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Introduced Predator Effects on a Threatened Anuran

A Dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Biological Sciences

by

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ABSTRACT

Introduced Predator Effects on a Threatened Anuran

by

Susan V. Christopher

A rapid reduction in global biological diversity is occurring, and effects from biological invasions are partially responsible. Many amphibian species in the western United States that have experienced population declines are thought to be negatively affected by introduced aquatic predators, including non-native species of fish, bullfrogs (*Rana catesbeiana*) and crayfish. I conducted field studies and manipulative experiments to determine the role of several introduced aquatic predators on the decline of a threatened anuran, the California red-legged frog (*Rana aurora draytonii*).

California red-legged frog tadpoles were palatable to introduced largemouth bass, bluegill, brown bullhead, and western mosquitofish, while tadpoles, metamorphs, and juveniles were consumed by introduced bullfrogs. Fish had stronger effects than bullfrogs or crayfish on red-legged frogs in this study. At a landscape scale, a negative correlation between sites occupied by adult red-legged frogs and introduced fish was greater than that of bullfrogs and red-legged frogs,

since the frog occurred at 78% of the sites where bullfrogs were present but only 52% of the sites with introduced fishes. Red-legged frog reproduction was significantly lower at ponds with introduced fish and bullfrogs compared to ponds with red-legged frogs alone, and reductions were greater with fish and bullfrogs than with only bullfrogs. Bullfrog predation rates on red-legged frogs in a river system were low since only 1 of 47 adult bullfrogs collected had consumed a red-legged frog, even though red-legged frogs were abundant at the collection site. The abundances of all life stages of red-legged frogs declined following the introduction of centrarchid fishes at one pond, but appeared to be unaffected by bullfrogs.

There was a significant positive association between the presence of introduced fishes and bullfrogs in central coastal California. Red-legged frog tadpoles displayed antipredator behaviors to free-ranging fish, crayfish and bullfrogs in mesocosms, but did not respond to chemical or visual cues from these predators. The local coexistence of red-legged frogs with introduced predators is probably maintained by immigration from nearby source sites. Preliminary information on red-legged frog dispersal suggests that there is high connectivity among frog habitats in the region studied.

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CHAPTER 1
A REVIEW OF REDUCTIONS IN BIOLOGICAL DIVERSITY,
BIOLOGICAL INVASIONS AND AMPHIBIAN DECLINES

ABSTRACT

A rapid reduction in global biological diversity is occurring. Anthropogenic alterations of the physical and biotic components of natural habitats are resulting in a dramatic change in the composition of many communities throughout the world, with an overall decline in the number and variety of organisms. These changes affect the structures, functions, evolutionary processes, and stability of biotic systems.

One of the causes for reductions in biodiversity is biological invasions. Native assemblages are often replaced by species that have been introduced through the actions of humans. Because most biological invasions are associated with relatively few exotic species, and because any given exotic species can negatively affect several native species, biological invasions often result in a net loss of biodiversity.

Invasive exotic species usually favor human-altered habitats, live in close association with humans, and have “weedy” population characteristics. Most cases where introduced species have been biologically disruptive can be categorized as exotic predators that consume native species of prey. Native assemblages that occur

in spatially restricted areas, such as oceanic islands and aquatic habitats, appear to be more vulnerable to biological invasions than those that inhabit continental areas.

The fossil record indicates that amphibians have been more resilient than other groups in surviving or recovering from past mass extinction events. However, amphibians appear to be more vulnerable than many other groups to changing environmental conditions in recent times. Many species of amphibians depend on aquatic habitats for reproduction. In the western United States, aquatic habitats have often been targeted for the purposeful introduction of exotic species. In many cases, entire aquatic communities have been replaced with those dominated by exotic species. These introductions have often been followed by the decline or elimination of native amphibians species.

In reviewing the literature on recent declines in biodiversity, biological invasions, and amphibian declines, the effects of introduced predators on native prey species emerge as a common theme. In this dissertation, I detail studies of introduced predator effects on a threatened native anuran, the California red-legged frog (*Rana aurora draytonii*). In areas where the California red-legged frog remains, it is thought to be negatively affected by introduced fishes (including species of bass, sunfish, catfish, and mosquitofish), bullfrogs (*R. catesbeiana*), and red swamp crayfish (*Procambarus clarkii*). Prior to the present study, little was known about the interactions between these introduced predators and the California red-legged frog.

I. REDUCTIONS IN BIOLOGICAL DIVERSITY

A major extinction event caused by human activities is currently taking place, and biodiversity is becoming substantially reduced. Biodiversity has been defined as “the natural variety and variability among living organisms, the ecological complexes in which they naturally occur, and the ways in which they interact with each other and with the physical environment” (Redford and Richter 1999 page 1247). Although biodiversity can be examined at global, ecosystem, community, species, population, and genetic scales (Noss 1990, Redford and Richter 1999, Naeem et al. 1999), most attention has been directed towards the loss of species. Approximately 490 animal and 580 plant species have gone extinct worldwide within the past 400 years (May et al. 1995). If current extinction rates continue, at least half of all species could be lost within 100 years (Pimm et al. 1995, Naeem et al. 1999).

Future extinction rates could be 10 times recent extinction rates (Pimm et al. 1995). There may be time lags between habitat destruction and the subsequent extinction of species, called extinction debt, thus the observed effects of recent habitat disturbance and loss of biodiversity may not be reliable indicators of long-term species losses (Tilman et al. 1994, Loehle and Li 1996). These factors indicate that current estimates of extinction rates may grossly under represent the magnitude of human-induced extinctions.

The primary causes for recent declines in native biodiversity include the loss or alteration of habitats and the effects of biological invasions (Mack et al. 2000). Deforestation, agricultural development, and water projects are often cited as types of habitat alterations that affect species richness (Moyle and Leidy 1992, Reid 1992, Allan and Flecker 1993). Most cases in which an introduced species is thought to be responsible for the extinction of native species can be categorized as exotic predators reducing native prey species (King 1980, Simberloff 1981; reviewed in Section II Part 4, this chapter).

Mass Extinctions of the Past

Mass extinctions have occurred periodically throughout geological history. The mass extinction in the Permian resulted in the elimination of more than 90% of marine invertebrate species and half of their families (Hickman et al. 1986). The mass extinction in the Cretaceous removed the dinosaurs as well as 48% of other documented genera throughout the world (Scott 1937, Russell 1979). Over 60% of the large mammals from the Americas, Europe and northern Asia, and at least 19 genera of North American birds, became extinct at the end of the Pleistocene (Martin and Kline 1984, Owen-Smith 1989, Holman 1991). Raup and Sepkoski (1986) observed that mass extinctions have occurred once every 26 million years.

Although climate change is thought to be responsible for many past mass extinction events, anthropogenic factors and biological invasions may have played a role in some past mass extinction events. A large number of extinctions took place

shortly after human occupancy in many areas (Balmford 1996; also see Flannery 1995). The elimination of the megaherbivores in the Americas and Australia in the late Pleistocene coincided with the arrival of humans who hunted these animals (Martin 1984, Owen-Smith 1987, Flannery 1995), however, the causes of extinction remain controversial. Natural invasions of plant and animal species due to changes in physical barriers to their geographic ranges have also preceded mass extinction events (reviewed in Section II Part 1, this chapter).

A precise comparison between extinction rates estimated from the fossil record and recent times probably cannot be made due to major differences between these data sets (Regan et al. 2001). Nevertheless, it is certain that extinction rates have increased dramatically within the past 100 years (Pimm et al. 1995, Regan et al. 2001). The present extinction interval has been compared to the mass extinction event that occurred at the end of the Cretaceous (Arrandale 1988).

Significance of the Present Mass Extinction Event

Because at least 99% of all species that ever lived are now extinct, extinction may be considered the normal fate of species (Gould 1993). Even on isolated continents, evolution usually does not result in a static equilibrium of species (Simpson 1980). Because the rates of familial origination decline over time, and extinction rates tend to stay the same, long-term taxonomic evolution results in a decrease in diversity (Gilinsky and Bambach 1987). Past partial extinctions have resulted in discontinuous distributions, in which species are restricted to smaller and

more disjunct habitats relative to the areas formerly occupied (Scott 1937). Many species that have recently gone extinct or are considered threatened with extinction exist in small disjunct populations (Moyle and Leidy 1992, Pimm et al. 1995). Because of random environmental variation, it is probably just a matter of time before these small populations become extinct (Hanski et al. 1995). Major international (Reid 1992), United States (Arrandale 1988), state and local (Redford and Richter 1999) efforts have been directed towards preserving the world's biodiversity. Because all species will disappear over time anyway, are these efforts worthwhile? Aside from desires to preserve species for their potential benefits to human medicine, agriculture, and for the enjoyment of future generations, what reasons justify attention to this issue by biologists?

On a geologic time scale, it probably makes no difference whether humans attempt to reverse the current mass extinction trend. Even following a great change in global climate or a nuclear holocaust, the resulting extinctions would likely be followed by radiations and dominance by novel groups, as has occurred subsequent to every other mass extinction event (Stanley 1975, Conway 1992, Feduccia 1995). Recovery to pre-disturbance biodiversity levels following mass extinctions may take up to 10 million years (Gould 1993). The duration of this recovery period may be increased due to environmental stresses caused by anthropogenically-produced toxins released into the environment.

The biodiversity changes expected to occur as a result of the present crisis are among the largest known from human history, and go well beyond the loss of

species. Soil fertility, water quality, atmospheric chemistry, and many other local and global environmental conditions, are controlled by both the diversity and identity of species living within a community (Carroll et al. 1996, Naeem et al. 1999). Ecosystem services provided by particular organisms regulate the flows of energy and materials through ecosystems (Naeem et al. 1999, Duffy 2002). Species diversity has been positively correlated with ecosystem productivity, higher stability, and greater adaptability to changing environmental conditions and perturbations in comparison to depauperate communities (MacArthur 1955, Elton 1958, Hutchinson 1959, Frank and McNaughton 1991, Naeem and Li 1997, Naeem et al. 1999, McCann 2000; but see May 1973, Tilman 1996, Huston 1997, Pfisterer and Schmid 2002).

The Role of Theory in Biodiversity Conservation

Biodiversity management requires the implementation of community ecology theory that has been developed over the past century (Western 1992). For example, Gleason's (1926) view of random assemblies of organisms was succeeded by theories regarding the balance of nature (Elton 1930, Egerton 1973), island biogeographic theory incorporating colonization and extinction processes (MacArthur and Wilson 1967), equilibrium theory (Simberloff and Wilson 1969, Connell and Sousa 1983), and community assembly sequence (Drake 1991, Grover and Lawton 1994). The role of keystone species, those organisms that have a primary role in determining the ecological characteristics of communities

disproportionate to their abundance, also has been investigated (Paine 1966, Brooks and Dodson 1965, Menge and Sutherland 1976, Simberloff 1991). Debate on whether the control of community structure is through predators (top-down forces) (Hairston et al. 1960, Menge and Sutherland 1976, Mills and Forney 1988, Vanni et al. 1997) versus resources (bottom up forces) (White 1978, Hunter and Price 1992) or a combination (Fretwell 1977, Hugie and Dill 1994), continues as studies of food web structure proceed. Investigation into indirect effects (Holt 1984, Schmitt 1987, Wootton 1994, Miller and Travis 1996) and trophic cascades (Paine 1980, Carpenter et al. 1985, Strong 1992) continues to further our understanding of community dynamics.

The development of methods for responding to the biodiversity crisis also requires the integration of evolutionary principles into the theory of community ecology (McPeck and Miller 1996). Investigations into speciation through mutations, impediments to gene flow, polyploidy, and hybridization are essential for exploring the mechanisms leading to the diversification of taxa (Ehrlich and Raven 1969, Bush 1975, McPeck and Miller 1996).

Biodiversity conservation requires an understanding of the structure and dynamics of metapopulations, which are subpopulations distributed on islands of suitable habitat embedded in a landscape of unsuitable habitat and linked by dispersal (Levins 1969, Hanski and Gilpin 1991). The application of these ideas requires the identification of source habitats (where birth rates exceed death rates); sink habitats (where birth rates are lower than death rates); and, core (one very large

population) and satellite populations (several smaller populations). The role of dispersal has become increasingly important in understanding the dynamics of metapopulations (Taylor 1990, Hansson 1991, Doak and Mills 1994).

Thus ecological principles that have been developed over the past 100 years recently have been applied to biodiversity conservation. The management of biodiversity requires exploration in a wide range of spatial and temporal scales (Noss 1992). The implementation of ecological theories calls for the integration of multiple disciplines, the need for more ecological information, and the testing of new ideas (Western 1992).

