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Decline of Ranid Frog Species in Western North America: Are Bullfrogs (*Rana catesbeiana*) Responsible?

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ABSTRACT. — **The decline of ranid frog species native to western North America is a pattern alluded to by many workers. We review the factors cited as having caused these declines, using, as primary examples, some of the ranid species native to California. We present explicit statements of four major alternative hypotheses: 1) bullfrog introduction, 2) habitat alteration, 3) predation by introduced fishes, and 4) commercial exploitation. Additionally, we review data relating to four other factors suggested as having caused declines: 1) toxicants, 2) pathogens and parasites, 3) acid rain, and 4) catastrophic mortality. Notably, data do not exist that suggest that the often-invoked bullfrog hypothesis is most compelling. Some factors, like commercial exploitation, are untestable because the putative causal conditions no longer exist, whereas others, like catastrophic mortality, are difficult to test because of their unpredictability. Perhaps the most neglected but potentially important alternative is predation by introduced fishes. Existing data cannot distinguish adequately among three major testable alternatives: bullfrogs, habitat alteration, and introduced fish predation. In the absence of satisfactory data, the chronological priority of fish introductions over those of bullfrogs and the greater access fish may have to earlier ranid life stages make the fish predation hypothesis more compelling. Several alternative hypotheses are confounded because existing correlative data support at least two alternatives equally well. Manipulations of testable alternatives are imperative to distinguish causal factors.**

Over a century ago, Lockington (1879) observed that populations of *Rana aurora* in the vicinity of San Francisco were diminishing. Since that time, investigators have repeatedly suggested that nearly every ranid frog species native to western North America has experienced reductions in range or declines in sizes of local populations (Table 1); these reductions seem to be a recent phenomenon. Although several factors have been suggested or inferred to be causal in these declines, one factor, interactions of native ranids with introduced bullfrogs (*Rana catesbeiana*), continues to be most frequently invoked (Jameson, 1956; Lardie, 1963; Dumas, 1966; Black, 1969; Moyle, 1973; Licht, 1974; Conant, 1975, 1977; Bury and Luckenbach, 1976; Green, 1978; Vitt and Ohmart, 1978; Baxter and Stone, 1980; Bury et al., 1980; Applegarth, 1983; Nussbaum et al., 1983). This emphasis has resulted in widespread acceptance of bullfrogs as *the primary cause* of ranid declines by both wildlife management personnel and segments of the research community (J. M. Brode and N. J. Scott, Jr., pers. comm.) and in citation of bullfrogs as a case where introduction of a vertebrate may be altering community structure (Moyle, 1973; Bury and Luckenbach, 1976; Hammerson, 1982*a*; Applegarth, 1983; Nussbaum et al., 1983). However, data unequivocally supporting the bullfrog hypothesis appear to be minimal. Here we review evidence for this hypothesis and for a number of alternatives that potentially explain declines of western ranids. Additionally we suggest ways in which each might work, show how alternatives may be confounded, and suggest data needed for their resolution.

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TABLE 1. Sources suggesting decline in ranid frogs in western North America.

Taxon	Suggested causes of decline[1]	Geographic area	Sources[2]
Rana aurora aurora	A	British Columbia, Oregon, and Washington	14[a], 16, 23[a], 25, 27, 33
Rana aurora draytonii	A, C, E	California	2, 3, 6, 12, 24, 28, 29, 31, 32, 42
Rana boylii	A, C, H	California, Oregon	3, 6, 31, 33, 37, 40
Rana blairi	A, C, D, F	Arizona, Colorado, and New Mexico	1, 15, 20, 21
Rana cascadae	A	Oregon and Washington	14[a], 33, 41
Rana chiricahuensis	A, F	New Mexico	1
Rana muscosa	D	California	3, 11, 17, 26, 39
Rana onca	A, C, D	Nevada, Utah	8, 13, 22, 34, 36[b]
Rana pipiens	A, C, D, F, H	Colorado, Montana, New Mexico, and Wyoming	1[c], 4, 5, 10, 20, 21
Rana pretiosa	A, B, C	British Columbia, Oregon, Montana, Utah, and Washington	5, 14, 27, 30, 33, 35
Rana tarahumarae	C, F, G	Arizona and Mexico (Sonora)	1, 7, 9, 18, 19
Rana yavapaiensis	A, C, F, G	Arizona, California, and Mexico (Sonora)	1[c], 9[c], 38[c]

[1] Suggested causes: A) competition with or predation by bullfrogs; B) competition with leopard frogs; C) habitat alteration; D) fish predation; E) commercial exploitation; F) toxicants; G) acid rain; H) catastrophic mortality.

[2] Sources: 1) Applegarth (1983), 2) Banta and Morafka (1966), 3) Basey and Sinclear (1980), 4) Baxter and Stone (1980), 5) Black (1969), 6) Bury and Luckenbach (1976), 7) Bury et al. (1980), 8) Committee on Rare and Endangered Wildlife Species (1966), 9) Conant (1977), 10) Corn and Fogleman (1984), 11) Cory (1963), 12) Cowan (1979), 13) Cowles and Bogert (1936), 14) Dumas (1966), 15) Frost (1983), 16) Green (1978), 17) Grinnell and Storer (1924), 18) Hale (1983), 19) Hale and May (1983), 20) Hammerson (1982*a*), 21) Hammerson (1982*b*), 22) Honegger (1975), 23) Jameson (1956), 24) Jennings and Hayes (1985), 25) Lardie (1963), 26) Leviton (1972), 27) Licht (1974), 28) Lockington (1879), 29) McKeown (1974), 30) Morris and Tanner (1969), 31) Moyle (1973), 32) Myers (1930), 33) Nussbaum et al. (1983), 34) Platz (1984), 35) Shay (1973), 36) Stebbins (1951), 37) Sweet (1983), 38) Vitt and Ohmart (1978), 39) D. Bradford (pers. comm.), 40) R. Hansen (pers. comm.), 41) R. O'Hara (pers. comm.), 42) S. Sweet (pers. comm.); annotations: a) reported as *Rana*, b) reported as *R. fisheri* and *R. pipiens fisheri*, c) reported as *R. pipiens*.

