians have declined or disappeared throughout the world (Barinaga 1990; Wake 1991). These declines have been alarming, in part, because the causes have often not been evident, and declines have occurred in some of the best preserved environments on earth. One such area is the Sierra Nevada of California at high elevation, where at least two of five species of aquatic-breeding amphibians, *Rana muscosa* (mountain yellow-legged frog) and *Bufo canorus* (Yosemite toad), have been declining (Phillips 1990). Population declines or disappearances of these amphibians have been reported from many locations in the Sierra Nevada, including sites within Yosemite, Sequoia, and Kings Canyon National Parks, and from several wilderness areas within and outside these parks. Most of these declines appear not to be associated with any obvious change in the terrestrial environment or in pattern of land or recreational use. Both species recently have become candidates for federal listing as endangered or threatened.

A number of hypotheses have been proposed for recent amphibian population declines, but little information is available in most cases (Barinaga 1990; Wyman 1990). In the western United States, acid deposition does not appear to be the cause of recent population declines of *R. muscosa* and *B. canorus* in the Sierra Nevada, nor *R. piptiens* and *B. boreas* in the Rocky Mountains (Corn et al. 1989; Bradford et al. 1992; Corn & Vertucci 1992). Drought in the western U.S. from 1986 to the present may have been detrimental to some amphibian populations, but population declines of *R. muscosa*, *B. canorus*, and some other species were evident before this time. Moreover, *R. muscosa* inhabits primarily permanent waters that persist even during prolonged droughts (Zweifel 1955; Mullaly & Cunningham 1956; personal observation).

In the Sierra Nevada, it is generally recognized that several species of introduced salmonid fishes have profoundly affected the distribution of at least *R. muscosa* within the past century by eliminating the species from nearly all waters inhabited by fish (Grinnell & Storer 1924; Bradford 1989). Presumably, these eradications occurred largely by predation on tadpoles (Hayes & Jennings 1986), which are restricted to permanent wa-

ter during the two to three summers required to reach metamorphosis (Zweifel 1955; Cory 1962). Despite such reductions, *R. muscosa* remained an abundant and widespread species in the Sierra Nevada until at least the 1960s in the many locations not inhabited by fish (Bradford et al., unpublished manuscript). It is in these fishless waters that recent population declines and disappearances have been reported. Thus, predation by introduced fishes appears not to be the direct cause of more recent population declines of *R. muscosa*.

We suggest that introduced fishes may have indirectly caused population declines in *R. muscosa* by isolating remaining populations. Prior to 1870, virtually all of the thousands of lakes at high elevation in the Sierra Nevada (>2500 m) were barren of fish (Christenson 1977); many or most of these probably were inhabited by *R. muscosa* (Grinnell & Storer 1924). Populations of *R. muscosa* presumably were connected to one another via waterways, because *R. muscosa* inhabits streams as well as lakes, and both adults and tadpoles are closely tied to water (Zweifel 1955). Upon elimination of *R. muscosa* from many sites by introduced fish, remaining populations were isolated. Thus, extinction of population fragments by natural causes may have become more likely, largely because of reduction in the size of remaining populations and the fact that the population size of many temperate amphibians is sensitive to fluctuations in the physical environment (Pechmann et al. 1991; Sjogren 1991). Moreover, re-establishment of locally extinct populations by colonization would have been impeded by fragmentation (Wilcox 1980; Hanski 1989; Hanski & Gilpin 1991).

Regardless of the cause of local extinctions of *R. muscosa* in recent decades, the impediment posed by introduced fish to the persistence of remaining populations and recolonization of extinct ones represents a potentially serious management dilemma for the National Park Service. *Rana muscosa* is a protected native species potentially threatened by several introduced species comprising a popular sport fishery. The inherent conflict challenges the National Park Service mandate to protect native biota and ecosystems under its stewardship.

The purposes of the present study are (1) to determine the current distribution of remaining populations of *R. muscosa* relative to the distribution of introduced

fishes; (2) to use this information to estimate the degree of isolation of remaining *R. muscosa* populations from one another by the presence of introduced fishes in intervening waters; and (3) to compare this estimate to the degree of isolation expected to have existed prior to fish introductions. The study focuses on Sequoia and Kings Canyon National Parks, California, because these parks include a large portion of the range of *R. muscosa* in the Sierra Nevada (Zweifel 1955), and because backcountry rangers were available to conduct field surveys over much of the area.