II. BIOLOGICAL INVASIONS

Introduced, exotic, or non-native species are species that have been transported through human activities from their native geographic ranges to new communities or locations in which they did not evolve. Introduced species have attracted the attention of biologists since Elton (1958), and interest by both community ecologists and conservation biologists in exotic introductions has recently been increasing (reviewed in Lodge 1993a, Williamson 1996, Sakai et al. 2001). Most countries have between 100 and 10,000 introduced species (Lodge 1993b), and there are approximately 4500 introduced plants and animals in the United States alone (Windle 1993). The addition of species to ecosystems by

human introduction may be greater than recent species losses (Hobbs and Mooney 1998).

Biological or biotic invasions have been defined as those instances when an introduced species proliferates, spreads, and persists, usually disrupting native species and ecosystems (Mack et al. 2000). Biological invasions can alter community composition, productivity, nutrient cycling, and hydrology of ecosystems (Vitousek 1990, Mack et al. 2000). Biological invasions have been considered to be one of the factors responsible for recent global environmental change (Vitousek et al. 1996) and loss of biodiversity (Mack et al. 2000). There are dramatic examples of the loss of native species due to the effects of exotic species (Smith 1968, Simberloff 1981, Atkinson 1985, Williamson 1996). In California, 30 to 37 (67 - 82%) of the 45 federally listed threatened and endangered animal species are thought to be negatively affected by introduced species (Steinhart 1990). There is increasing concern about the invasion of non-native species in areas that have been set aside for natural resource protection (Usher et al. 1988, Macdonald et al. 1989, Drost and Fellers 1995, Knapp et al. 2001).

Williamson (1996) reviewed the predictions from computer simulations of biological invasions. He found that the presence of introduced species increased the susceptibility of communities to invasion by other species. Each successive invasion led to a new set of coexisting species, and these sets of species have been called alternate states of a community (Connell and Sousa 1983). These predictions have been supported by observations of introduced species facilitating the

establishment of other introduced species (Gagne 1979, Williamson 1996, Simberloff and Von Holle 1999, Adams et al. 2003).

Below I provide a review of the literature on biological invasions. First, I provide a brief overview of biological invasions known from the fossil record. Second, I discuss the factors that are thought to affect the success of biological invasions, including the characteristics of invasive species, communities that are susceptible to invasion, and habitats that are vulnerable to invasions. Third, I briefly describe the typical population dynamics of an invading species. Fourth, I review the types of exotic species effects on native biota. I examine patterns in the mechanisms whereby exotic species alter the abundance and occurrence of native species by quantifying cases reported in the literature. Fifth, I describe how population and community theory forms the foundation for investigations of biological invasions, and how the study of introduced species can and has contributed to these fields. I limited this part of my review to three topics: the importance of predation and competition in structuring communities, island biogeographical theories, and the persistence of species and populations.

Historical Examples of Biological Invasions

Climate change and tectonic movements have changed physical barriers to the geographic limits of biotas through time. When a physical barrier breaks down, biotic interchange between two formerly separated biotas takes place. Biotic interchange has occurred frequently during the last 25 million years. Examples

include an interruption of the Tethys seaway permitting the interchange of terrestrial organisms of Asia and Africa in the early Miocene; contact between Australia and New Guinea with southeast Asia; the formation of the Central American land bridge in the Pliocene connecting North and South America; the opening of the Bering Strait enabling interchange of the marine biotas of the North Pacific and Arctic-Atlantic in the middle Pliocene; and, an intermittent land bridge connecting the terrestrial biotas of Asia and North America throughout the Paleogene and Neogene (reviewed in Vermeij 1991). Vermeij (1991) concluded that these cases of biotic interchange showed the following patterns: 1) most cases of biotic interchange are highly asymmetrical, with movement of more species in one direction across the former barrier than movement in the other direction, 2) biotas that have the higher number of invading species in asymmetrical interchanges also have higher species diversity; thus, invading species may have evolved under conditions with greater competition, predation, diseases, and need for higher reproductive performance, 3) biotas that underwent mass extinction before an interchange were more susceptible to invasion, and 4) most instances of biologic invasions from these historic cases of biotic interchange *were not* followed by the extinction of native species in invaded areas.

One of the cases of biotic interchange that appears to have led to extinctions in the receiving biota is the Great American Interchange (Simpson 1980, Vermeij 1991) which took place in the late Miocene or early Pliocene (about 7 to 8 million years ago) when the Panamanian Isthmus joined North and South America

(Simpson 1980, Marshall et al. 1982). This biotic interchange was asymmetrical, as there were more species from North America that invaded South America than South American species that invaded North America (Simpson 1980). A higher percentage of native (75%) than immigrant families (25%) went extinct in South America following the interchange. Of the extinctions that occurred in North America, about equal proportions were of immigrant (45%) and native (55%) families (Marshall et al. 1982). Fifty percent of mammalian genera present in South America today are derived from North American immigrants (Marshall et al. 1982), but only three mammal species of South American origin occur in the non-tropical regions of North America (Simpson 1980). Although familial mammalian diversity increased in both North and South America after the appearance of the Panamanian Isthmus, the numbers of families present today are similar to those prior to the exchange, as predicted by MacArthur-Wilson equilibrium theory (Simpson 1980, Marshall et al. 1982).

Natural invasions also occurred historically when groups of organisms underwent range adjustments in response to climatic change. For example, during the advance of the Wisconsinan Laurentide ice sheet in the Pleistocene, the Northern Plains region of the United States received a wave of immigrant animal species from areas to the north and east (Holman 1995). The effects of this invasion differed among taxa. The native amphibian and reptile fauna of the Plains remained relatively stable in comparison to avian and mammalian faunas (Holman 1991).

Mechanisms that may be responsible for the elimination of native species following invasions by new species during past events of biotic interchange include competitive exclusion, predation, an inability to withstand changes in habitat, pressures from pathogens and parasites introduced with the invading species, and an inability to adapt or diversify in response to changing conditions (Holman 1991, Vermeij 1991). These same mechanisms are thought to be responsible for recent declines in native species following human-caused species introductions (discussed below). However, negative effects from biological invasions on native species appear to be more common in recent human-caused species introductions than in historic cases of biotic interchange (Vermeij 1991).

Establishment of Introduced Species

Approximately 10% of species introductions become established (Williamson 1996). Many introductions are successful only after the failure of multiple earlier introductions (Sax and Brown 2000). Inappropriate climate, unsuitable microhabitats, and predation or competition from native species, are the major causes for the failure of establishment following introduction (Levins and Heatwole 1973, Crawley 1986, Lodge 1993a, Moyle and Light 1996). In addition, demographic effects such as high extinction probability of small founding populations (Gilpin and Soule 1986) and reduced population growth rates when the number of individuals in the population is below a threshold level (Allee et al. 1949) can also influence the probability of establishment. Due to random fluctuations in

the biological and physical environment, rare chance events that occur at just the right time can result in the establishment of an introduced species (Crawley 1989, Sax and Brown 2000).

Characteristics of Invading Species and Invaded Communities

Certain life history traits may predispose species to be successful colonists when introduced. Some of the traits that promote establishment include broad environmental tolerance, high phenotypic plasticity, ability to reproduce sexually and asexually, high fecundity, short time to sexual maturity, rapid population expansion, and high dispersal ability (Taylor et al. 1984, Mollison 1986, Brandao and Paiva 1994, Williamson 1996, Sakai et al. 2001). The establishment of an introduced species may also be influenced by the length of time the species is introduced to a given area and the number of repeated introductions (Rejmanek 1989, Williamson 1996). A newly established population is likely to be less genetically diverse than the population from which it is derived (Barrett and Kohn 1991), due to being founded by a small number of initial colonists and genetic drift during colonization (Sakai et al. 2001). Multiple introductions can increase the genetic diversity of invasive populations, and increased genetic diversity may increase the population's potential for adaptive evolution in the new environment (Sakai et al. 2001). Once established, factors that enable some introduced species to persist include positive association with humans and human-altered environments (Moyle 1986, Passera 1994), possessing high competitive ability for resources,

potential for rapid evolutionary change, and long-lived individuals with low mortality rates (reviewed in Sakai et al. 2001).

Differences between native communities also influence the success of invasions. Rejmanek (1996) found that the susceptibility of communities to biologic invasions is related to latitude: the likelihood of invasion is low in the tropics and toward the poles, and highest at 40 to 45°. Two similar communities may not be equally invulnerable due to differences in assembly history (Diamond 1975, Robinson and Dickerson 1987, Drake 1991). The chance of establishment of an introduced species may be increased by the absence of co-adapted enemies, including predators, competitors, parasites and endemic diseases (Crawley 1986, Ashton and Mitchell 1989, Case 1991, Reimer 1994; reviewed in Mack et al. 2000). Invasions may be less successful in communities with diverse functional groups and relatively large numbers of species (Elton 1958, Brown 1989, Ross 1991, Vermeij 1991, Tilman 1997; but see Moyle and Light 1996, Levine and D'Antonio 1999, Stachowicz et al. 2002). Case (1991) attributed invasion resistance of species-rich communities to strong interactions between members of the resident community, which create an “activation barrier” that repels invaders. In a subtidal marine invertebrate community (Stachowicz et al. 2002) and a prairie grassland (Naeem et al. 2000), native species diversity was inversely correlated with invasion success because limiting resources (open space, light, and nutrients) were used more efficiently by native communities with higher diversity than those with lower diversity and an equal number of individuals. Invasions are more likely to succeed if introductions

occur when the densities of one or more native species are reduced (Elton 1958, Moyle and Light 1996). Finally, invasions may be more successful if other introduced species are already present, and there are mutualistic interactions among the introduced species (Simberloff and Von Holle 1999, Adams et al. 2003).

Early researchers proposed that biological invasions were more successful in communities with vacant niches (Nowak 1975, Simberloff 1981, Price 1984, Walker and Valentine 1984, Williamson 1996). Others argued that vacant niches do not exist, and only appear to be “vacant” because we do not understand how resources are being used (Herbold and Moyle 1986, Allison et al. 1996). However, there are cases in which an introduced species fills a functional role that no native species occupied, such as the introduction of carnivores to islands that lack top predators.

Vulnerable Habitats: The Role of Disturbance

Many authors suggest that introduced species have a greater probability of becoming established in disturbed compared to pristine habitats (Moyle 1986, Brown 1989, Hobbs 1989, Williamson 1996, Moyle and Light 1996, Ross et al. 2001). Communities in disturbed habitats often contain few species, and the idea that they are more vulnerable to invasions is a variant of the vacant niche hypothesis (Brown 1989, Hobbs 1989, Pimm 1989, Ross 1991). Alternatively, introduced species may be competitively superior to native species in disturbed habitats if they are better adapted to human-altered conditions (Moulton and Pimm 1983, 1986; Moyle et al. 1986, Brown 1989). Weeds and human-commensals (such as the

Norwegian rat and house sparrow) have a long history of association with human-modified environments, and these habitats are novel for native species (Sax and Brown 2000).

Although the role of disturbance in the establishment of exotic species differs among taxa and community types (Lodge 1993b), some generalizations can be made. Types of human-caused disturbance which favor the establishment of exotic plant and animal species include road construction and maintenance, water pollution and eutrophication, agriculture, livestock grazing, land clearing, stream channelization, streams with regulated streamflow, and artificial impoundments (Moyle 1986, Ramakrishnan and Vitousek 1989, Dudley and Collins 1995, Mack et al. 2000). Habitats in which the natural disturbance regimes (i.e., floods, fires) have been altered are also prone to invasion (Dudley and Collins 1995, Mack et al. 2000). For example, the distribution of exotic fish species in a northeastern United States watershed was explained by alterations of stream habitat (due to mining and agriculture), and was not influenced by the distribution and diversity of native fish species (Ross et al. 2001). In the western United States, exotic species such as sunfish, bass, carp, catfish, and bullfrogs thrive in modified habitats (e.g., reservoirs, irrigation canals, aqueducts) created by water projects (Bury and Whelan 1984, Moyle 2002). Relatively undisturbed streams in the western United States are not easily invaded by these species, possibly because they do not possess adaptations to cope with periodic floods and droughts (Baltz and Moyle 1993). However, during

mild climatic conditions, these species often spread into undisturbed habitats from adjacent reservoirs or irrigation channels (Moyle 1986, Moyle and Light 1996).