In this review, we use *R. aurora* and *R. boylii* as primary examples of declining western ranids. This emphasis is because both our own data and much of that of others relating to ranid decline concern these taxa. However, the arguments we present may apply to the other taxa listed in Table 1 as well, with certain differences reflective of their respective life histories.

Discussion of the pattern of decline among western North American ranid frogs would be incomplete without addressing whether the currently observed pattern is in fact recent or if it extended into aboriginal times. No evidence exists that ranid frog populations were much exploited prior to the human population influx generated by the discovery of gold in California in 1848. Most authors indicate that aboriginals in western North America avoided eating frogs, or amphibians in general (Powers, 1877; Kroeber, 1925; Driver, 1937; Aginsky, 1943; Bright, 1978; Levy, 1978; Wallace, 1978*a*), and Wallace (1978*b*) emphasized the Southern Yokuts' repugnance to the idea of eating frogs. Moreover, unlike other aquatic vertebrates (mostly fishes and turtles), frogs are absent from aboriginal food middens (McKern, 1922; Miller, 1955; Schulz and Simons, 1973; Schulz, 1979). Thus, our subsequent discussion of various hypotheses assumes that frog population declines of significance did not occur before 1850.

THE HYPOTHESES

The Bullfrog Hypothesis.—This hypothesis implicates bullfrogs (*R. catesbeiana*) as the most important causal

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agent in frog population decline, either from competition with or predation on native ranids. Bullfrogs were first introduced to western North America in California in 1896 (Heard, 1904), probably as a result of the decline of commercially exploited populations of the native ranid *R. aurora* (Jennings and Hayes, 1985). The origin of the bullfrog hypothesis is vague, but a progression is observed from early predictions that the area occupied by bullfrogs would increase with time (Storer, 1922, 1925, 1933*a*, *b*) to documentation of the dramatic and rapid expansion of the bullfrog (Stebbins, 1951, 1954; see also Wright and Wright, 1949). Eventually, this was followed by suggestions that bullfrogs might be responsible for the concurrent disappearance of endemic *Rana* (Jameson, 1956; Lardie, 1963; Dumas, 1966; Black, 1969; Moyle, 1973; Shay, 1973; Licht, 1974; Conant, 1977; Green, 1978; Vitt and Ohmart, 1978; Baxter and Stone, 1980). Moyle (1973) explicitly suggested that bullfrogs were probably the most important factor influencing the decline of native ranids and marshalled evidence that remains the basis of frequent citations by other authors (see references in Table 1). That evidence, based primarily on samples from 95 localities within the San Joaquin drainage basin of California, can be summarized as follows: 1) bullfrogs were the most frequently encountered ranid frog species, 2) no red-legged frogs (*R. aurora*) were found, 3) yellow-legged frog (*R. boylii*) abundance was inversely correlated with bullfrog abundance among sites, 4) bullfrogs occupied areas that had once had yellow-legged frogs, and 5) captive bullfrogs ate juvenile yellow-legged frogs soon after the latter were introduced into their enclosure.

Moyle (1973) suggested that bullfrogs might eliminate native ranids by either predation or competition. Field evidence that bullfrogs prey on native California ranids is unavailable. Furthermore, data are also unavailable to evaluate competition, which requires a manipulative experiment to establish its occurrence unequivocally (Wiens, 1977). Nevertheless, other anuran studies provide some insight into the likelihood of each mechanism.

Few data suggest that predation by bullfrogs might be responsible for ranid frog decline. *Rana catesbeiana* unquestionably pursue (Stewart and Sandison, 1972) and eat post-metamorphic life stages of other anurans (see summary in Applegarth, 1983). However, inferring the importance of predation from dietary studies remains tenuous because numbers of prey eaten mean little without data on population sizes of prey species.

Interspecific competition between either premetamorphic (Rose, 1960; Licht, 1967; DeBenedictis, 1974; Woodward, 1982*a*) or post-metamorphic anurans (Inger and Greenberg, 1966) has been rarely demonstrated, and the only convincing evidence is from manipulations within experimental enclosures (Licht, 1967; Wilbur, 1977, 1982; Smith-Gill and Gill, 1978; Travis, 1980). Competition among amphibians appears associated with resource-limited conditions frequent at high population densities (Licht, 1967; Wilbur, 1980; Woodward, 1982*a*, *b*; Smith, 1983). Such densities are rarely attained in the larval and post-metamorphic environments of the ranid frogs we discuss (Calef, 1973; Licht, 1974; Hayes, unpubl. data). Although the greatest potential for observing competitive effects exists in denser larval environments, high larval mortality seems to prevent densities from reaching the levels necessary for competitive effects to be significant (Macan, 1966; Calef, 1973; Licht, 1974). While we do not imply that competition between native ranids and bullfrogs is unworthy of testing, indications that it may be rare because the requisite resource-limited conditions are infrequent (Wiens, 1977, 1984; Connell, 1983) suggest it should be examined after more compelling alternatives.