Study Area and Background Biology

Sequoia and Kings Canyon National Parks lie adjacent to one another along the western slope of the Sierra Nevada and jointly comprise 3498 km², 73% of which lies above 2500 m elevation (Fig. 1). The parks contain a total of 2801 lakes designated on 1:24,000 scale maps of the United States Geological Survey, 95% of which lie above 2500 m elevation. These high lakes are mostly glacial in origin and lie in the headwaters of four major river systems (San Joaquin, Kings, Kaweah, and Kern) that flow into the San Joaquin Valley. Most of the land above 2500 m elevation lies in designated wilderness areas; use is restricted to recreational backcountry activities, with access only by foot or pack animal.

Within the parks *R. muscosa* has disappeared from

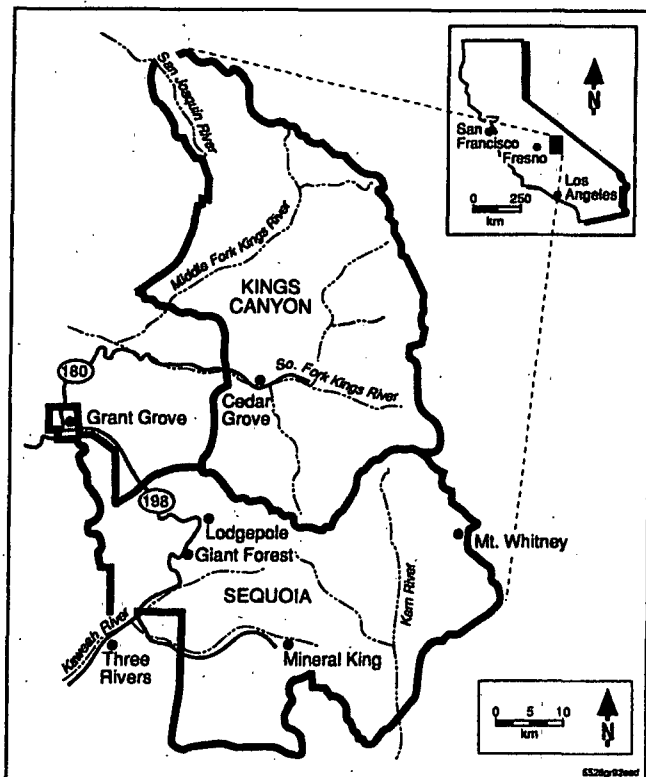


Figure 1. Location map of Sequoia and Kings Canyon National Parks, California

about half of the sites where it was extant two to three decades ago, including all sites within some drainage systems (Bradford et al., unpublished manuscript). *Rana muscosa* historically occurred in suitable habitat throughout most of the Sierra Nevada above about 2000 m elevation, ranging between extremes of 1400 and 3660 m (Zweifel 1955; Mullaly & Cunningham 1956). Tadpoles are largely restricted to permanent still water, usually deeper than 1 m (Bradford 1989). Adults typically live in or immediately adjacent to water throughout the year and usually overwinter in water under ice (Zweifel 1955; Mullaly & Cunningham 1956; Bradford 1983). Both tadpoles and adults are often extremely abundant in ponds, lakes, and meadows with permanent pools; they often inhabit streams, but at lower densities (Grinnell & Storey 1924; Zweifel 1955).

Prior to European colonization, waters within the parks were largely barren of fish because fish could not move up the steep stream gradients created by glaciation (Christenson 1977). *Oncorhynchus aguabonita* (golden trout) inhabited streams (and possibly a few lakes) at the southern edge of Sequoia National Park (Schreck & Behnke 1971); *O. mykiss* (rainbow trout) may have reached high elevation (>2500 m elevation) in some major streams elsewhere within unglaciated regions of the parks (Christenson 1977, personal communication). However, waterfalls and other barriers prevented these populations from penetrating lakes at high elevation. During the past century, four species of fish were both systematically and casually introduced by pack animal, aircraft, and backpack to many locations within the parks and became established within the geographic range of *R. muscosa*: *Oncorhynchus aguabonita*, *O. mykiss* spp., *Salmo trutta* (brown trout), and *Salvelinus fontinalis* (brook char) (California Department of Fish and Game records). These species (and hybrids) are now established in most streams and lakes in the parks (National Park Service records).