Introduced species that favor human-modified habitats and habitat fragmentation can have synergistic effects on native species. Habitat fragmentation increases the chance of extinction due to stochastic factors (demographic or environmental) as a result of smaller populations occupying smaller habitats (Gilpin and Soule 1986, Shaffer 1990, Fagan et al. 2002). Fragmentation can also increase the probability of extinction for a native species by increasing the contact zone between the native and introduced species, and smaller fragments may lack refugia for native species from the exotic species (Moyle 1976, Hobbs 1989, Suarez et al. 1998). Exotic species that thrive in human-modified habitats may decrease the effective habitat area for species that occupy the interior of undisturbed habitats if the exotics compete with, prey upon, or parasitize the native species (Harris et al. 1996).

Vulnerable Habitats: Spatially-Restricted Habitats

Evidence exists that invasions are more likely to be successful in spatially restricted habitats, such as oceanic islands (Magnuson 1976, Macdonald et al. 1989). Over 90% of the mammals present in both New Zealand and Hawaii, and 67% of the mammals on the Galapagos Islands are exotic species (Thornton 1971). In contrast, less than 10% of the mammals of North America and Australia are exotic species (Brown 1989). In addition, extinctions caused by introduced species are

more likely to occur on islands than on continents (Collar and Stuart 1985, Brown 1989, Macdonald et al. 1989).

It is often argued that mainland species invade islands more readily than island species invade mainlands (Elton 1958, Carlquist 1965). In fact, there are very few island species that are known to invade continents (Brown 1989). The phenomenon of more invading species being from continents than islands may be a simple matter of probability, because there are more mainland than island species (Simberloff 1989, Williamson 1996), and mainland populations tend to be larger (Brown 1989). Alternatively, mainland species may be inherently superior to island species because they have greater ability to resist a wide diversity of potential enemies, tolerate a wide range of abiotic conditions, and use a broad range of resources (Simberloff 1989, Sax and Brown 2000). This follows from the assumption that species that are likely to be introduced are abundant and widespread in their native ranges, and the same characteristics responsible for their dominance in their native range should enable these species to establish and persist on islands with lower diversity (Sax and Brown 2000).

Islands may be more susceptible to the effects of biological invasions in part because of decreased levels of species richness and evenness in comparison to continental habitats (Moulton and Pimm 1986, Fox and Fox 1986, Loope and Mueller-Dombois 1989). More speciose communities are hypothesized to be more resistant to biological invasions than less speciose communities, in what is termed “biotic resistance” (Loope and Mueller-Dombois 1989, Pimm 1989, Vermeij 1991).

The species-area relationship for insular habitats has a steeper slope and lower intercept than similar non-isolated habitats (MacArthur and Wilson 1967). Some authors have observed that the number of species per genus is lower on islands than in similar-sized continental areas (Simberloff 1984). Birds of prey and large carnivores are usually absent from islands because there is inadequate habitat or prey to maintain their populations, and amphibians, land mammals, and freshwater fish are often absent because they cannot easily disperse to islands. In addition, island populations are inherently vulnerable to extinction because of decreased immigration rates and reduced genetic variability due to past bottleneck effects (Loope and Mueller-Dombois 1989) and stochastic effects on small population size (Williamson 1981, Rey 1984).

Fragmented continental habitats (Coblentz 1990), lakes (Magnuson 1976), and freshwater drainages (Gido and Brown 1999) may function ecologically much like oceanic islands. Depauperate native communities are characteristic to these types of spatially-restricted habitats, and may be responsible for increased vulnerability to invasions. For example, native fish species diversity in most freshwater habitats of the western United States was naturally low, and presently these systems have more introduced than native fish species (Gido and Brown 1999, Moyle 2002). The rate of establishment of an invading species is relatively rapid and interactions with the native community are often strong in spatially-restricted habitats (Nowak 1975).

Invasion Dynamics

In a homogeneous environment, a successful newly established organism will usually increase its population size exponentially at its intrinsic rate of natural increase (Nowak 1975). Its distribution will expand by means of random diffusion at a roughly constant rate of expansion (Nowak 1975, Williamson 1996). The conceptually simplest theory of spatial spread incorporating exponential population increase and random diffusion developed by Skellam (1951) gives the deterministic linear partial differential equation

$$\partial n / \partial t = rn + D(\partial^2 n / \partial x^2 + \partial^2 n / \partial y^2)$$

where n is the population size, t is time, and x and y are the spatial dimensions. The parameters r and D are the intrinsic rate of natural increase and the diffusion coefficient, respectively. The rate of population growth at the front of the wave may be slightly greater than after the colonist has become established owing to a time lag for resident predators and parasites to switch to using the invading organism (Nowak 1975). The rate of advance will be slower if population growth is not maximal due to age structure, Allee effects (Allee et al. 1949, Lewis and Kareiva 1993, Williamson 1996), or if invasion success requires the evolution of adaptations to the new environment (Mack et al. 2000, Sakai et al. 2001).

In a heterogeneous environment, the rate of spread of an introduced species depends on the size and distribution of available habitat patches, the distance between suitable patches (Mooney and Drake 1989), the frequency of migrations or rate of dispersal, and ability to expand under different habitat conditions (Passera

1994). Nowak (1975) described the processes of species range expansion in heterogeneous landscapes. Macroexpansion occurs when the range is increased overall by small groups of individuals dispersing across less suitable areas to high-quality patches. Fluctuations in population sizes sometimes lead to the extinction of local populations. This is followed by a stage of microexpansion in which the gaps in the distribution are filled by dispersal. The more heterogeneous the environment, the greater the time until population size remains relatively constant (Nowak 1975).

After an introduced species is established, it usually persists over ecological time (Coblentz 1990). An introduced species may attain higher densities in novel habitats than in its native habitat due to a lack of co-adapted enemies (Lampo and De Leo 1998).

Effects of Biological Invasions

Human-caused species introductions may be responsible for reducing global biodiversity because relatively few introduced species have been responsible for displacing many native species (Lodge 1993b, Vitousek 1994, Mack et al. 2000). Biological invasions can also be responsible for altering habitats, disrupting evolutionary processes, and changing ecosystem functions such as fire regimes and nutrient cycling (Breytenbach 1986, Mack et al. 2000). These types of community and ecosystem effects have been demonstrated in 2 - 40% of cases where exotic species have successfully become established (Ebenhard 1988, Lodge 1993a, Simberloff 1991, Williamson 1996). Predicting whether introductions will be

disruptive to native communities is difficult because of the complexity and dynamics of natural systems (Courteney 1979, Breytenbach 1986).

Most studies of the effects of introduced species have been concerned with ecological time, or tens to a few hundreds of generations (Williamson 1981). It is still too early to determine the magnitude of effects that introduced species will have on the evolution of native species (Williamson 1996). Estimates of the time needed for speciation to occur range from 100,000 to 10 million years (Vermeij 1991, Knowlton et al. 1993). However, introduced species have already been shown to exert strong selective pressures on some native species (Benkman 1989, Abrams 1996, Kiesecker and Blaustein 1997a, 1998).

Types of Effects From Introduced Species

I reviewed accounts of introduced species effects on native communities from 11 sources (Appendix A). Within these publications, I found 1000 cases of pairwise interactions between an introduced species and a native species. I included only cases in which the introduced species had successfully become established. I tallied the accounts (pairwise interactions) according to the mechanism by which an introduced species affected a native species. I performed a similar tally by mechanism for accounts in which introduced species effects led to the extinction of a native species. Only 14 accounts indicated there were no apparent effects of the exotic on the resident species; however, the reviewed literature was inherently biased toward reporting accounts in which there was an effect. Of the 986 accounts

in which there was an effect, 601 (61%) determined that the effect was of an introduced carnivore or herbivore using native prey. There were 237 (24%) accounts that listed competition between the introduced species and a native species as the mechanism responsible for changes in native communities. Habitat alteration caused by an introduced species that negatively affected a native species was cited in 108 (11%) cases. Introduced parasites and diseases comprised 25 (3%) of the cases, and hybridization accounted for 13 (1%) cases.

Local extinctions of native species were documented in 554 (56%) of the 986 accounts in which there were introduced species effects. The type of interaction that led to extinction was given in 548 accounts. Predation accounted for 337 (61%) and competition 179 (33%) of these accounts. Habitat alteration leading to an extinction was documented in 24 (4%) of the accounts; parasites and diseases were responsible for 7 (1%) of the extinctions; and, hybridization accounted for 1 extinction (<1%).

Of the 554 accounts of extinctions, 474 (86%) occurred in spatially-restricted habitats, including oceanic islands, ponds, lakes, reservoirs, estuaries, small river or stream systems, and sand dunes. The time required for extinction to occur following the introduction of an exotic species was reduced on islands compared to continents. On islands, extinctions have been documented 9 - 100 years after the establishment of an introduced species, whereas on continents it may take centuries (Herbold and Moyle 1986, Williamson 1996). However, extinction rates on islands are relatively high even in the absence of introduced species (Simberloff 1976).

The importance of predation as the primary mechanism for invasive species effects on native species is consistent with the findings of Simberloff (1981). An introduced predator is more likely to cause the extinction of a native species if it is a generalist, and can avoid predator-prey cycles by subsisting on other species as vulnerable native species dwindle in numbers (Williamson 1996). Prey species that have not coevolved with certain types of predators, and populations which lack prior experience with particular predators, generally do not display appropriate antipredator responses (Grubb 1972, Woodward 1983, Kats et al. 1988, Ducey and Brodie 1991, Chivers and Smith 1995, Gamradt and Kats 1996). For example, bird colonies on oceanic islands which lack native predators had higher extinction rates following introductions of non-native predators than those that evolved with native predators (Atkinson 1985, Balmford 1996). The ability to recognize and respond to predators may have both a learned (Conover 1987, Maloney and McLean 1995) and a genetic basis (Kats et al. 1988, Ducey and Brodie 1991, Sih and Kats 1994, Kiesecker and Blaustein 1997a). Antipredator adaptations of prey that are effective against native predators, however, may not be adequate for coexistence with introduced predators (Courteney 1979, Reimer et al. 1990, Gamradt and Kats 1996, Gillespie 2001). Many communities have been invaded by multiple predators (Gamradt and Kats 1996, Kiesecker and Blaustein 1998), and effects from multiple predators may be greater than those predicted by summing the effects of single predators (Sih et al. 1998, Peckarsky and McIntosh 1998). Prey may avoid sites with introduced predators that they formerly occupied, and this may contribute to

apparent prey declines (Gamradt et al. 1997). Introduced predators can also have effects that cascade through lower trophic levels (Flecker and Townsend 1994, Schoener and Spiller 1999, Nystrom et al. 2001).

Introduced herbivores have had dramatic effects on island plant communities where large mammalian herbivores were not native (Thorne 1967). Most island flora lack the chemical or morphological defenses displayed by plants from areas with large mammalian herbivores. The introduction of herbivores to islands has been followed by decreases in plant biomass, primary production, species diversity, and species extinctions (Coblentz 1978).

Competition was demonstrated most often in cases where introduced and native species were similar. Petren and Case (1996) found that competitive displacement occurred rapidly because an introduced gecko was better able to exploit limited food resources than a native gecko due to a slightly larger body size, faster running speed, reduced intraspecific interference while foraging, and superior ability to find and exploit clumped resources. Bolger's (1991) studies of the same pair of gecko species indicated that the introduced species dominated resources because its aggressive behavior caused the native species to use sites with lower quality resources. An introduced mudsnail was able to displace a native mudsnail because the introduced snail had a lower mortality rate, which contributed to its ability to be a better competitor for shared food resources (Byers and Goldwasser 2001).

One of the most significant types of habitat alteration caused by introduced species was introduced plants that overgrow other plants and convert entire communities to monospecific stands, which are often of little value to native animal species. Non-indigenous plant species can affect native species through excessive shading, decreased water availability, changes in productivity, litter accumulation, changes in nutrient cycling, and alteration of soil chemistry (Versfeld and van Wilgen 1986, Vitousek and Walker 1989, Vitousek 1990, Williamson 1996). Introduced aquatic plants often cover the entire water surface, resulting in reduced water movement, decreased oxygen infusion from the atmosphere, altered rates of evapotranspiration, and almost a complete loss of light penetration (Ashton et al. 1986). The production and accumulation of large quantities of organic matter from invasive aquatic plants promote bacterial activity, leading to a detritus-based food web and eutrophication (Ashton et al. 1986).