The Habitat Alteration Hypothesis.—This hypothesis implies that human-in-

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duced habitat alterations have reduced or eliminated populations of endemic *Rana*. It implies that certain physical aspects of the habitat are critical to survival of frog populations and that their modification or removal reduces or eliminates those populations. For instance, Banta and Morafka (1966), Moyle (1973), and Hammerson (1982*a*) discuss localities at which they initially observed or had historical records of endemic *Rana* occurrence, but later found these sites in an altered condition without frogs. Banta and Morafka (1966) suggested that the destruction, artificial drainage, and cleaning of natural ponds were the types of alterations that extirpated these populations. Moyle (1973) did not specify types of habitat alteration but implied that removal of riparian cover and damming and the reduction of stream flow were important to frog population disappearance. Moreover, Moyle documented an inverse correlation between abundance of endemic *R. boylii* and degree of human-induced modifications of stream habitats. Hammerson (1982*a*) presented frequency data suggesting decline in populations of *R. pipiens* in Colorado, but suggested only in passing that unspecified habitat changes might account for these population trends.

Although introduction of bullfrogs may be considered an alteration of habitat, we restrict habitat alteration to mechanical changes of topography or vegetation, the meaning implied by most workers. Critical aspects of the habitat are rarely identified, but for western ranids, suitable oviposition and nursery sites and refuges for post-metamorphic frogs, especially hibernating adults (Nussbaum et al., 1983), are probably critical (see also Wells, 1977). For *R. boylii*, oviposition site suitability appears to be determined in part by the presence of a solid substrate in flowing water (Storer, 1925; Fitch, 1936; Wright and Wright, 1949; Zweifel, 1955); this species is absent from sites that seem otherwise appropriate but lack such substrates (Fitch, 1938). Similarly, populations of *R. a. draytonii* are associated with deep-water pools fringed by thick vegetation (Zweifel, 1955; Hayes, unpubl. data), which may provide a refuge from predation or from unfavorable environmental conditions for post-metamorphic individuals, especially adults.

Physical conditions of the habitat are undoubtedly important to survival; temperature might be especially important. Among ranid frogs, high temperatures are tolerated least during early embryonic development (Kuramoto, 1978), and breeding is probably restricted to sites and time intervals where embryos can avoid lethal temperatures (Moore, 1942; Zweifel, 1977). Embryonic *R. boylii* have a critical thermal maximum (CTM) of <26°C (Zweifel, 1955), and *R. a. draytonii* may have a similarly low tolerance because it breeds during the colder season (Storer, 1925). Furthermore, the related *R. a. aurora* has the lowest known embryonic CTM of any North American ranid (21°C; Licht, 1971). In contrast, oviposition and developmental characteristics of *R. catesbeiana* (including an embryonic CTM of 32°) allow it to withstand higher temperatures (Moore, 1942). Therefore, habitat alterations that increase water temperature, such as removal of riparian vegetation or reductions in stream flow, might favor bullfrogs.

Habitat alteration may also affect the probability of local frog population survival simply by eliminating adjacent populations. Scattered data suggest that western ranid frog populations often exist in small demes (Storm, 1960; Brown, 1975; R. W. Hansen, D. C. Holland, and R. K. O'Hara, pers. comm.; Hayes, unpubl. data). Maintenance of deme size depends on recruitment and immigration. Extinctions of local demes or adjacent populations result in greater distances between populations (Moyle, 1974; Terborgh, 1976) and may decrease the probability of immigration. How important decreases in immigration are to the probability of deme survival is poorly understood in general (Diamond, 1976) and unknown for frogs, but

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it is probably important because local extinctions, a frequent occurrence in small populations (Whitcomb et al., 1976; Fritz, 1979), produce complete dependence on immigration for population replacement.

A Neglected Alternative: Fish Predation.—A third alternative suggests that introduced fish are responsible for ranid declines (Hammerson, 1982*a*). Neglected in part because of the belief that introduction of transplanted and exotic fish had few effects on California's native aquatic fauna (Curtis, 1942), this hypothesis may have originated from Grinnell and Storer's (1924) comment that local declines of *R. muscosa* were known to be caused by trout (*Salmo* spp.) and charr (*Salvelinus* spp.) introductions. Cory (1963) developed the idea, and these authors are probably the sources of other quotes (Leviton, 1972; Basey and Sinclear, 1980). Based on this idea, abundance of *R. muscosa* tadpoles has been used to suggest fish population size in lakes of the southern Sierra Nevada mountains of California (Zardus et al., 1977).

The fish hypothesis assumes that frog declines are caused by predation. Voris and Bacon (1966) concluded that fish are more effective than most organisms at preying on tadpoles; Heyer et al. (1975) amplified that conclusion, noting that fish are the only purely aquatic predators capable of eliminating anurans from pond systems. However, while fish do prey on various anuran life stages (Pearse, 1915–16; Ball, 1948; Lowry, 1966; Heman et al., 1969; Cochran, 1983), the assessment of the impact of fish predation on anuran populations remains inconclusive. The effects of fish predation have usually been inferred indirectly from the absence of anuran breeding or larvae in certain habitats (Cory, 1963; Whitaker, 1971; Merrell, 1977; Hurlbert and Mulla, 1981; Smith, 1983; Woodward, 1983), decreases in larval survivorship in certain ponds (DeBenedictis, 1974), disappearance of larval or adult anuran populations following fish introductions (Liem, 1961; Cory, 1963; Bovbjerg, 1965; Macan, 1966; McCoid and Fritts, 1980), or distinctive behaviors interpreted as escape responses in larval and even post-metamorphic anurans (Cory, 1963).