Methods

Current Distribution of *Rana muscosa* and Fish

Surveys to determine the status of anurans and fish were conducted over a large portion of the parks above 2500 m elevation by National Park Service backcountry rangers in 1989 and 1990. Rangers were instructed in identification and survey methodology for the aquatic-breeding amphibians inhabiting the parks at high elevation: *R. muscosa*, *Pseudacris* [= *Hyla*] *regilla* (Pacific chorus frog), and *Bufo* spp. They searched shorelines of selected lakes, 0.5 ha or larger shown on 1:24,000 topographic maps, at least once between June and September during the daytime in good weather, when tadpoles tend to concentrate in warm shallows near shore and adults are most conspicuous (Bradford 1984; 1989). Rangers were instructed to search all

shorelines and near-shore waters at a rate slow enough to avoid detection failures. These searched areas were termed "lake-sites" because, in addition to the lakes, they included adjacent small ponds and pools when present. Rangers selected lake-sites within their territories in a nonrandom manner; selection was deliberately moderately biased toward lake-sites most likely to contain suitable habitat for amphibians. At each lake-site the presence or absence of tadpoles and metamorphosed individuals of each species was recorded. For convenience we classified the areas surveyed into distinct "survey basins" in which the lowest elevation was near the lowest lake and no lakes (or only one) occurred downstream from the basin.

Data for some sites were obtained in the same fashion by a team engaged in amphibian surveys for other purposes (Bradford et al. 1993). In addition, some data were obtained by rangers and by this team for sites other than lake-sites. These included small isolated lakes not shown on maps, ponds in meadows, and streams. Finally, data for some current locations of *R. muscosa* (defined as 1987 or later) were obtained from sightings recorded by other National Park Service staff.

During the surveys, the presence or absence of fish was also determined by direct observation or information from fishermen in the field. In addition, an extensive park database was used that included data for fish distribution based on direct observations, California Department of Fish and Game stocking records since 1970, and National Park Service fish surveys.

Isolation of *Rana muscosa* by Introduced Fishes

Because of logistical constraints in the extremely rugged terrain, not all backcountry lake-sites that potentially could contain *R. muscosa* or fish were searched in any one area. Consequently, it was not possible to delineate the distribution of all remaining sites of *R. muscosa* nor to determine the total number of *R. muscosa* sites connected to one another via fishless waters in a given area. Instead, we delineated networks of *R. muscosa* sites that were connected to one another via fishless drainage channels, and we compared these present fishless networks ("present networks") to those expected for the same sites assuming that no fish had been introduced to the Sierra Nevada ("former networks"). To delineate the present networks, we plotted all sites surveyed for or known to contain *R. muscosa* or fish on 1:24,000-scale quadrangles. We assumed fish to be present in permanent streams downstream from an established fish population. Drainage channels connecting two *R. muscosa* sites that did not meet the above criteria were assumed to be fishless. Thus, the number of *R. muscosa* sites in a present network may be an overestimate of the actual number in some cases.

We reconstructed the approximate former networks of *R. muscosa* sites by estimating the original distribution of native fish in streams. We defined fishless areas as

the watershed upstream from a topographic barrier to upstream fish colonization. Most of these barriers were obvious because they consisted of waterfalls, cataracts, or steep gradients formed by glacial action. A few cases were less clear, but a barrier was inferred if native fish were known to have been absent in lakes at the headwaters of the streams (Christenson 1977).

We computed a measure of "connectivity" for both present and former networks to estimate the degree to which populations are or were connected to one another by fishless drainage channels. Connectivity is defined as the mean number of potential dispersal "links" between *R. muscosa* sites within the fishless networks. A link is a drainage channel connecting two sites. The number of such links per network equals $n - 1$ (where n = number of *R. muscosa* sites in the network) because the drainage system is dendritic in pattern and two sites are virtually never connected by more than one drainage channel.