Hybridization of introduced species with native species has led to the loss of genetic diversity in native communities (Krueger and May 1991). The extinction of native populations by hybridization with introduced species can occur through genetic assimilation or outbreeding depression (Huxel 1999). Native species have also been eliminated when hybrids have higher fitness than native species (Moyle et al. 1986).

Relevance of Studies on Introduced Species

Introduced species offer valuable opportunities to study basic processes in community ecology and population biology (Sakai et al. 2001). Much of the understanding of the ecology of invasions and the effects of introduced species is based on ecological principles developed for natural communities. Many of these principles have been the subject of ongoing debate. Studies of biological invasions have been equated with natural experiments, with the processes involved in community and ecosystem change occurring at faster rates than in native communities (Sakai et al. 2001). Below I summarize the history of community theory on competition and predation, island biogeography, and persistence, and suggest how studies of introduced species can advance the development of community theory.

Competition and Predation

The role of competition in structuring ecological communities has long received much attention (MacArthur 1972, Cody 1974, Wiens 1977, Diamond 1978, May 1978, Tilman 1982, Schoener 1983). Competition theory predicts that morphologically similar species cannot coexist (Hutchinson 1959), and there may be limits to the number of species per genus that can coexist (Elton 1946). Brown and Wilson (1956) described “character displacement” by observing that two species that have a small portion of their geographic ranges overlapping have greater body size differences in regions of sympatry than in regions of allopatry. May and

MacArthur (1972) described “limiting similarity” as how similar the ecological niche of two species can be for coexistence to occur. Gause’s (1934) principle states that if the resources used by two species are too similar, over time one species will be eliminated through competitive exclusion.

The importance of competition in natural communities is likely to be underestimated because competition is expected to decrease over time as species coevolve or are extirpated from areas of sympatry (Brown and Wilson 1956, MacArthur and Levins 1967, Schoener 1975, Connell 1980). Communities that are undergoing invasion provide a natural experiment regarding the role of competition in altering community composition (Diamond and Case 1986, Brown 1989). Studies of introduced species effects have suggested that communities vary in the importance of competition as a structuring force, and competitive exclusion is at one end of the continuum (Milligan 1985, Bolger 1991). The outcome of competition between an introduced species and a native species is influenced by the type of habitat, the degree of habitat disturbance (Simberloff 1984, Moyle et al. 1986), and the ability of the native species to compress or shift its niche (Werner 1984, Moyle 1986).

Many ecologists, however, have questioned the importance of competition in structuring ecological communities (Strong 1983, Wiens 1983, Sih et al. 1985). In many communities, predation seems to be more important than competition in determining the abundance and distribution of species (Paine 1966, Connell 1975, Zaret 1980), as is the case with introduced predators (Simberloff 1981). The

importance of coevolved antipredator adaptations for coexistence of prey with predators can be investigated where predators have been introduced.

Island Biogeography

The basic premise of island biogeography theory is that the number of species on an island is determined by a balance between the immigration of species new to the island and the local extinction of those already present (MacArthur and Wilson 1967, MacArthur 1972). Immigration rates increase with decreasing distance between the island and the mainland, and extinction rates increase with decreasing size of the island. Brown and Kodric-Brown (1977) stated that extinction rates may also be dependent on distance to the mainland, because a declining population may be “rescued” by new immigrants. Another prediction is that immigration and extinction rates are affected by the number of species already present on the island, where immigration rates decrease and extinction rates increase with increasing numbers of resident species.

Island biogeography theory has gained support from the study of supersaturated nonequilibrium island faunas. Wilcox (1978) studied land-bridge islands in Baja California that are shrinking in size due to rising sea levels, and found that species diversity is declining through an increase in extinction rates. Critics of island biogeography theory have asserted that there are no data that suggest that a new immigrant is balanced by an extinction, let alone causes one (Williamson 1981). They suggest that equilibria in the number of species on islands

are the result of numerous ecological processes that operate at random, and extinction rates may be constant and diversity-independent.

Island biogeography theory predicts that interspecific competition would be responsible for most introduced species effects in spatially-restricted habitats. However, most cases of introduced species effects on island biota are from the introduction of predators such as cats, rats, and mammalian herbivores (Simberloff 1981, Williamson 1996). Further, it has been suggested that island biogeography theory cannot adequately explain the effects of introduced species because these effects often far exceed what is predicted by theory (Simberloff 1981, Coblenz 1990).

Persistence

Connell and Sousa (1983 page 791) defined persistence “to indicate that a population or species either did not become extinct during a given period of time and in a given area, or if it did, that it recolonized the area within the time span required for one turnover of all individuals of that species in that place.” The likelihood of extinction has been related to temporal variability in mean population density (Vucetich et al. 2000), the size or extent of habitat (Murdoch 1979, Connell and Sousa 1983), spatial heterogeneity (Smith 1972), stochastic processes (Leigh 1981, Grossman et al. 1982, Goodman 1987a), assembly sequence (Drake 1991), and the effective size of ecosystems (Crowley 1978). For some species the key to persistence is the interconnectedness of subpopulations, whereby dispersal from

suitable habitat patches results in recolonization following local extinctions (Crowley 1981, Goodman 1987b, Taylor 1990, Sjogren 1991, Gulve 1994). Because most introductions fail multiple times before successfully becoming established (Williamson 1996, Sax and Brown 2000), study of the factors which determine establishment success can contribute to community theory relating to persistence.

III. AMPHIBIAN DECLINES

An apparent global decline of amphibians was first noted in the late 1980s (Barinaga 1990, Blaustein and Wake 1990, 1995; Phillips 1990, Wyman 1990, Wake 1991, 1998; Pechmann and Wilbur 1994). Reports have detailed worldwide amphibian population declines, range reductions, regional extirpations, and species extinctions (Corn and Fogelman 1984, Clarkson and Rorabaugh 1989, Crump et al. 1992, Phillips 1994, Drost and Fellers 1996, Fisher and Shaffer 1996). A recent analysis of 936 studies indicated that there was a rapid global decline in amphibian populations from the late 1950s to the late 1960s, and another rapid decline in North America from 1970 to the late 1990s (Houlahan et al. 2000, Alford et al. 2001). Determining a universal cause of the decline is complicated because (a) not all species in a given area are declining (Fisher and Shaffer 1996); (b) some species appear to be declining in pristine areas (Bradford 1989, Kagarise-Sherman and Morton 1993, Drost and Fellers 1996, Green and Sherman 2001); and

(c) populations in some regions are declining more than populations in other regions (Wake 1991, Blaustein 1994).

Much public attention has been focused on abnormally large numbers of deformed frogs from many regions, perhaps with implications for humans (Kaiser 1997, Reaser and Johnson 1997). Recently, however, naturally occurring trematodes were found to be a primary agent responsible for amphibian limb abnormalities (Sessions and Ruth 1990, Johnson et al. 1999).

Hypotheses for the Cause of Amphibian Declines

Amphibians appear to be especially vulnerable to environmental changes because they live in both aquatic and terrestrial habitats, have permeable skins and unshelled eggs, and are both carnivores and herbivores throughout their life cycles (Vitt and Caldwell 1990, Blaustein 1994, Stebbins and Cohen 1995, Kiesecker and Blaustein 1997b). Originally amphibian declines were purported to indicate global environmental collapse (Blaustein 1994, Morell 1999). Because most species of amphibians have complex interactions with geologic, climatic, and floristic factors, they are among the first organisms to disappear when natural habitats undergo anthropogenic alteration (Duellman and Sweet 1999). In North America, many threatened amphibian species depend on mesic habitats that have become less abundant during the present interglacial interval and persist in localized patches of favorable habitat that occur as outlying areas in their former ranges (Duellman and Sweet 1999). Due to their ability to persist in small microsites, many species of

amphibians are regional endemics or relict taxa, which renders them more prone to extinction (Bury et al. 1995, Bury 1999, Duellman and Sweet 1999).

Amphibian populations are known to fluctuate widely over time, which can result in local extinctions, even under natural conditions (Pechmann et al. 1991, Berven 1990, Pechmann and Wilbur 1994, Blaustein et al. 1994a, Bertram and Berrill 1997). Historically, local extinctions of these small populations were followed by recolonization from adjacent areas, but habitat fragmentation has impeded or eliminated this process in many areas (Bradford et al. 1993, Blaustein et al. 1994a, Green 1997). Wide fluctuations in local amphibian population size are due to highly variable survival of larvae (Pechmann and Wilbur 1994, Alford and Richards 1999). Models of populations with highly variable recruitment suggest that these populations might be expected to decrease during more than 50% of time intervals (Alford and Richards 1999). Evidence for these predictions has come from the analyses of long-term amphibian field data (Meyer et al. 1998, Alford and Richards 1999, Alford et al. 2001).

Hypotheses that explain amphibian declines in apparently undisturbed habitats include the effects of ultraviolet radiation (Blaustein et al. 1994b, 1995, 1996; Anzalone et al. 1998, Lizana and Pedraza 1998), acidic deposition (Corn et al. 1989, Harte and Hoffman 1989, Corn and Vertucci 1992, Dunson et al. 1992, Bradford et al. 1994, Long et al. 1995), and climate change (Pounds and Crump 1994). Amphibian populations at higher elevations and on the western margins of continents appear to be most at risk for extinction (Wake 1991). Aquatic-breeding

amphibian species tend to have greater fluctuations in populations sizes in comparison to terrestrial-breeding species (Alford and Richards 1999, Marsh 2001). These patterns are consistent with the expected effects of major climatic changes, especially decreases in precipitation (Duellman and Sweet 1999).

Others suggest that instead of one global culprit, many amphibian populations are declining due to various local factors that may act synergistically. Local factors include the destruction or alteration of habitat (Brode and Bury 1984, Fellers and Drost 1993, Petranksa et al. 1993, Pechmann and Wilbur 1994, Davidson et al. 2001), chemical pollutants (Hall and Henry 1992, Richards et al. 1993, Fontenot et al. 1994, Russell and Hecnar 1995, Davidson et al. 2001), the presence of introduced aquatic predators and competitors (Moyle 1973, Hayes and Jennings 1986, Bradford 1989, Drost and Fellers 1996, Fisher and Shaffer 1996, Kiesecker and Blaustein 1998, Lawler et al. 1999, Rosen and Schwalbe 2002; see below), and the spread of diseases and pathogens (Carey 1993, Blaustein et al. 1994b, Anderson 1995, Laurance et al. 1996, Berger et al. 1998). Drastic rapid amphibian declines suggest the action of a pathogen, and gradual declines with decreased recruitment over successive years are more likely to be the result of habitat degradation (Carey et al. 1999, Duellman and Sweet 1999, Carey 2000) or predation on early life-stages by introduced species (Chapters 2 and 3).

Sudden declines in frog populations in protected areas of Australia, Brazil, and Central America have shown a spatio-temporal pattern consistent with the directional spread of a pathogen (Laurance et al. 1996, Lips 1999). Infection by a

chytrid fungus (*Batrachochytrium dendrobatidis*) has recently been documented at sites worldwide where rapid mass mortalities of amphibians have occurred (Berger et al. 1998, Lips 1998, 1999; Carey et al. 1999, Morell 1999, Rollins-Smith et al. 2002, Green and Sherman 2001, Fellers et al. 2001). Chytrid fungi are not known to parasitize other vertebrate species (Berger et al. 1998). *Batrachochytrium dendrobatidis* infects the keratinized epidermal cells of amphibians (Longcore et al. 1999), and can be fatal to postmetamorphic amphibians (Berger et al. 1998, Pessier et al. 1999). Recently, some amphibians were found to produce antimicrobial peptides that effectively inhibit growth of *B. dendrobatidis*, and may prevent infection by chytrids from becoming fatal (Rollins-Smith et al. 2002). However, environmental factors such as cold temperatures, UV-B, or chemical pollutants could possibly decrease the synthesis and release of these peptides (Rollins-Smith et al. 2002).

Some animals that had a primary infection of chytrid fungus also had a secondary infection by a pathogenic bacterium (*Aeromonas hydrophila*) that causes red-leg disease in amphibians (Taylor et al. 1999). Chytrid fungi and *Aeromonas* bacteria are normally found in most aquatic habitats (Powell 1993). It is not known whether environmental factors have recently weakened the immunological defenses of infected individuals (Carey 1993, Pounds and Crump 1994, Carey et al. 1999, Morell 1999, Carey et al. 2001), or whether chytrid fungi only recently become pathogenic to amphibians through the natural evolution of new pathogenic forms (Daszak et al. 1999, Carey 2000).