California ranids may have evolved under conditions of limited fish predation, which may have increased the impact of introductions. California possesses a depauperate native fish fauna (Miller, 1958; Moyle, 1976*b*). Salmonids (*Oncorhynchus* spp., *Salmo* spp., and *Salvelinus confluentus*), cottids (*Cottus* spp.), two cyprinids (*Gila crassicauda* and *Ptychocheilus grandis*), and one centrarchid (*Archoplites interruptus*) are the only native fishes that may prey on vertebrates. The salmonids occasionally prey upon frogs or tadpoles (Lowry, 1966; Calef, 1973); however, they, many cottids, and *P. grandis* use deeper- or swifter-water habitats or exhibit migratory behaviors that probably limit their co-occurrence with susceptible ranid life stages (Taft and Murphy, 1950; Chapman and Bjornn, 1969; Moyle, 1976*b*; Moyle et al., 1982). Although the remaining native fishes, *A. interruptus*, *G. crassicauda* and some *Cottus* spp. frequently use the shallower, slower-water habitats with greater cover (Murphy, 1948; Miller, 1963; Moyle, 1976*b*) similar to those used by ranid tadpoles and frogs, foraging behavior and prey composition data for these species suggest that frog life stages are infrequent prey. Today, the California fish fauna includes about 50 transplanted and exotic species mostly from eastern North America (Smith, 1896; Moyle, 1976*a*; Hubbs et al., 1979; Shapovalov et al., 1981; McGinnis, 1984; Saiki, 1984), 17 of which are extensively naturalized (Taylor et al., 1984). Over half of the naturalized species are piscivores that are implicated in (Curtis, 1942; Miller, 1961; Moyle and Nichols, 1973, 1974; Moyle, 1974, 1976*a*, *b*; Schoenherr, 1981; Minckley, 1983) or have been shown to cause (Meffe, 1985) the decline of native western North American fishes via pre-

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dation. Several of these species are known to prey on frogs or their premetamorphic stages (Pearse, 1915–16; Ball, 1948; Heman et al., 1969; Grubb, 1972; Cochran, 1983).

While vulnerability of western *Rana* tadpoles to fish predation has not been examined directly, native ranids may show especially great vulnerability to introduced versus native fishes. Tadpoles of species infrequently exposed to predators have been shown to be highly vulnerable, either because of their greater activity (Woodward, 1983) or palatability (Kruse and Francis, 1977), but may also be vulnerable because of an inability to escape novel predators (see Eckhardt, 1972; Minckley, 1983; Meffe, 1985). Lewis and Helms (1964) found that ranid larvae were more vulnerable than fish to fish predation, which may result from the more limited stamina tadpoles exhibit (Wassersug and Feder, 1983) because recent data suggest that the mechanical efficiency of tadpole locomotion does not differ significantly from that of fishes (Hoff and Wassersug, 1985; Wassersug and Hoff, 1985). The apparent palatability of larval *R. aurora* suggests that they may be vulnerable (Hayes, unpubl. data). Native California predatory fish feed primarily by sight on prey in the water column or on organisms exposed on accessible surfaces, only infrequently disturbing aquatic vegetation or benthic sediment (Ware, 1971, 1973; Tippets and Moyle, 1978). This mode of feeding allows some benthos-dwelling organisms, such as tadpoles, to avoid predation because they are rarely exposed (Johannes and Larkin, 1961; Schutz, 1969; Efford and Tsumura, 1973). Native and introduced fish species also show markedly different foraging behaviors. Available data suggest that introduced centrarchids (sunfishes) may be more maneuverable than native salmonid predators (Webb, 1983), but whether ranid tadpoles, highly maneuverable swimmers (Wassersug and Hoff, 1985), are at greater risk to predation by centrarchids because of the latter's maneuverability is not known. Many of the centrarchid and ictalurid (catfish) transplants are also generalized predators that often feed by disturbing vegetation or benthic sediment (Ball, 1948; Keast and Webb, 1966; Turner 1966*a*, *b*) and may exhibit unusual behaviors to obtain prey (Baylis, 1982). Because larvae of ranid frogs native to California use benthic sediment, aquatic vegetation, or rocky crevices as refuges (Cory, 1963; Calef, 1973; our data), a critical investigation of tadpole responses when exposed to the novel foraging behaviors of transplanted and exotic fish would be instructive. Finally, a key aspect of predation by centrarchid species naturalized in western North America is their habit of preying on the eggs of aquatic vertebrates (Huish, 1957; Bennett, 1962; Goodson, 1965; Applegate and Morais, 1967; Grubb, 1972). Eggs may even comprise a substantial portion of the diet of the less piscivorous species (e.g., *Lepomis macrochirus*). Anuran eggs are rarely reported as prey (Pearse, 1915–16); this may result from the ichthyological perspective of dietary studies of fishes and the similarity of ranid frog eggs to those of fish. Thus, fish (particularly sunfish) predation of ranid frog eggs may prove a fertile area of investigation.

We suspected that fish might be responsible for declines of native frogs when we noted an inverse relationship between the abundance of introduced fish species and the abundance of the endemic ranids *R. a. draytonii* (Table 2) and *R. boylii* (Table 3) within and between drainage systems. Localities where introduced fishes were abundant rarely had native ranids, and when ranids were present, their populations appeared small, suggesting conditions marginal for their survival. Moyle (1973) reported a similar negative relationship between *R. boylii* numbers and fish abundance and noted that the fish fauna at sites with bullfrogs tended to be dominated by the introduced fishes

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TABLE 2. Relationship between numbers of endemic and non-endemic ranid frogs and fishes for 15 sites in California. Spearman Rank correlation coefficients (r_s) marked by an asterisk (*) are significant ($P < 0.05$) and N = 15 and df = 13 for all comparisons. Data collection methods are in Appendix A.

Frog taxon	Fish	
	Endemic	Non-endemic
Rana aurora draytonii		
Adults and subadults (>50 mm SVL)	.124	−.799*
Juveniles and larvae	.393	−.768*
Rana catesbeiana		
Adults and subadults (>65 mm SVL)	−.410	.723
Juveniles and larvae	−.257	.901*

TABLE 3. Post-metamorphic *Rana boylii* density above and below barriers to fish movement from three northern California drainages. Differences in frog density were significant (two-tailed Mann-Whitney *U*-test, $U = 540$, $P < 0.05$). Data collection methods are in Appendix B.