Results

Abundance and Distribution of Sites Currently Inhabited by *R. muscosa* and Introduced Fish

At least one lake-site was searched in each of 95 survey basins in 1989 or 1990 (Table 1). These basins were scattered throughout the parks at high elevation and included headwaters of the four river systems in the parks. The 95 basins contained 1275 lakes, 45% of the 2801 lakes in the parks.

A total of 312 lake-sites were searched for *R. muscosa* and fish in 1989 or 1990 (Table 1), 24.5% of the lakes in the basins. Of these, *R. muscosa* was found in 109 (34.9%), with tadpoles occurring in 66 of these. Fish were found at 142 (45.5%) of the 312 lake-sites searched (Table 1). At lake-sites where both *R. muscosa* and fish were present, *R. muscosa* was typically restricted to smaller bodies of water where fish were absent.

Fifty-three lake-sites were surveyed in both 1989 and 1990. *Rana muscosa* was found at 22 of these sites: ten during both years, eight in 1989 only, and four in 1990 only. Fish were found at 31 of the 53 sites: 23 during both years, three in 1989 only, and five in 1990 only.

Table 1. Results of surveys for *R. muscosa* and fish in lake-sites in 1989 and 1990.

No. of survey basins	95
Total no. lake-sites in basins	1,275
No. lake-sites searched	312
No. lake-sites containing <i>R. muscosa</i>	
Tadpoles present	66
Tadpoles absent	39
Unspecified stage	4
Total	109
No. lake-sites containing fish	142

Survey basins and lake-sites are defined in text. At least one lake-site was surveyed in each basin. *R. muscosa* and fish were considered present at a site if they were observed in either 1989 or 1990.

Distribution of Current *R. muscosa* Sites Relative to Distribution of Introduced Fish

The current sites inhabited by *R. muscosa* are largely separated from one another by introduced fish in intervening waterways (Fig. 2a). For the lake-sites searched (systematic survey, $n = 109$) and for all known sites within the basins surveyed ($n = 152$), the size of present fishless networks averages only 1.4 and 1.5 *R. muscosa* sites, respectively. Most networks consist of only one site, and the largest network for the 152 known sites is eight.

This situation contrasts to that for former fishless networks, the condition prior to fish stocking (Fig. 2b). For the same sites described above, means of 5.2 lake-sites and 6.3 known sites comprise the former networks, and the largest network for the 152 known sites is 29. This difference in number of sites per network differs significantly between present and former networks ($p < 0.001$ for both the systematic survey and all known sites, Kolmogorov-Smirnov Test).

Rana muscosa sites are dramatically more isolated from one another by fish at present than in prestocking conditions. The connectivity of *R. muscosa* sites in present versus former networks differs by approximately 10-fold. That is, for 109 lake-sites, the mean number of potential dispersal links per network averaged only 0.43 in present networks but 4.15 in former ones. For all known sites ($n = 152$), these values are 0.52 and 5.3, respectively. This difference is also evident when the number of *R. muscosa* sites that are isolated from all other sites (number of sites/network = 1 in Figure 2) are compared. At present, 53% of the lake-sites in present networks are isolated from all other sites by fish, whereas only 4.6% of the lake-sites in former networks are so isolated. For all known sites, these values are 49% and 4.6%, respectively.

The median nearest-neighbor distance between present fishless networks, measured via connecting drainage channels shown on 1:24,000-scale maps, was 2.4 km; the range was 0.1 to 21 km.

Discussion

Extent of Isolation of Remaining *R. muscosa* Populations by Introduced Fish

We have assumed in this study that drainage channels are the primary routes of dispersal for *R. muscosa*. This seems reasonable because tadpoles are entirely aquatic, and juvenile and adult frogs do not stray far from water (Zweifel 1955; Mullaly & Cunningham 1956). In two summers spent in the field observing hundreds of frogs, the senior author never found juveniles or adults more than a meter or two from standing or running water in regular drainages, even during summer rainstorms.

We also assumed that the presence of fish in water-courses presents a significant impediment to dispersal.