Fungi in the family Saprolegniaceae have also been found to be pathogens of amphibians. Tadpoles were recently discovered with infections of *Aphanomyces* sp. (Berger et al. 2001). *Saprolegnia ferax* has been responsible for amphibian embryo mortality in the Pacific Northwest (Blaustein et al. 1994c), with mortality increasing with exposure to ultraviolet-B radiation (Kiesecker and Blaustein 1995).

There is evidence that other amphibian population declines are the result of infection by iridoviruses (*Ranavirus*), which are pathogens of fish, amphibians and reptiles (Collins et al. 2001). Outbreaks of iridoviral disease have resulted in mass mortality (primarily of larvae), and the disease has recurred annually within a few populations (Daszak et al. 1999). Secondary infections by opportunistic bacteria have also been found in individuals infected by iridoviruses (Cunningham et al. 1996, Jancovich et al. 1997, Bollinger et al. 1999).

The presence of pathogens may alter species interactions, such as by differentially affecting competitively superior species, and this may consequently influence community structure (Kiesecker and Blaustein 1999). Introductions of exotic fish species and bullfrogs may not only reduce native amphibian populations through direct effects of these predators (Hayes and Jennings 1986, Fisher and Shaffer 1996, Gamradt and Kats 1996, Hecnar and M'Closkey 1997; see below), but may also aid in the spread of diseases which affect native amphibians (Seymour 1970, Richards and Pickering 1978, Srivastava and Srivastava 1978, Daszak et al. 1999, Mao et al. 1999, Collins et al. 2001, Fellers et al. 2001). Bullfrogs have stronger resistance to *B. dendrobatidis* than other amphibian species because they

produce additional types of antimicrobial peptides, which appear to permit survival by maintaining low levels of infection (Rollins-Smith et al. 2002).

Many amphibian species that have experienced dramatic declines are thought to be negatively affected by introduced aquatic predators (Moyle 1973, Hayes and Jennings 1986, Bradford et al. 1993, Jennings and Hayes 1994, Stebbins and Cohen 1995, Fisher and Shaffer 1996, Knapp and Matthews 2000, Gillespie 2001, Pilliod and Peterson 2001). Several non-native fish species are suspected to be responsible for eliminating or drastically reducing aquatic-breeding amphibians through predation on larvae (Macan 1966, Bradford et al. 1993, Fellers and Drost 1993, Drost and Fellers 1995, Gamradt and Kats 1996, Funk and Dunlap 1999, Knapp and Matthews 2000, Pilliod and Peterson 2001, Matthews et al. 2001, Gillespie 2001; see Chapter 3 for a comprehensive review of introduced fish effects on amphibians). Bullfrogs also have been suggested to be a cause of population declines of native ranid frogs (Moyle 1973, Bury and Luckenbach 1976, Hammerson 1982, Lannoo et al. 1994, Kupferberg 1997; see Chapter 2 for review). Bullfrogs are native to the eastern United States (Wright and Wright 1949, Stebbins 1985), and have been introduced throughout the world (Storer 1922, Bury and Whelan 1984). Adult bullfrogs consume tadpoles (Cohen and Howard 1958, Corse and Metter 1980, Stuart and Painter 1993, Cook 1997, Cook and Jennings 2001), juvenile frogs (Stewart and Sandison 1972, Smith 1977, McAlpine and Dilworth 1989, Stuart and Painter 1993, Werner et al. 1995, Cook and Jennings 2001), and adult ranid frogs (McAlpine and Dilworth 1989, Twedt 1993, Cook 2002). Competition between the

larvae of bullfrogs and other amphibian species may also affect native amphibian populations (see Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999). Introduced crayfish, especially red swamp crayfish (*Procambarus clarkii*), are thought to have contributed to the decline of native amphibians (Gamradt and Kats 1996; see Chapter 3 for review). Crayfish prey on amphibian larvae (Reynolds 1978, Gamradt and Kats 1996, Axelsson et al. 1997) and eggs (Gamradt and Kats 1996, Axelsson et al. 1997, Punzo and Linstrom 2001). Red swamp crayfish are aggressive and will attack adult amphibians, causing injuries and excluding some amphibians from potential aquatic breeding sites (Fauth 1990, Gamradt et al. 1997, Axelsson et al. 1997, Nystrom et al. 2001).

One of the reasons that introduced aquatic predators can have such strong effects on native amphibians is because amphibian larvae and eggs may not display appropriate antipredator defenses to these novel predators (Woodward 1983, Kats et al. 1988, Ducey and Brodie 1991, Chivers and Smith 1995, Gamradt and Kats 1996, Kiesecker and Blaustein 1997a). In addition, several species of introduced aquatic predators that prey on native amphibians co-occur due to antipredator adaptations that allow them to coexist with each other (Hayes and Jennings 1986, Adams et al. 2003; see Chapter 4 for review). Therefore, native amphibian species are often exposed to pressures from more than one introduced predator (see Chapter 4). In some cases, the effects of multiple predators are additive (Nystrom and Abjornsson 2000, Nystrom et al. 2001), but in other cases they are not (Fauth 1990, Sih et al. 1998). Multiple introduced predator effects may also act synergistically with

environmental factors, especially anthropogenic alteration of habitats (Hayes and Jennings 1986). Several introduced aquatic predator species may be mutualistic, and these interactions increase invasion success. For example, the presence of introduced fish species increases the success of invasion by bullfrogs because fish prey on aquatic invertebrates, which are predators of bullfrog larvae (Werner and McPeck 1994, Smith et al. 1999, Adams et al. 2003). Fish avoid preying on bullfrog larvae because they are unpalatable (Kruse and Francis 1977, Cecil and Just 1979) or too large (Heyer et al. 1975).

The Need for Research on Amphibian Declines

More than 200 amphibian species worldwide are considered threatened under the IUCN Red List (Baillie and Groombridge 1996). Although habitat protection is thought to be the most effective technique for preserving amphibian populations, regulatory agencies often overlook the fact that many other uses of protected lands (such as grazing, flood control, water diversions, logging, mining, fish stocking, and intensive recreational use) are inconsistent with protecting amphibian habitat (Duellman and Sweet 1999). The common perception is that effective conservation efforts undermine these economic interests.

Although the need to understand factors that affect amphibian populations is an important issue in conservation biology, the study of amphibian declines also provides an opportunity to examine factors affecting ecosystem processes and community structure. Because amphibians constitute a large proportion of the

biomass of some ecosystems (Burton and Likens 1975, Petranka and Murray 2001), and since amphibians are one of the few groups of organisms that provide a link in nutrient flows between aquatic and terrestrial systems (Seale 1980, Stebbins and Cohen 1995), substantial decreases in the numbers of amphibians could affect entire ecosystems (Dickman 1968, Vitt and Caldwell 1990). A change in the abundance of amphibians may have direct and indirect effects on other community members, and some of these effects may cascade through several trophic levels (Seale 1980, Blaustein and Wake 1995).

Much has been learned about the causes for amphibian declines in local areas since 1990, when many researchers began investigating whether isolated accounts of amphibian declines and extinctions were part of a global trend. However, further study of the biology of amphibians must be performed to be able to separate natural population fluctuations from declines caused by human activities (Pechmann and Wilbur 1994). More work is needed to determine if the magnitude of population declines or the frequency of extinctions has increased relative to baseline levels, and if amphibians are more imperiled than other groups (Pechmann et al. 1991, Blaustein et al. 1994a, McCoy 1994, Pechmann and Wilbur 1994).

IV. CASE STUDY: INTRODUCED PREDATOR EFFECTS ON A THREATENED ANURAN

My research addresses the causes of decline in a native amphibian species. Amphibians are an interesting group for study because, although they have been relatively more resilient than other groups during past mass extinction events, they appear to be more vulnerable during present declines in biodiversity. Many amphibian species depend on aquatic habitats for reproduction. In the western United States, aquatic habitats have often been targeted for the purposeful introduction of exotic species that incidentally prey on native amphibians. These introductions have been highly successful and are thought to be responsible for considerable changes in resident communities, due in part to the spatially-restricted nature of these aquatic habitats and their relatively depauperate native communities. The introduction of a few target species (i.e., game fishes) has been followed by the replacement of native species by other introduced species, such as planktivorous and other small fish, bullfrogs, and crayfish (Moyle 1973, Magnuson 1976, Hecnar and M'Closkey 1977). Habitat alterations, such as the creation of impoundments with reduced vegetation, water diversions, vegetation removal, and stream channelization are often associated with the presence of introduced fish species and bullfrogs, and have direct negative effects on native frogs (Moyle 1973, Hayes and Jennings 1986). Owing to complex interactions between native amphibians and several species of introduced aquatic predators, and the confounding effects of habitat alteration on

these interactions, manipulative experiments are needed to demonstrate causal relationships between introduced predators and native amphibians (Hayes and Jennings 1986).

In the following chapters, I describe studies of a threatened amphibian, the California red-legged frog (*Rana aurora draytonii*). Populations of the California red-legged frog declined dramatically in the late 1800s due to overharvesting for human consumption (Jennings and Hayes 1985, Stebbins 1985). During the past 100 years, the habitat of this frog has been drastically altered or eliminated (Hayes and Jennings 1986, 1989; Jennings 1988, Jennings et al. 1992, Davidson et al. 2001). This subspecies has been eliminated from 70 percent of its former range (U. S. Fish and Wildlife Service 2002). I conducted studies on the California red-legged frog in the only region where large, contiguous populations remain, the central coast of California (Jennings et al. 1992, Davidson et al. 2001, U. S. Fish and Wildlife Service 2002). In this and other areas where the frog is still present, it is thought to be threatened by introduced aquatic species, including many species of fish, bullfrogs, and crayfish (Hayes and Jennings 1986, Jennings et al. 1992, Cook and Jennings 2001).

Prior to the present study, it was not known which mechanisms may be responsible for California red-legged frog declines, and whether the California red-legged frog could persist in areas where introduced species are present. I conducted studies on the effects of several predators that have been introduced throughout California (adult bullfrogs, four fish species, and one crayfish) on the California red-

legged frog. I also examined antipredator behaviors displayed by California red-legged frog tadpoles in response to these introduced predators.

In Chapter 2 I investigate predation by the bullfrog on the California red-legged frog in natural and experimental situations. In Chapter 3 I detail a similar set of studies involving the California red-legged frog and four introduced fish species, as well as an introduced crayfish. In Chapter 4 I discuss how multi-species interactions and environmental factors may influence the interactions between the California red-legged frog and these introduced predators in the central coast of California.

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CHAPTER 2

INTERACTIONS OF INTRODUCED BULLFROGS AND CALIFORNIA

RED-LEGGED FROGS: PREDATION EFFECTS

AND ANTIPREDATOR DEFENSES

ABSTRACT

I studied the effects of introduced bullfrogs (*Rana catesbeiana*) on the federally threatened California red-legged frog (*R. aurora draytonii*), in coastal central California. At a landscape scale, a survey of 95 sites revealed that California red-legged frogs were common in this region, and their occurrence was related to the presence of bullfrogs. California red-legged frogs were present at 89 and bullfrogs at 18 of the sites surveyed. At a pond scale, I compared measures of the recruitment of California red-legged frogs at sites with and without bullfrogs. While the number of California red-legged frog egg masses did not differ between sites with and without bullfrogs, larvae and metamorphs (frogs which had metamorphosed that season) were significantly more abundant in ponds lacking bullfrogs. The presence of bullfrogs did not affect microhabitat use by California red-legged frog tadpoles in ponds. Of 47 bullfrogs collected from a river site for diet analysis, only one had consumed an adult red-legged frog even though metamorph, juvenile and adult red-legged frogs occurred at high densities at the time of collection. Crayfish and fish dominated the diets of bullfrogs collected in the field.

Bullfrogs consumed larval and post-metamorphic California red-legged frogs in artificial ponds (mesocosm scale). Bullfrogs decreased the number of California red-legged frog metamorphs to 50% of the original number within 24 hours even when alternative prey (crayfish and fish) were present. Bullfrogs significantly reduced the survivorship of large California red-legged frog larvae in artificial ponds within 24 hours when refugia for the larvae were present. The presence of adult bullfrogs in artificial ponds affected microhabitat use by large California red-legged frog tadpoles, but this could have been due to physical disturbance from bullfrogs rather than antipredator responses of tadpoles. In an experimental flow-through system (microcosm scale), large California red-legged frog larvae did not respond to chemical cues from an adult bullfrog or adult red-legged frog by altering activity levels or refuge use. Evidence presented here indicates that introduced bullfrogs may reduce California red-legged frog densities through predation on larvae, metamorphs and adult frogs, but that bullfrogs may not be important to broad distribution patterns. Environmental conditions and interactions with other native and introduced species may affect the strength of bullfrog effects.