Parameter	Above barriers fish absent (N = 30)	Below barriers fish present (N = 18)
Rana boylii mean density (frogs/meter stream)	0.72	0.22
Range in frog density	0.47–0.97	0.07–0.37

Lepomis cyanellus and *Gambusia affinis*. Coupled with Moyle's previously noted inverse correlation between *R. boylii* and *R. catesbeiana* numbers, this may imply that the observed negative relationship could be reduced to the effects produced by introduced fishes.

Two facts make fish predation a more compelling hypothesis for ranid declines than the interactions with bullfrogs previously discussed. The first is historical priority: 35 species of exotic and transplanted fishes were released in California between 2 and 36 years prior to 1896, the earliest known date of bullfrog introduction (Smith, 1896; Curtis, 1942; Moyle, 1976*a*, *b*; Jennings and Hayes, 1985). At least six of these species, all predatory, had well-established populations in the lowland Sacramento-San Joaquin drainage by the early 1890s, some with populations sufficiently large to support a commercial trade (Wilcox, 1895; Smith, 1896). Of these species, some of the catfishes (*Ictalurus* spp.) and the basses (*Micropterus* spp.) probably co-occurred with frog populations because of their similar habitat requirements (see Moyle, 1976*b*). The second fact is ecological: although bullfrogs and even their tadpoles can eat anuran eggs and larvae (Ehrlich, 1979; Corse and Metter, 1980), post-metamorphic frogs are the more typical prey of bullfrogs (see summary in Applegarth, 1983), whereas fish have greater access to anuran eggs and larvae simply because of their specialization for aquatic life. Ranid larvae in the non-feeding, yolk-resorbing period immediately after hatching may be most vulnerable; larvae remain attached by adhesive glands to benthic substrates, moving only occasionally (Caldwell et al., 1980). Most predation on ranid larvae occurs during this early developmental period (Herreid and Kinney, 1966; Calef, 1973; Efford and Tsumura, 1973; Licht, 1974).

It is noteworthy that bullfrogs appear to have an advantage over native frogs under conditions of predation by fish (Table 2). Bullfrogs experience higher premetamorphic survivorship (Cecil and Just, 1979) when compared to the western ranid frogs studied (Turner, 1960; Calef, 1973; Licht, 1974; Hayes, unpubl. data). Their eggs and larvae appear to be less vulnerable than those of other anurans, which may be because of lesser palatability (Walters, 1975; Kruse and Francis, 1977) or reduced larval activity (Woodward, 1983), which would reduce their exposure to predators. These patterns may also reflect use of permanent aquatic sites that have a more consistent predation risk (Woodward, 1983); bullfrogs evolved in eastern North America, which has a diverse array of native predatory fishes.

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A Historical Alternative: Commercial Exploitation.—Elsewhere (Jennings and Hayes, 1985), we have suggested that substantial frog harvests in California prior to 1900 probably caused the decline of formerly extensive populations of *R. aurora.* This hypothesis is not testable since conditions postulated to have caused declines no longer exist. Commercial exploitation appears to have produced a parallel decline among populations of the introduced bullfrog in California in the late 1960s (Treanor and Nicola, 1972), but there is no evidence that declines among native ranids resulted from this latter exploitation.

OTHER ALTERNATIVES

In addition to the hypotheses discussed above, several other possible causes of frog declines remain uninvestigated, although some of these have been suggested for other western ranid species (see Hammerson, 1982*a*; Hale and May, 1983; Nussbaum et al., 1983; Corn and Fogleman, 1984). Some of these hypotheses may be trivial, yet the most basic data are unavailable to eliminate any of them.

Toxicants.—A diverse array of often novel compounds (pesticides, herbicides, heavy metals, and others) are known to have deleterious effects on various life stages of ranid frogs (Logier, 1949; Kaplan and Overpeck, 1964; Mulla et al., 1966; Rosato and Ferguson, 1968; Tuck and Crabtree, 1970; Weis, 1975; Hall and Swineford, 1980; Monhanty-Hejmadi and Dutta, 1981). Except for a few dramatic anecdotes (Fashingbauer, 1957; and review in DeWitt and George, 1960), field observations that suggest toxicant-induced mortality among North American ranid frogs are limited (Herald, 1949; Hoffman and Surber, 1949; Boyd et al., 1963; Ferguson, 1963; Mulla, 1963; Meeks, 1968). The early use of thallium and other compounds as rodent control agents in California probably killed many nontarget vertebrates (Linsdale, 1931, 1932). More recently, the use of agricultural and mosquito control pesticides, particularly DDT (Cory et al., 1971; von Rumker et al., 1974), is linked to population declines of a variety of organisms (Stickel, 1975).

Although frog populations were monitored for pesticide load levels (Cory et al., 1970), pesticide effects on frogs were not studied (L. R. Cory, pers. comm.). Nevertheless, existing literature provides data useful in showing how toxicants may be important in frog declines. Larval stages appear to be more sensitive to toxicants than are embryonic and post-metamorphic stages (Mulla et al., 1966; Meeks, 1968; Lande and Guttman, 1973; Hall and Swineford, 1980). Hyperactivity and prolonged premetamorphic development are sublethal responses which can increase vulnerability to predation (Cooke, 1971; Yeung, 1978). Notably, *R. catesbeiana* appears more resistant to the effects of toxicants than some other ranid frogs (Logier, 1949; Newsom, 1958; Ferguson, 1963; Meeks, 1968; Weis, 1975), and even larval bullfrogs tolerate an impressive array of pesticides (Mulla, 1963, 1966; Mulla et al., 1963), data contrary to the contention of Cecil and Just (1979), who suggested that bullfrogs should be a sensitive model for measuring the impact of natural habitat contamination. Comparable data for western ranid frogs are unavailable. In summary, toxicants may have been responsible for ranid frog mortality, but since the use of at least chlorinated hydrocarbons (DDT, etc.) postdates the period of significant decline in at least one species (e.g., *R. aurora*) by at least 30 years, it is unlikely that those toxicants were responsible for the noted decline. Linkage of toxicants, however, to other declines remains inferential.