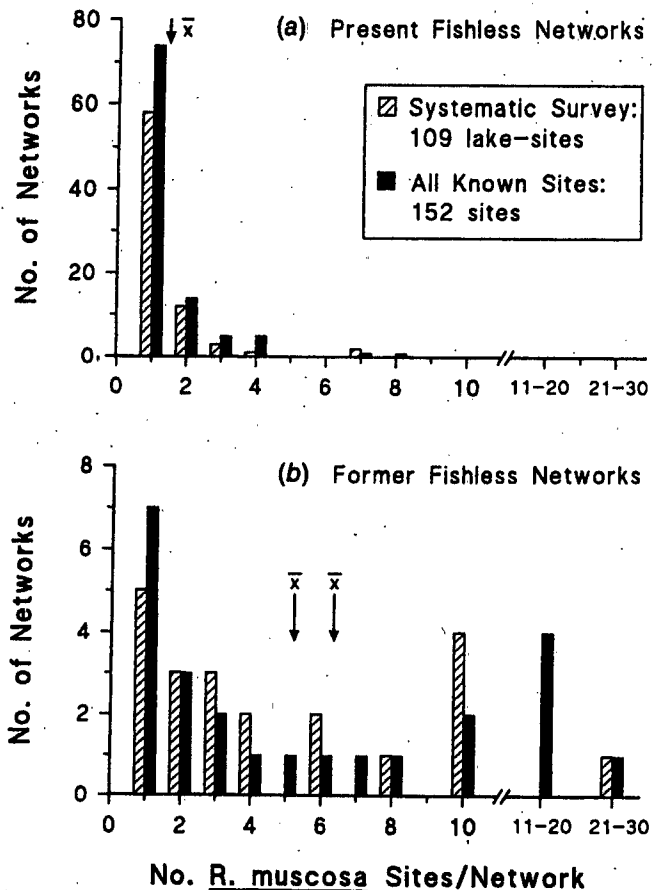


Figure 2. (a) Number and size of present fishless networks containing *R. muscosa* sites. For example, "3" on the x-axis refers to a group of three *R. muscosa* sites connected to one another at present by drainage channels in which fish are not known to be present. "Systematic Survey" refers to the survey of lake-sites for presence or absence of *R. muscosa* and fish in 1989 or 1990 (Table 1). "All Known Sites" refers to the systematic survey plus sightings of *R. muscosa* in both lake-sites and nonlake-sites within the survey basins, documented by various individuals from 1987 to 1990. For the systematic survey, total number of networks is 76 and mean number of sites per network is 1.43. For all known sites, these values are 100 and 1.52, respectively. (b) Number and size of expected former fishless networks of *R. muscosa* sites—networks prior to fish stocking. Sites and definitions as in (a) above. For the systematic survey, total number of networks is 21 and mean number of sites per network is 5.15. For all known sites, these values are 24 and 6.34, respectively.

In the absence of fish, *R. muscosa* adults are often found in, or near stream pools (Zweifel 1955; Mullaly & Cunningham 1956; Bradford 1984). Successful breeding may occur at such sites, provided that the water persists for the two to three summers required for tadpoles to reach metamorphosis (Zweifel 1955; Cory 1962). More-

over, many juvenile and adult frogs typically move from lakes into fishless streams during snowmelt, and then retreat to the lake as the streams dry (personal observation).

In contrast, tadpoles or metamorphosed individuals are rarely seen in streams or lakes inhabited by fish (Grinnell & Storer 1924; Bradford 1989). Tadpoles (and possibly juvenile frogs) are attacked and presumably consumed by fish (Hayes & Jennings 1986; Bradford 1989), whereas adults are likely to be too large to be eaten by the relatively small fish typical of high-elevation waters. Consequently, the effective dispersal distance may be determined by the vagility of adults. This, however, is virtually unknown for *R. muscosa*. Based on observations of telemetered and marked adults (Bradford 1984), individuals often reside within a small area for most of their activity season (<100 m²). For adult *R. pretiosa* in Yellowstone National Park, the activity range over several years averaged 0.9 ha, which included migration from hibernacula averaging about 400 m away (Turner 1960). The maximum dispersal distance for *R. pretiosa* was 1.3 km, whereas the maximum dispersal distance observed for other anurans varies between tens of meters and a few kilometers (Turner 1960). In a study of 59 populations of *R. lessonae* in Sweden, extinction between the 1950s and late 1980s occurred in 10 populations isolated by 1.0 km or more from other populations, but in no populations closer than this distance (Sjogren 1991). Thus, for present networks of *R. muscosa* populations currently separated from each other by fish-inhabited waters, the nearest-neighbor distance between such networks (median = 2.4 km) may represent a substantial barrier to dispersal between sites.