INTRODUCTION

There are dramatic examples of the loss of native species following the introduction of non-native predators (Simberloff 1981, Atkinson 1985, Lodge 1993, Williamson 1996). Because predation is a strong selective force, prey evolve antipredator adaptations that increase their chance of survival (Lima and Dill 1990, Endler 1991). Prey are particularly vulnerable to introduced predators since they may not possess appropriate defenses against predators with which they lack prior experience (Woodward 1983, Kats et al. 1988, Ducey and Brodie 1991, Chivers and Smith 1995, Gamradt and Kats 1996, Kiesecker and Blaustein 1997). Determining how introduced species affect native organisms is important for predicting the impacts of invasions (Lodge 1993) and understanding the factors that structure communities (Simberloff 1981).

Introductions of bullfrogs (*Rana catesbeiana*) have been suggested to be responsible for population declines of native ranid frogs in western North America (Moyle 1973, Bury and Luckenbach 1976, Hammerson 1982, Schwalbe and Rosen 1988, Leonard et al. 1993, Lannoo et al. 1994, Kupferberg 1997). Bullfrogs are native to the eastern United States (Wright and Wright 1949, Stebbins 1985). They were introduced to many areas west of the Rocky Mountains beginning in the early 1900s (Storer 1922), and subsequently spread throughout the western United States (Storer 1925, Wright and Wright 1949, Bury and Luckenbach 1976, Stebbins 1985). The presence of introduced bullfrogs is negatively correlated with the presence of

native frog species in many areas (Dumas 1966, Moyle 1973, Hammerson 1982, Schwalbe and Rosen 1988, Hayes and Jennings 1988, Lannoo et al. 1994, Fisher and Shaffer 1996, Kupferberg 1997, Batista 2002). The role of bullfrogs in the decline of native frogs remains ambiguous, however, because there have been concurrent habitat alterations and introductions of other exotic predators in most cases (Hammerson 1982, Hayes and Jennings 1986, Jennings et al. 1992).

Because frogs possess complex life cycles, there are a variety of potential interactions between bullfrogs and native frogs. Competition between the larvae of bullfrogs and other ranid frog species has been demonstrated in some enclosure experiments (Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999), but not in others (Adams 2000). Predation by adult bullfrogs on other ranids has been suggested to be more important than competition between larvae or adults in natural systems (Stewart and Sandison 1972, Hayes and Jennings 1986, McAlpine and Dilworth 1989, Cook 1997). Adult bullfrogs are generalist predators (Korschgen and Baskett 1963, Bury and Whelan 1984, Clarkson and DeVos 1986, Schwalbe and Rosen 1988), and their diets include tadpoles (Cohen and Howard 1958, McKamie and Heidt 1974, Schwalbe and Rosen 1988, Corse and Metter 1980, Stuart and Painter 1993, Cook 1997), juvenile or small species of frogs (Dickerson 1906, Stewart and Sandison 1972, Smith 1977, McAlpine and Dilworth 1989, Stuart and Painter 1993, Werner et al. 1995, Cook 1997), and adult ranid frogs (McAlpine and Dilworth 1989, Twedt 1993, Cook 2002). The importance of frogs in the diets of bullfrogs probably varies seasonally depending on juvenile frog availability (see

Korschgen and Baskett 1963, Corse and Metter 1980, Platt and Fontenot 1993).

Bullfrog larvae prey on tadpoles of other species in experimental situations (Ehrlich 1979, Kiesecker and Blaustein 1997), although they are thought to be mainly herbivores, detritivores, or scavengers of dead animal material in the wild (Dickerson 1906, Bury and Whelan 1984, Kupferberg 1997).

Introduced bullfrogs may have only minor effects on the northern red-legged frog, *Rana aurora aurora* (Green 1978, Twedt 1993, Adams 2000, Kiesecker et al. 2001, Pearl et al. 2004). Although bullfrogs prey on adult northern red-legged frogs, population effects may not be large because juvenile and adult northern red-legged frogs are mainly terrestrial (Dumas 1966, Licht 1986, Twedt 1993, Pearl et al. 2004) whereas bullfrogs are highly aquatic (Wright and Wright 1949, Dumas 1966, Green 1978, Clarkson and DeVos 1986, Licht 1986, Twedt 1993, Werner et al. 1995, Pearl et al. 2004). In addition, northern red-legged frog larvae display effective antipredator behaviors in the presence of introduced bullfrogs, altering microhabitat use, decreasing activity, and increasing refuge use when exposed to chemical cues of adult and larval bullfrogs (Kiesecker and Blaustein 1997, 1998). Because northern red-legged frog larvae from sites with bullfrogs displayed these behaviors and allotopic tadpoles did not, Kiesecker and Blaustein (1997) proposed that these antipredator behaviors resulted from natural selection over 60 years following bullfrog introduction.

In contrast, bullfrogs have been suggested to contribute to declines of California red-legged frogs, *R. a. draytonii* (Moyle 1973, Hayes and Jennings 1986,

Fisher and Shaffer 1996). The bullfrog is now widely established throughout the historic range of the California red-legged frog (Moyle 1973, Bury and Luckenbach 1976, Fisher and Shaffer 1996). Juvenile and adult California red-legged frogs are highly aquatic throughout most of the year (Storer 1925). In aquatic habitats spatial distributions and microhabitat use of California red-legged frogs are similar to those of bullfrogs (Moyle 1973, Cook 1997) and spatial overlap increases during seasonal drying of aquatic habitats (Cook 1997), prolonged periods of drought (Moyle 1973), and following habitat alterations that reduce refugia (Hayes and Jennings 1986). Few published studies have investigated the role of bullfrogs in California red-legged frog declines (but see Moyle 1973, Jennings and Hayes 1985, Hayes and Jennings 1986, Cook 1997, Lawler et al. 1999).

Tadpoles of many species of amphibians can recognize predators through water borne olfactory cues released by predators (Petranka et al. 1987, Kats 1988, Sih and Kats 1991). Tadpoles respond to predators by increasing refuge use (Petranka et al. 1987, Kats 1988, Lima and Dill 1990, Kiesecker and Blaustein 1997), avoiding areas with predators (Sih et al. 1992, Kats and Sih 1992), decreasing activity (Lawler 1989, Wilson and Leftcort 1993, Kiesecker and Blaustein 1997), shifting activity periods (Holomuzki 1986, Sih et al. 1992), and altering their morphologies (Van Buskirk and Relyea 1998, Relyea 2001). No previous studies have addressed whether California red-legged frogs display effective antipredator behaviors to introduced bullfrogs. Because behavioral responses to predators occur at the same time scales as direct predation effects,

understanding the role of adaptive behavioral mechanisms is critical to understanding species interactions (Werner 1992).

I studied interactions between California red-legged frogs and bullfrogs through field studies and experimental manipulations (Table 2.1) to determine the mechanisms in which the bullfrog may negatively affect the California red-legged frog. I focused on whether predation by adult bullfrogs on several California red-legged frog life stages could regulate California red-legged frog distribution patterns and population densities. I surveyed 95 sites in coastal central California to determine if there was a relationship between the presence of bullfrogs and California red-legged frogs at a landscape scale. I compared the abundances of California red-legged frog egg masses, larvae, and metamorphs (frogs which had metamorphosed that season) between ponds with and without bullfrogs to determine if the presence of bullfrogs affected California red-legged frog recruitment at a pond scale. I also sampled California red-legged frog tadpoles across five pond microhabitats to determine if tadpoles used different microhabitats in the presence versus absence of bullfrogs. To assess the importance of California red-legged frogs in bullfrog diet, and to determine which life stages are consumed, I examined the stomach contents of bullfrogs collected from a river where metamorph, juvenile and adult California red-legged frogs (as well as other potential prey) were abundant. At the mesocosm scale, I used artificial ponds to determine if bullfrogs would consume large California red-legged frog tadpoles and metamorphs, and if bullfrogs display preference among 3 common prey types (California red-legged frog metamorphs,

crayfish and fish). I tested whether California red-legged frog larvae display antipredator behaviors in the presence of adult bullfrogs using both free-ranging bullfrogs in artificial ponds and chemical cues from bullfrogs in microcosms. Examination of the distributions, abundance, and interactions of California red-legged frogs and bullfrogs should provide information about the role of introduced bullfrogs in California red-legged frog declines, as well as potential bullfrog effects on other native anuran species.

NATURAL HISTORY

Bullfrog

The bullfrog is the largest frog in North America, and individuals have been recorded to 203 mm snout-urostyle length (Conant 1975). The bullfrog has a dorsal coloration of dark gray, brownish olive, or greenish, and is characterized by the lack of dorsolateral ridges on the body (Wright and Wright 1949, Conant 1975, Stebbins 1985). The native range of the bullfrog is from Nova Scotia to central Florida, from the Atlantic coast to the western edge of the Great Plains and central Texas (Conant 1975). The original distribution of the bullfrog is not well known because it had been introduced widely throughout North America by the early 1900s (see Bury and Whelan 1984). Bullfrogs have been introduced throughout the world, and are currently established throughout most of western North America (Hammerson 1982, Nussbaum et al. 1983, Jennings and Hayes 1985, Clarkson and DeVos 1986,

Schwalbe and Rosen 1988), Hawaii (Storer 1922), Vancouver Island (Green 1978), Europe (Albertini and Lanza 1987, Stumpel 1992), Jamaica (Mahon and Aiken 1977), and Brazil (Batista 2002). This species prefers large, permanent bodies of water (Conant 1975, Bury and Whelan 1984, Stebbins 1985, Werner and McPeck 1994), but individuals have also been found to temporarily occupy vernal pools (Balfour and Morey 1999) and intermittent streams (Moyle 1973). Bullfrogs often occur in habitats that also have fish, particularly species native to the eastern United States (Moyle 1973, Hayes and Jennings 1986, Werner and McPeck 1994, Adams et al. 2003). Bullfrogs evolved with a variety of predatory fish species, and bullfrog larvae developed unpalatability (Kruse and Francis 1977, Cecil and Just 1979, Werner and McPeck 1994) and behavioral responses to water borne predator chemical cues (Pearl et al. 2003) as mechanisms that allow them to coexist with fish. In fact, the survivorship of bullfrog larvae may dramatically increase in the presence of bluegill (*Lepomis macrochirus*), because bluegill depress populations of aquatic invertebrates that prey on bullfrog larvae and the larvae of other amphibian species that compete with bullfrog tadpoles (Hambright et al. 1986, Werner and McPeck 1994, Adams et al. 2003). Because bullfrogs occur at many fish hatcheries, they are often introduced with game fish during stocking (Corse and Metter 1980, Hammerson 1982).

Bullfrogs breed from April to July when the air temperature is about 27° C and water temperature is 20-21° C, with the breeding period beginning earlier in warmer climates (Wright and Wright 1949, Clarkson and DeVos 1986). In

California they breed in late April - July (Cook 1997, personal observation). Older females can lay two clutches per year, and there may be two peaks of breeding activity that are separated by approximately 4 weeks (Howard 1978, Clarkson and DeVos 1986). Bullfrogs have the largest clutch sizes of any amphibian species (Duellman and Trueb 1986), and the total number of eggs per female per clutch can exceed 20,000 (Howard 1978). The ability to lay two clutches per year, and the large number of eggs per clutch, results in exceptionally high reproductive potential for this species (Bury and Whelan 1984). Eggs are laid in a large film that floats on the surface of the water (Wright and Wright 1949). Wind usually breaks the egg mass into smaller packets that drift on the water's surface. Eggs hatch after 2-4 days (Clarkson and DeVos 1986). The tadpoles can grow to 178 mm long (Dickerson 1906). Tadpoles may overwinter one to three times in the northern parts of their range (Berven et al. 1979, Collins 1979, Werner and McPeck 1994). Tadpole growth and development stop as the water cools in the fall, resume when air temperatures rise above 12.8° C (Viparina and Just 1975), and tadpoles begin transforming in March - April (Clarkson and DeVos 1986). In warmer climates, where breeding starts in the spring, tadpoles from early clutches can metamorphose in late summer or fall of the same year (George 1940, Viparina and Just 1975, Cook 1997, Nie et al. 1999). The ability for tadpoles to metamorphose within the same year that eggs are laid can allow bullfrogs to survive seasonal drying of aquatic habitats, which occurs at many sites in the western United States (Cohen and Howard 1958, Cook 1997).