Pathogens and Parasites.—Wild frog population responses to pathogens and parasites are essentially unstudied, and most data are from captive frogs. Some viruses occur in ranid frogs, a few of which are known to be lethal (Nace et al., 1974). The Lucke virus has been

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linked to cold weather renal tumors (McKinnell and Ellis, 1972), and frogs with these tumors ultimately die in the laboratory (McKinnell, 1973). McKinnell et al. (1980) reported declines in Lucké virus coincident with declines of *R. pipiens*, but indicated there was no evidence for linking viruses to frog declines.

The bacterium *Aeromonas hydrophila* is linked to frog septicemia, a pathogenic condition commonly described as "red leg" (Ewing et al., 1961; Carr et al., 1976). Although frog septicemia has been reported from several wild ranid frog populations (Hunsaker and Potter, 1960; Franz, 1966; Treanor and Nicola, 1972; Lee and Franz, 1973; Hird et al., 1981) and may become epidemic among captive frogs (Gibbs et al., 1966; Glorioso et al., 1974; Nace et al., 1974), the influence of septicemia-associated bacteria on wild ranid populations is controversial. Red leg symptoms are also linked to bacteria other than *A. hydrophila* as well as to simple wounds and are expressed with some inconsistency, making epidemiology confusing (Gibbs, 1973). Inconsistencies make determination of pathogenic incidence from most studies impossible because pathogenicity has often been determined from symptoms alone, which emphasizes the importance of using a systematic method for studying pathogens (Gibbs et al., 1966). That pathogenic bacteria, such as *A. hydrophila*, are favored during the low temperature maintenance of captive frogs and that frogs may be stressed either during or following extended periods at low temperatures have been used to suggest that bacteria may be responsible for mortality following emergence from hibernation (Carr et al., 1976). However, even though *A. hydrophila* was isolated more frequently in spring than in fall samples of *R. pipiens* from Minnesota, no evidence indicated that *A. hydrophila* was the primary cause of declining populations (Hird et al., 1981). Additionally, whether pathogenic bacteria comprise part of the normal gut flora of ranid frogs or not is unclear (Van der Waaij et al., 1974; Carr et al., 1976). That understanding as well as identification of susceptibility differences to *A. hydrophila* between native western ranids and introduced bullfrogs would be instructive in addressing the hypothesis that bullfrogs may behave as a vector for this pathogen.

Data on the incidence of helminth parasitism in populations of native frogs and bullfrogs in western United States are relatively limited (Ingles, 1932*a*, *b*, 1936; Turner, 1958; Waitz, 1961; Lehmann, 1965; Walker, 1965; Moravec, 1984). Early observations that the introduced bullfrog does not appear to be parasitized by the array of helminths found in native frogs are noteworthy (Ingles, 1933). However, it is not known whether freedom from these parasites is important to the success of the adventitious bullfrog over native frogs (Ingles, 1933). Kennedy (1980, 1981) reports that some species of *Haematoloechus* trematodes are largely restricted to bullfrogs, but most western ranids were not examined for these parasites and any pathogenicity in such alternate hosts is unknown.

Acid Rain.—Acid rain is well known in Europe and northeastern North America (Haines, 1981; Cowling, 1982), but its effects in western United States remain poorly understood, even though local areas may have experienced acid rainfall since the 1960s (Liljestrand and Morgan, 1980; R. K. O'Hara, pers. comm.). Acid rain has been implicated in lowered pH of temporary pools, probably causing embryonic salamander mortality in northeastern United States (Pough, 1976; Pough and Wilson, 1977). Ranids could be affected by decreased pH through developmental anomalies (Tome and Pough, 1982; Pierce et al., 1984), reduced sperm motility and thus lowered fertilization effectiveness (Schlichter, 1981), interference with ion regulatory capabilities similar to those found in fish (Fromm, 1981; Freda and Dunson, 1985), or de-

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creased growth rates (Freda and Dunson, 1985). Field mortality as a result of acid rain has not been demonstrated in western North America as it has at frog breeding sites in Sweden (Hagström, 1977) and other parts of Europe (Honegger, 1981), although it has been suggested for *R. tarahumarae* in Arizona (Hale and May, 1983). Acid tolerance of western ranids remains unstudied (see Pierce, 1985); however, in the laboratory, *R. catesbeiana* embryos appear more acid sensitive than embryos of species more closely related to *R. aurora* and *R. boylii* (e.g., *R. sylvatica*; Tome and Pough, 1982).

Catastrophic Mortality.—We include in this category all mortality resulting from environmental catastrophe. Sweet (1983) suggested that recent declines of *R. boylii* were the result of scouring floods that occur about once every 500 years, whereas Corn and Fogleman (1984) implied that severe drought may have been responsible for the local extinction of Colorado *R. pipiens.* Bradford (1983) indicated that during some winters, almost all post-metamorphic *R. muscosa* in shallow lakes die, probably because of oxygen depletion. Because its larvae can overwinter under nearly anoxic conditions, this species probably can resist local extinction. Still, some winters may be so severe that local populations are extirpated. Hypotheses invoking catastrophic mortality are difficult to test because of the unpredictability of catastrophic events.

CONFOUNDED ALTERNATIVES

Existing data may support alternative hypotheses in several ways. We will not attempt to present an exhaustive list of confounded possibilities, but we use a few to illustrate how existing data support alternative interpretations.