Regardless of the magnitude of the impediment to frog dispersal posed by fish-inhabited streams, remaining populations of *R. muscosa* are dramatically more isolated from one another by the presence of fish in intervening waters than they were prior to the introduction of fish. The magnitude of this difference appears to be about 10-fold, based on the connectivity of remaining populations and the fraction of sites isolated from all other sites. Such isolation by fish may be even more extreme for ranid frogs in other situations, such as *R. cascadae* in Lassen Volcanic National Park, where only one remaining population is known (Fellers & Drost 1993).

Possible Effects of Isolation of *R. muscosa* Populations by Introduced Fish

The proximate causes for recent population disappearances of *R. muscosa* in the parks and elsewhere in the Sierra Nevada are not clear, nor is it evident whether such causes are natural or anthropogenic in origin (Bradford et al., unpublished manuscript). Mass mortality of *R. muscosa* has been observed in association with factors such as disease, predation, and winterkill, all of

which may be natural (Bradford 1983; 1991). Anthropogenic factors have been suggested, such as acidic deposition, increased ultraviolet radiation, range expansion of introduced fishes, researcher activities, and other human activities. No data are available concerning the ultraviolet radiation hypothesis, however, and available data for the other hypotheses are not supportive (Bradford et al. 1992; Bradford et al., unpublished manuscript).

Regardless of the proximate causes of population disappearances of *R. muscosa*, the isolation of *R. muscosa* by introduced fish may have had progressive, adverse effects on populations in at least two ways. First, increased isolation may have contributed to the extinction of some populations because smaller populations of organisms are generally more susceptible to extinction via stochastic events than are larger ones (Wilcox 1980; Hanski 1989; Hanski & Gilpin 1991). This effect may be especially pronounced in *R. muscosa* and many other temperate anurans because they often show wide swings in population size in response to environmental factors (Pechmann et al. 1991; Sjogren 1991). Second, increased isolation of *R. muscosa* populations may also have significantly reduced the probability of recolonization of a site where extinction occurred (Wilcox 1980; Hanski & Gilpin 1991). This effect may occur due to the decreased size of potential source populations, the increased distance from source populations, and direct predation on dispersing individuals (Hanski 1989; Sjogren 1991). Such reduction in recolonization probability may be particularly pronounced for *R. muscosa* in the Sierra Nevada because the establishment of introduced fish populations has been most extensive below 3000 m elevation, and stream connections between drainages containing abundant habitat for *R. muscosa* (lakes, ponds, and meadow pools) often lie below this elevation.

Conclusions and Management Implications

The remaining populations of *R. muscosa* in Sequoia and Kings Canyon National Parks appear to represent small fragments of former widespread populations, and such fragments appear to be largely isolated from one another by the presence of introduced fish in intervening waters. Such isolation may have contributed substantially to the extinction of local populations and impeded the recolonization of sites of extinction. These potential effects constitute indirect consequences of fish introductions, which may be further exacerbated with time as the ranges of fish continue to expand opportunistically during flood years. Ultimately these indirect effects may be as important as the direct effect of introduced fish eliminating *R. muscosa* populations by predation.

The decline of a native vertebrate such as *R. muscosa* in Sequoia and Kings Canyon National Parks should be a serious concern to the National Park Service. *Rana*

muscosa is a native vertebrate characteristic of aquatic communities at high elevation in the Sierra Nevada, and large fractions of such communities are contained within national parks. Moreover, there is no reason to think that population declines of *R. muscosa* will not continue. The National Park Service has tolerated the stocking and recreational taking of alien fish species in many national parks, whereas it has prohibited the introduction and taking of terrestrial animals and plants. Moreover, it has actively attempted to eradicate many alien terrestrial species, but rarely an alien fish species. If indeed fish introduced to the high Sierra Nevada are contributing to the extirpation of native *R. muscosa*, the Park Service may be compelled to reconsider these inconsistent practices.