In areas within the native range of the bullfrog, adult bullfrogs can move at least 1600 m in less than one year, and 1219 m in less than 3 weeks (Ingram and Raney 1943). Willis et al. (1956) reported adult movements of up to 2.8 km within a season and Ingram and Raney (1943) recorded distances of ≥ 205 meters in a period of two days. Although most long-distance movements probably follow streams, overland movements of at least 76 m also have been recorded (Ingram and Raney 1943).

Range expansion of the bullfrog in the western United States has been facilitated by the creation of favorable habitats such as permanent reservoirs and irrigation channels (Moyle 1973, Hammerson 1982, Clarkson and DeVos 1986, Lind et al. 1996). Human alterations of natural habitats such as riparian and aquatic vegetation removal, stream channelization for flood control, livestock trampling and grazing, introductions of exotic fish species, and sediment deposition from erosion, appear to favor bullfrogs (Moyle 1973, Hammerson 1982, Hayes and Jennings 1986, Zampella and Bunnell 2000; also see Adams et al. 2003). Alterations resulting in increased water temperatures appear to be especially important for the success of introduced bullfrogs (Moyle 1973, Howard 1978, Hayes and Jennings 1986). All bullfrog lifestages prefer warm water relative to other North American anurans (Bury and Whelan 1984; reviewed in Chapter 4).

California Red-legged Frog

The California red-legged frog (*Rana aurora draytonii*) is the largest native frog in California, with a body length up to 136 millimeters (Wright and Wright 1949, Stebbins 1985). The adults are characterized by reddish coloration on the abdomen and hind legs, prominent dorsolateral folds, and a tympanic membrane that is smaller in diameter than the eye (Dickerson 1906, Storer 1925). This subspecies occurs in the Coast Ranges of California from Marin County to Ventura County, and a few isolated localities in the Sierra Nevada, San Joaquin Valley, and southern California (Jennings and Hayes 1994, U. S. Fish and Wildlife Service 2002).

Historically, this species also was found throughout the Central Valley, the western slope of the Sierra Nevada from Shasta County to Tulare County, and the coastal regions of southern California, but almost all of these populations are now extinct (Stebbins 1985, Jennings and Hayes 1994, U. S. Fish and Wildlife Service 2002).

The northern red-legged frog (*R. a. aurora*) ranges from British Columbia to northern California (Stebbins 1985). The systematic relationship between these taxa is incompletely understood, and morphological, genetic, and behavioral data suggest that they may represent separate species (Hayes and Miyamoto 1984, Green 1985, Hayes and Kremples 1986).

California red-legged frogs inhabit streams, springs, ponds, marshes, sloughs, lakes, and reservoirs (Storer 1925, Wright and Wright 1949, McKeown 1974, Stebbins 1985). They are found primarily at aquatic sites that retain water at least through mid-summer, and they avoid stream reaches with high current velocity

(Storer 1925, Wright and Wright 1949, Jennings 1988, Hayes and Jennings 1988).

The adults prefer aquatic habitats with dense shoreline vegetation (Storer 1925, Jennings 1988, Hayes and Jennings 1988, Jennings and Hayes 1989, Rathbun et al. 1993, Christopher 1997). The presence of California red-legged frogs is associated with the maximum water depths of at least 70 cm (Hayes and Jennings 1988), although individuals may use areas with shallower water depths (Cook 1997).

Adults and subadults may be found far from water during winter rains (Storer 1925, Stebbins 1985, Rathbun et al. 1993, Bulger et al. 2003), and they can move substantial distances within aquatic and riparian habitats (Jennings and Hayes 1989, Rathbun et al. 1993).

Inland populations of the California red-legged frog are inactive in winter, whereas coastal populations may be active all year (Storer 1925, Jennings et al. 1992). Breeding can occur from November through April (Storer 1925, Wright and Wright 1949, Stebbins 1985, Hayes and Jennings 1986, Christopher 1996). Egg masses are usually laid in emergent vegetation at the margins of ponds or stream pools (Dickerson 1906, Storer 1925, Wright and Wright 1949, Jennings et al. 1992). Larvae usually metamorphose after 3.5 to 7 months (Dickerson 1906, Storer 1925, Jennings and Hayes 1989), but in some cases larvae may overwinter (Fellers et al. 2001). Red-legged frogs become reproductively mature at 2 to 3 years of age (Jennings and Hayes 1985) and can live up to 8 to 10 years (Jennings et al. 1992). The diet of adult California red-legged frogs includes fish, aquatic and terrestrial insects, tadpoles, and small frogs (Dickerson 1906, Sanders 1950, Hayes and

Tennant 1985). It is not known whether early life stages can detect and respond to chemical cues from the adults or other native predators. Spatial separation may reduce cannibalism because tadpoles undergoing metamorphosis and metamorphs often select microhabitats different than those used by the adults (see Hayes and Tennant 1985, Jennings et al. 1992, Christopher 1997).

The California red-legged frog is listed as threatened under the Endangered Species Act (U. S. Fish and Wildlife Service 1996). The first known population declines took place in the late 1800s, when populations were overharvested for human consumption (Jennings and Hayes 1985, Stebbins 1985). Over the past 100 years, the habitat of the California red-legged frog has been drastically altered or reduced due to urbanization, agricultural development, flood control practices, the creation of reservoirs, and livestock grazing (Hayes and Jennings 1986, 1988; Jennings 1988, Jennings et al. 1992, Stebbins and Cohen 1995, Davidson et al. 2001). In otherwise undisturbed habitats, populations are thought to have been reduced or excluded by introduced predators including bullfrogs, fish (Moyle 1973, Hayes and Jennings 1986, 1988; Stebbins and Cohen 1995), and crayfish (Jennings et al. 1992). Human alteration of aquatic habitats may result in conditions that are not only less suitable for California red-legged frogs, but that are favorable for introduced aquatic predators (Hayes and Jennings 1986, 1988; Jennings 1988, Jennings et al. 1992). Isolation of California red-legged frog populations due to habitat fragmentation and the presence of introduced predator populations may prevent recolonization following local extinctions (Jennings et al. 1992).

Range Overlap of the California Red-legged Frog and Bullfrog

The California red-legged frog has been eliminated from 70% of its historical geographic range (U.S. Fish and Wildlife Service 2002). The most severe reductions have occurred in the Central Valley and southern California (between the Santa Clara River system and the Mexican border), where this species has disappeared from approximately 99% of its former range (Jennings and Hayes 1994, Davidson et al. 2001). In addition, California red-legged frogs have been eliminated from 90% of their historic localities in the Salinas River system and the inner Coast Ranges (Jennings and Hayes 1994). The highest number of extant California red-legged frog populations is found in the central coast of California, from Pt. Reyes National Seashore, Marin County to Carpinteria, Santa Barbara County (Jennings et al. 1992, Jennings and Hayes 1994, Davidson et al. 2001, U.S. Fish and Wildlife Service 2002).

Bullfrogs were first introduced to California in 1896 and many introductions were for aquaculture (Heard 1904, Jennings and Hayes 1985). Introductions were performed after California red-legged frog populations had been depleted, and the continuing demand for frogs was probably the main cause for initial bullfrog introductions (Jennings and Hayes 1985). By the early 1900s bullfrogs were widespread throughout the state (Storer 1922, 1925; Slevin 1928, Jennings and Hayes 1985), and today the species is present in 55 of the state's 58 counties, being absent only from the Sierra Nevada above 1800 m elevation and from the deserts of

southern California (Moyle 1973, Bury and Luckenbach 1976, Stebbins 1985).

Bullfrogs are particularly common and reach high densities in California's Central Valley (Moyle 1973, Treanor 1975, Bury and Luckenbach 1976). Recent surveys indicate that it may still be expanding its range (Fisher and Shaffer 1996).

Bullfrogs are present only in scattered localities in the Coast Ranges of central California (Fisher and Shaffer 1996). The earliest accounts of bullfrogs in the central coast of California are from the 1930s (prior to 1933, Santa Barbara County, Storer (1933); prior to 1931, Gibraltar Lake, Santa Ynez River, Santa Barbara County, T. I. Storer Field Notebook #9, page 1441; prior to 1938, Alisal Ranch, Santa Barbara County, record from Richard Bond, T. I. Storer Field Notebook #11, page 2214b). Bullfrog introductions to Ventura County continued through the late 1940s, and a bullfrog hatchery was still in operation at that time (Sanders 1950). Bullfrogs are sympatric with California red-legged frogs in at least four coastal drainages systems, and are present (along with exotic fish) in at least 12 others where California red-legged frogs have been extirpated (Jennings et al. 1992). In summary, bullfrogs have been introduced throughout most of the California red-legged frog's historic range. In regions where the California red-legged frog has been extirpated, bullfrogs are common. California red-legged frogs remain widely distributed in California's central coast, where bullfrogs are less common than in other regions of the state.

STUDY DESIGN

I performed 4 field studies and 3 experiments that examined interactions between bullfrogs and California red-legged frogs at 5 scales (Table 2.1). Field studies can be confounded by multiple biotic and abiotic factors that vary among sites, and correlational analysis of field data cannot be used to infer causes from observed patterns. Simulated aquatic communities in mesocosms provide a compromise between the high degree of experimental control and reduced realism of laboratory studies, and the natural complexity and variability in field studies (Morin 1989, Wilbur 1989; see also Cooper and Barmuta 1993). Mesocosm studies can demonstrate interactions that otherwise would have been difficult to detect (Hairston 1989). Concordant results from a variety of approaches at different scales can increase confidence in the conclusions.

Each of the field studies and experiments I performed has subheadings in the Study Sites, Methods, and Results sections. The Discussion section ties together the results from these investigations and those from other studies.

Because the presence of introduced fish species can confound bullfrog and California red-legged frog interactions, the following studies were performed excluding possible fish effects. The effects of introduced fish on California red-legged frogs are treated separately in Chapter 3, and the interactions between fish, bullfrogs, and environmental factors on the decline of the California red-legged frog are considered together in Chapter 4.

Study Sites

Study 1

Distribution patterns of bullfrogs and California red-legged frogs were analyzed using data I collected in central coastal California. These data resulted from various other projects that had the common goal of determining the status of the California red-legged frog at each site. All sites included in this study met the habitat requirements for both California red-legged frogs and bullfrogs, and were within the geographical ranges of these species. Sites with native fish species were included in the dataset but sites with introduced fishes (centrarchids and ictalurids) were omitted from this study and used in a separate analysis (Chapter 3). Sites were divided into two groups: ponds and reservoirs (63 sites), and river and stream reaches (32 sites). The number of sites per county was: Ventura = 4, Santa Barbara = 74, San Luis Obispo = 12, Monterey = 1, and Santa Cruz = 4 (Appendix B).

Vandenberg Air Force Base (VAFB) was the primary study area, and surveys were conducted at 63 sites (Appendix C). VAFB is on the coast of northern Santa Barbara County, California, and contains 98,400 acres of dune system complexes, up faulted and folded ridges and mesas, and down faulted and incised canyons. Freshwater habitat on VAFB includes 85 kilometers of semi-permanent and permanent creeks, at least 283,800 m² of lakes and ponds, as well as lagoons, marshes and vernal pools (Coulombe and Cooper 1976, Coulombe and Mahrtdt 1976). VAFB is an exceptional area for California red-legged frogs because of the

high density of freshwater wetlands (see Appendix C). California red-legged frogs occur in at least 73 wetlands or ponds and 17 stream reaches on VAFB (unpublished data), and potential habitat exists at about 25 other wetlands that have not yet been surveyed (personal observation).

Bullfrogs occur at 17 wetlands or ponds and 5 stream reaches on VAFB (unpublished data). Of these at least 7 ponds and two stream systems also support introduced fish species (unpublished data). Bullfrogs may have invaded some sites on the base from off-base areas, and they also may have been introduced during game fish stocking at a few large ponds on VAFB, which was conducted from the mid-1960s through 1980 (California Department of Fish and Game 1969, 1972; Coulombe and Mahrtdt 1976, Cudd 1986).