The fish predation hypothesis suffers from the same deficiencies as the bullfrog predation hypothesis. We paraphrase from Kitching and Ebling (1967) the criteria considered necessary to demonstrate predation. They include that: 1) an organism cannot survive at a site outside its normal range unless it is somehow protected (isolated) from its suspected predator; 2) an inverse correlation exists between the distribution of the organism and the suspected predator, or alternatively, the organism is inaccessible to the suspected predator where they co-occur; 3) the suspected predator can inflict lethal damage on the prey; and 4) transplant experiments show that the suspected predator is responsible for the destruction of prey. Existing data fulfill criterion two for both fish and bullfrog predation hypotheses (see Tables 2 and 3, and bullfrog hypothesis section). Populations of *R. aurora* have been established successfully in central Nevada in isolation from fish (Linsdale, 1938), fulfilling criterion one. However, Nevada populations are isolated from bullfrogs as well, confounding these hypotheses. Data are also available for criterion three for both bullfrogs (Moyle, 1973) and fish (Hayes, unpubl. data). While these first three criteria are necessary, they are not sufficient conditions for an unequivocal field demonstration of predation. Thus, the data implicating predation by fish and bullfrogs remain confounded.

Data that appear to provide the best support for the bullfrog hypothesis, that *R. boylii* and *R. catesbeiana* abundance are inversely correlated and that *R. catesbeiana* occupies areas formerly occupied by *R. boylii* (Moyle, 1973), could support the habitat alteration hypothesis equally well. *Rana catesbeiana* is known to require warmer, lentic water habitats with limited emergent cover (Wright, 1932; George, 1940; Treanor, 1975*a*, *b*), whereas *R. boylii* requires cooler, lotic waters with greater vegetative cover (Storer, 1925; Zweifel, 1955). Because these requirements correspond well to Moyle's (1973) habitat descriptions for these species, an alternative and more parsimonious interpretation of the inverse correlation in abundance is that habitat partitioning has occurred. Similarly, the observation that bullfrogs now occupy

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areas previously occupied by native ranids could be explained by habitat changes eliminating *R. boylii* and favoring *R. catesbeiana* rather than by competitive exclusion or predation. Moyle (1973) implied this alternative when he suggested that alteration of foothill streams has increased the amount of suitable bullfrog habitat, indicating that bullfrogs seem to be most abundant in warm pools created behind small dams or streams denuded of their riparian cover. Hammerson (1982*a*) similarly indicated that a parallel sort of habitat creation favored bullfrogs in Colorado.

Furthermore, the hypothesis implicating habitat alteration would be confounded with the bullfrog or fish hypotheses if alterations decreased predator-avoidance opportunities from bullfrogs or fishes, such as reducing refuges available for post-metamorphic frogs. Increased predation by bullfrogs is probable where refuges have been eliminated; habitats occupied by bullfrogs appear more open (Moyle, 1973; Treanor, 1975*b*) than those used by *R. aurora* and *R. boylii* (Moyle, 1973; Green, 1978; Hayes and Jennings, unpubl. data). Further, some habitat changes that decrease vegetative cover are known to increase water temperature (Gray and Edington, 1969). Increases in thermal regime that favor bullfrogs may be confounded with habitat alteration that increases the susceptibility of native ranids to bullfrog predation.

Factors may also act synergistically, further confounding attempts to separate their contributions to ranid declines. For example, riparian habitat alteration may amplify the sluicing effect of flooding (Cooke and Reeves, 1976) believed to be detrimental to *R. boylii* (Sweet, 1983; R. W. Hansen and D. C. Holland, pers. comm.).

CONCLUSIONS AND THE DIRECTION OF FUTURE RESEARCH

Clearly, causal mechanisms in declines of *R. aurora* and *R. boylii* are potentially complex. The answer to our query, "Are bullfrogs responsible?," remains ambiguous. For localities from which *R. aurora* and *R. boylii* have disappeared, any mechanism of decline is invariably confounded with at least one alternative because variables that allow alternatives to be eliminated were not observed or measured, or because alternatives cannot be excluded on the basis of present data. We also acknowledge that declines may have been caused by multiple factor interactions or synergisms, but because unequivocal data are unavailable to eliminate the possibility that a single factor has been involved in most of the declines among different taxa, the latter possibility cannot simply be dismissed.

Existing data can be substantially improved in several ways. First, future work should emphasize alternatives testable through manipulations. Manipulations that attempt to test hypotheses are essential for unequivocally determining causal factors. This is crucial for distinguishing between the effects of bullfrogs and fish, which, for example, may operate through the same mechanism, predation. Second, long-term demographic studies of populations at specific sites are necessary to differentiate short-term population fluctuations from longer-term declines. Few quantitative data illustrate ranid frog population decline; rather, what exist are data that indicate sites where historical populations occurred. For example, Colorado populations of *R. pipiens* suggested to be locally extinct (Corn and Fogleman, 1984) require long-term monitoring to confirm extinction. Long-term data are not only needed to correlate putative causal mechanisms with declines, but are also required to test all hypotheses involving unpredictable catastrophic mortality. Third, in addition to investigating the interactions that may be occurring between bullfrogs and native ranids, it may be as useful to investigate the conditions that favor bullfrog survival. Most forms of human-effected environmental changes

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that we have reviewed, with the possible exception of acid rain, may give bullfrogs a selective advantage over that of the native western ranid taxa. Furthermore, the differing habitat requirements between the ecologically most similar and putatively interacting *R. a. draytonii* and *R. catesbeiana* may be sufficient to allow significant partitioning (see Zweifel, 1955; Hayes, unpubl. data). Finally, except for limited surveys on geographically restricted taxa (see Hale and May, 1983; Platz, 1984), documentation of the spatial distribution of extant western native ranid frog populations is non-existent. Such data are imperative to predicting which of the remaining frog populations are most susceptible to extinction.