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Literature Cited

- Barinaga, M. 1990. Where have all the froggies gone? *Science* 247:1033-1034.
- Bradford, D. F. 1983. Winterkill, oxygen relations and energy metabolism of a submerged dormant amphibian, *Rana muscosa*. *Ecology* 64:1171-1183.
- Bradford, D. F. 1984. Temperature modulation in a high-elevation amphibian, *Rana muscosa*. *Copeia* 1984:966-976.
- Bradford, D. F. 1989. Allotopic distribution of native frogs and introduced fishes in high Sierra Nevada lakes of California: Implication of the negative effect of fish introductions. *Copeia* 1989:775-778.
- Bradford, D. F. 1991. Mass mortality and extinction in a high-elevation population of *Rana muscosa*. *Journal of Herpetology* 25:174-177.
- Bradford, D. F., M. S. Gordon, D. F. Johnson, R. D. Andrews, and W. B. Jennings. Acidic deposition as an unlikely cause for amphibian population declines in the Sierra Nevada, California.
- Bradford, D. F., C. Swanson, and M. S. Gordon. 1992. Effects of low pH and aluminum on two species of declining amphibians in the Sierra Nevada, California. *Journal of Herpetology* 26:369-377.
- Christenson, D. P. 1977. History of trout introductions in California high mountain lakes. Pages 9-18 in Proceedings of a Symposium on the management of high mountain lakes in California's national parks. California Trout, Inc., San Francisco, California.
- Corn, P. S., and F. A. Vertucci. 1992. Ecological risk assessment of the effects of atmospheric pollutant deposition on western amphibian populations. *Journal of Herpetology* 26:361-369.
- Corn, P. S., H. W. Stolzenburg, and R. B. Bury. 1989. Acid precipitation studies in Colorado and Wyoming: Interim report of surveys of mountain amphibians and water chemistry. Biological Report 80 (40.26). U.S. Fish and Wildlife Service, Washington, D.C.
- Cory, L. 1962. Life-history and behavior differences between ranids in isolated populations in the Sierra Nevada. *American Zoology* 2:515.
- Fellers, G. M., and C. A. Drost. 1993. Disappearance of the Cascades frog *Rana cascadae* at the southern end of its range. California, U.S.A. *Biological Conservation* 65:177-181.
- Grinnell, J., and T. I. Storer. 1924. Animal life in the Yosemite. University of California Press, Berkeley, California.
- Hanski, I. 1989. Metapopulation dynamics: Does it help to have more of the same? *Trends in Ecology and Evolution* 4:113-115.
- Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: Brief history and conceptual domain. *Biological Journal of the Linnean Society* 42:3-16.
- Hayes, M. P., and M. R. Jennings. 1986. Decline of ranid frog species in western North America: Are bullfrogs (*Rana catesbeiana*) responsible? *Journal of Herpetology* 20:490-509.
- Mullaly, D. P., and J. D. Cunningham. 1956. Ecological relations of *Rana muscosa* at high elevations in the Sierra Nevada. *Herpetologica* 12:189-198.
- Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: The problem of separating human impacts from natural fluctuations. *Science* 253:892-895.
- Phillips, K. 1990. Where have all the frogs and toads gone? *Bioscience* 40:422-424.
- Schreck, C. B., and R. J. Behnke. 1971. Trout of the upper Kern River basin, California, with reference to systematics and evolution of western North American *Salma*. *Journal of the Fisheries Research Board of Canada* 28:987-998.
- Sjogren, P. 1991. Extinction and isolation gradients in metapopulations: The case of the pool frog (*Rana lessonae*). *Biological Journal of the Linnean Society* 42:135-147.
- Turner, F. B. 1960. Population structure and dynamics of the western spotted frog, *Rana p. pretiosa* Baird & Girard, in Yellowstone Park, Wyoming. *Ecological Monographs* 30:251-278.
- Wake, D. B. 1991. Declining amphibian populations. *Science* 253:860.
- Wilcox, B. A. 1980. Insular ecology and conservation. Pages 97-117 in M. E. Soule and B. A. Wilcox. *Conservation biology*. Sinauer Associates, Sunderland, Massachusetts.
- Wyman, R. L. 1990. What's happening to the amphibians? *Conservation Biology* 4:350-352.
- Zweifel, R. G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boylei* group. University of California Publications on Zoology 54:207-292.