The belief that bullfrogs cause declines of native frogs has led to the suggestion that, to relieve native frogs, bullfrog populations should be reduced by relaxing commercial and sport harvest regulations (Moyle, 1973; Bury and Luckenbach, 1976). However, unless it is shown experimentally that bullfrogs do in fact cause declines, uncontrolled density reductions may not only be futile, but undesirable because bullfrogs themselves are an important resource (Treanor and Nicola, 1972; Treanor, 1975*a, b*; Jennings and Hayes, in prep.). Rather, we believe the most useful next step would be to execute field experiments of the sort we have suggested, carefully designed to sort decisively among the factors causal in frog declines.

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APPENDIX A

Methods for Data in Table 2

Localities are listed in Table 4. All sites except 3 and 4 had historical records or sightings of *R. a. draytonii*. On the same day, each site was sampled diurnally for fish and frogs (all life stages), and supplementally sampled at night for frogs. Frog and fish numbers were scored similarly to Moyle (1973), except that both were scored identically. Values were 0 = no individuals observed, 1 = one or two, 2 = three to 10, 3 = 10 to 20, 4 = more than 20. Categories scored were adults or subadults, and larvae or young juveniles for *R. a. draytonii* and *R. catesbeiana*, and endemic and nonendemic fish. Endemic fish were those species present within the historic range of *R. a. draytonii*. Thus, *Gila orcuttii*, although probably not historically occurring at site 13, was an endemic because it historically co-occurred with *R. a. draytonii* elsewhere. Fish numbers were estimated by direct observation, but seining was used to determine species composition (Table 4). Stream sample locations were 100 meters of stream length, except for sites 3 and 7. Site 3 was an artificial pond ca. 300 m^2 in a small drainage and site 7 was a pond ca. 900 m^2. Streams were moderate-sized (3–7 m wide), variable depth (0.4–2.4 m), with a low gradient (<1%), and sampled under low flow conditions (0.05–0.12 m/sec). Sites were sampled twice each over the period 1978–1981 during either September, October or November, except for sites 8, 9 and 13, which were sampled four times. We averaged values for each category and compared all frog categories with the two fish categories using a Spearman rank correlation (Zar, 1974). Because eight tests were performed, we conservatively adjusted α to 0.00625. The critical value for rejection of the null hypothesis ($r_s = 0$) at this $\alpha_{df=13}$ is $r_s = 0.736$.

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TABLE 4. Localities sampled and fish species composition.

Locality[1]	Fish species composition[2]	
	Endemic	Non-endemic
1) Freshwater Creek	LS	GA
2) Stony Creek	MC, PG, SG	LM
3) Big Chico Creek	CA, GC, MC, PG, SG	GA, LC
4) Wyandotte Creek	GC, CA	GA, LC, LM, MS
5) Corral Hollow Creek	LS	—
6) Pioneer Pond	—	GA, LC
7) Del Puerto Creek	LS	—
8) Pico Creek	CA, EN, GC, SG	—
9) Pico Pond	CA, GC	MS
10) Ellysly Creek	GC	GA, LC
11) San Simeon Creek	CA, GC, SG	—
12) Cayucos Creek	GC	GA, LC, LM
13) Cañada de la Gaviota	CA, GC, GO, SG	—
14) Refugio Creek	GC	—
15) Malibu Creek	GC, GO	GA, LC

[1] All localities are in California. Counties for localities numbered as in the table are: 1-2) Colusa, 3-4) Butte, 5) San Joaquin, 6) Amador, 7) Stanislaus, 8-12) San Luis Obispo, 13-14) Santa Barbara, and 15) Los Angeles.

[2] Endemics: CA = *Cottus asper*, EN = *Eucyclogobius newberryi*, GC = *Gasterosteus aculeatus*, GO = *Gila orcuttii*, LS = *Lavinia symmetricus*, MC = *Mylopharodon conocephalus*, PG = *Ptychocheilus grandis*, SG = *Salmo gairdneri*. Non-endemics: GA = *Gambusia affinis*, LC = *Lepomis cyanellus*, LM = *Lepomis macrochirus*, MS = *Micropterus salmoides*.

APPENDIX B

Methods for Data in Table 3

Study sites were tributaries of Little Stony Creek in Colusa County, and Salt and Grindstone creeks in Glenn County, California. The Salt Creek tributary was sampled on 10 June, 13 July, 4 August, and 23 September 1981; the Grindstone Creek and Little Stony Creek tributaries were sampled once each on 15 and 22 August 1981, respectively. Study streams were small (1-2 m wide), shallow (0.08-0.4 m), with a moderate gradient (1-4%), and sampled under low flow conditions (0.1-0.4 m/sec). Sites were chosen so that a vertical barrier (2.0-5.2 m) prevented fish access to the stream reaches above the barriers at each sampling location. Clear water, limited aquatic vegetation, and limited benthic sediment (5-20% of bottom) permitted determination of the presence or absence of fish by direct observation. The absence of fish above the barrier in the Salt Creek drainage was confirmed by electroshocking and below the barrier, the fish species were *Salmo gairdneri*, *Catostomus occidentalis*, *Lavinia symmetricus*, *Mylopharodon conocephalus*, *Ptychocheilus grandis*, *Lepomis cyanellus*, and *Cyprinus carpio*, the last two species being rare (N. A. Villa, pers. comm.). Sample locations consisted of three 30-m lengths of stream each above and below the vertical barrier at each site except for the Salt Creek tributary, where six 30-m stream lengths were sampled above the barrier, three in each of two tributaries. At each sample location, ranid frogs (exclusively *R. boylii*) were counted during diurnal (mostly between 1400-1600 h) surveys and the number of frogs per meter of stream was used as a relative measure of frog density. We used a Mann-Whitney *U* test to compare differences in frog densities above and below barriers (Zar, 1974).

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