Studies 2 & 3

Studies of bullfrog effects on recruitment of California red-legged frogs (*Study 2*) and microhabitat use of larvae in ponds (*Study 3*) were conducted at 6 VAFB ponds that lacked introduced centrarchid or ictalurid fishes (Figure 2.1). These ponds are permanent except during prolonged drought conditions. Three ponds (30, 36, 39) contained bullfrogs and California red-legged frogs, and three ponds (77, 79, 91) contained only California red-legged frogs. Ponds 30, 36, and 39 were the only fishless ponds at VAFB where bullfrogs and red-legged frogs were sympatric. Ponds 30 and 36 were manmade ponds, and 39 was a natural dune swale pond that was fishless at the time of the study (but see Chapter 4). Ponds 77, 79,

and 91 were natural dune swale ponds, and were selected as the control sites because introduced predators probably never occurred in these ponds, and these sites appeared to exemplify “ideal” California red-legged frog habitat (e.g., structurally complex shore and emergent vegetation, presence of deep water, not modified by humans; See Appendix D).

Study 4

I assessed bullfrog predation in the field by collecting bullfrogs from the Santa Ynez River drainage, Los Padres National Forest, Santa Barbara County, California (U. S. G. S. 7.5' Little Pine Mtn. Quadrangle, 34° 31' N, 119° 38' W). The collection area was the upstream third of Gibraltar Reservoir, the Santa Ynez River between Gibraltar Reservoir and the confluence of Mono Creek, and the lowermost kilometer of Mono Creek. Because upper Gibraltar Reservoir has been filled by sediment, this area dries to isolated pools in the late summer and fall. The Mono debris dam contributes to the lack of surface flows downstream of the dam in late summer, but subsurface flows maintain water in isolated pools in this reach of Mono Creek.

This site was selected for studying bullfrog diet because it was the only area known to me that had high densities of bullfrogs, adult and juvenile California red-legged frogs, crayfish, and fish (see Methods). This study was also used to examine multiple introduced predator interactions (Chapter 4). There were no sites (ponds or streams) on VAFB that had high densities of both California red-legged frogs and

bullfrogs (see Appendix E). The Santa Ynez River site is the only area in the central coast region where I have detected high recruitment of California red-legged frogs despite the presence of introduced predators.

Experiments I, II & III

Experiments I and II used artificial ponds (described in Methods) that were placed on a level open field at VAFB. There were no structures or trees that shaded the ponds; however, overcast conditions were common during the experiments. Experiment III was performed using a gravitational flow-through system (Petranka et al. 1987) on an outdoor porch shaded by a large tree (San Luis Obispo County, California). All experiments were subject to natural light and climate conditions.

METHODS

Study 1: Distribution Patterns

Survey data were used to examine the frequency of co-occurrence of bullfrogs and California red-legged frogs to determine whether California red-legged frogs tended to be absent from sites where bullfrogs were present. The presence of fish was determined using existing data (California Department of Fish and Game 1969, 1972; Coulombe and Mahrtdt 1976, Cudd 1986, U. S. Forest Service 1993, 1994; Swift et al. 1997), visual surveys (shallow, clear streams), and sampling (at sites without existing data, sites suspected to have fish based on

connectivity to other fish sites, and sites likely to have been stocked). Fish sampling was conducted using hoop net traps (fiberglass hoop diameter 50.8 centimeters, 4 hoops and 2 throats per trap, mesh size 3.2 centimeters, netcoated black nylon #15 knotted netting; “The Shorty” Miniature Hoop Net, Nylon Net Company, Memphis, Tennessee).

Visual encounter surveys (Crump and Scott 1994, Crisafulli 1997) for frogs were conducted between 1994 and 1999. Surveys were conducted at night using high-intensity focused-beam lights (Wheat Cap Lamps, Model 5800-H, Koehler Manufacturing Company, Marlborough, Massachusetts) to detect frog eyeshine. Surveys were conducted in the water by wading or using float tubes and all potential habitats at each site were thoroughly searched. Numbers of each frog species seen by age class (adult, juvenile, metamorph; see Appendix E for size categories) were recorded. Each site was surveyed 1 – 15 times, and California red-legged frogs were considered absent only if they had not been observed after 2 - 4 surveys. Eighty-two percent of the surveys took place between April 1 and September 30, which is the peak period to detect both bullfrogs and California red-legged frogs in this region. Many sightings of California red-legged frogs were obtained during the peak of their breeding season (February and March), and these sites were also surveyed later in the season for bullfrogs.

Ninety-five sites met the criteria described above and received enough surveys to detect all frog species that were present. The null hypothesis that the

presence of California red-legged frogs was independent of the presence of bullfrogs was tested using a Fisher exact test (Systat 5.2.1, Evanston, Illinois).

Study 2: Reproduction in Ponds, and

Study 3: Microhabitat Use of Larvae in Ponds

I compared the relative abundances of California red-legged frog egg masses, larvae, and metamorphs at 3 ponds with and 3 ponds without bullfrogs. Repeated trapping using hoop net traps (described above) was used to verify the absence of introduced centrarchid and ictalurid fish species at these sites. The purpose of this study was to determine whether the presence of bullfrogs affected the recruitment (reproductive success) of California red-legged frogs in ponds through direct or indirect effects.

Visual surveys for California red-legged frog egg masses were conducted from 19 January 1997 through 16 March 1997. Each of the sites was surveyed twice, and the order of the surveys was haphazard. All areas were thoroughly searched by wading or float tube. A flag was tied near each egg mass with an identifying number to prevent recounting egg masses during the subsequent survey.

The abundance and microhabitat use of larvae at each site was determined using unbaited, galvanized hardware-cloth two-funnel traps (Gee's minnow traps, 42 cm long, 19 cm diameter at ends, 21 1/2 cm maximum diameter, funnel openings 3 – 3.5 cm, mesh 5 mm; Model MT2, Nylon Net Company, Memphis, Tennessee) (Adams et al. 1997). Each pond received 30 traps on each of 3 sampling sessions.

Traps were arrayed along 6 transects per pond, with transects perpendicular to shore and 5 traps per transect. Transect locations were determined by mapping the sites, numbering potential transect locations (34 - 48 per site) on the maps, and randomly selecting 6 transect locations per site. Transects were marked by placing a post (PVC pipe) into the pond substrate, which extended at least 20 cm above the water surface. Posts were positioned in the open water 1 m away from the perimeter band of emergent vegetation (if present) or at water depth 40 cm (Pond 36). Each transect had one trap placed in each of 5 microhabitats in the littoral zone, which sampled three lateral zones (shore, emergent vegetation, open water) and two heights within the water column (near surface, benthic; Figure 2.2). Traps were set at 1400 hours and checked at 2200 hours encompassing both day and night hours. Traps were not deployed overnight because some of the traps were completely submerged to sample deeper microhabitats and anoxic conditions lethal to tadpoles may occur overnight in some ponds (unpublished data).

Each pond was sampled 3 times from 23 May - 4 August 1997, except for Pond 30 that dried down during the study and was sampled only twice. Pond 30 had a layer of soft mud substrate 50-80 cm thick that did not dry out completely during the study, but the layer of water on top of the mud became too shallow (< 11 cm) to be able to use the traps effectively. The order in which the ponds were sampled during the first session was haphazard. Sampling was repeated over two more sessions with the order of the ponds the same as for the first session. Tadpoles at all

stages of metamorphosis were counted, including metamorphs that had recently undergone transformation.

Because the number of larvae captured by traps may be affected by larval activity, which in turn may be affected by the presence of predators, surveys for metamorphs were also conducted. In addition, if bullfrogs prey intensively on juvenile frogs in lentic habitats, decreases in the numbers of metamorphs may occur even if bullfrogs do not affect the number of larvae. The numbers of metamorphs present at the 6 ponds were estimated using visual encounter surveys conducted during the peak period of metamorphosis. Estimating the peak of metamorphosis at each site was complicated by high variation in the timing of metamorphosis among individuals and sites (personal observation). In addition, a large proportion of California red-legged frogs emigrate into upland habitats within a few weeks of metamorphosis (Chapter 4), and thus cannot be found during visual surveys of aquatic habitats. Peaks of metamorph activity were estimated based on the stages of development of tadpoles caught in traps for Studies 2 and 3, and observations of metamorph activity at these sites during previous years (Appendix E). Ponds where water levels dropped due to seasonal drying tended to have tadpoles with increased rates of development, and these ponds were surveyed earlier in the survey period. Accordingly, Pond 30 was surveyed on 5, 6, and 7 July 1997, and all other ponds were surveyed from 15 August - 23 September 1997. One pond (Pond 91) still had untransformed tadpoles until the end of September, since transforming frogs with tails could be seen resting on aquatic vegetation during the metamorph surveys.

Surveys could not be performed after late September 1997 because low nightly air temperatures at VAFB greatly reduced the number of frogs active at or near the water's surface, and thus reduced the number that could be found during visual surveys (personal observation). As a consequence Pond 91 was surveyed late within the sampling period (13 - 23 September 1997). Three surveys were conducted at each pond separated by 4 - 16 days (Appendix F). Visual encounter surveys for metamorphs began immediately after total darkness (2100 hours for Pond 30 and 2045 hours for the others) and followed the methods described in Study 1.

The null hypotheses were: 1) the numbers of California red-legged frog egg masses, tadpoles, and metamorphs are not different between sites with and without bullfrogs (Study 2), and 2) the proportions of California red-legged frog tadpoles trapped in each of the 5 microhabitats would be similar for ponds with and without bullfrogs, indicating that larvae did not alter microhabitat use in the presence of bullfrogs (*Study 3*). Because other factors (habitat suitability, predators, competition between bullfrogs and red-legged frogs) may also contribute to any observed differences between ponds with and without bullfrogs, bullfrog predation alone could not be considered to be completely responsible for any observed differences. The object of this study, however, was to determine if sites where California red-legged frogs coexist with bullfrogs were sources or sinks for red-legged frog populations (Pulliam 1988, Dias 1996), when all pond-scale factors are included.

In Study 2, the total number of egg masses found at each pond was used for analysis. The numbers of tadpoles caught during each sampling session was

calculated and the mean number of tadpoles trapped per pond was used for analysis. It was not possible to identify individual metamorphs in this study, but it was unlikely that the same individuals were counted more than once during consecutive surveys due to the length of time between surveys and the emigration of metamorphs into upland habitats shortly after metamorphosis (Chapter 4, Appendix E). Therefore, cumulative numbers of metamorphs observed at each site were used for analysis. Because ponds differed in size (Appendix D) and metamorphs were observed only in the littoral zones of the ponds, the cumulative number of metamorphs observed per pond was divided by pond perimeter (obtained from the VAFB geographic information system, BTG, Santa Maria, California). Mann-Whitney U tests (Systat 5.2.1, Evanston, Illinois) were used to determine whether total numbers of egg masses, mean number of tadpoles trapped, and density of metamorphs differed between ponds with and without bullfrogs. The replicates were the 3 ponds in each category (bullfrogs/no bullfrogs).

For Study 3, the numbers of tadpoles trapped in each microhabitat were pooled across all transects for each sampling session, and the mean proportion of tadpoles in each microhabitat across the sampling sessions was calculated for each pond. Proportion values were arcsine square root transformed. Pond 36 was dropped from the analysis because no tadpoles were obtained. Because data for microhabitat B were the most similar for bullfrog and non-bullfrog ponds, microhabitat B data were dropped from the final analysis to maintain independence of the remaining response variables. Data met the assumptions for normality and

homoscedasticity (Lilliefors test and Levene's test, respectively; Systat 5.2.1, Evanston, Illinois). The effects of the independent factor (presence or absence of bullfrogs) on the dependent variables (transformed proportions of tadpoles trapped in each microhabitat) were analyzed using MANOVA (Systat, Inc., Version 5.2.1, Evanston, Illinois). Ponds were used as replicates in the analysis.

Study 4: Bullfrog Predation in the Field

To examine bullfrog predation on California red-legged frogs in the field when several types of prey are available, adult bullfrogs were collected for stomach content analysis. Bullfrogs were collected on 8 August 1996, 15 August 1996, and 5 September 1997. Stream pools at the collection site were shallow enough (20 to 40 centimeters deep) for bullfrogs to potentially have access to all aquatic, semi-aquatic and terrestrial prey types. California red-legged frogs were abundant at the time of bullfrog collection (e.g., minimum numbers of adult, juvenile, and metamorph California red-legged frogs seen during collecting: 8 August 1996 - 10, 0, 31; 15 August 1996 - 17, 1, 15; 5 September 1997 - 10, 0, 13). Pacific treefrogs (*Pseudacris regilla*) and western toads (*Bufo boreas*) also were very abundant along the edges of the pools and in the dry riverbed. Invertebrates, crayfish (*Procambarus* sp.), western mosquitofish (*Gambusia affinis*), sunfish (*Lepomis* sp.), three-spine stickleback (*Gasterosteus aculeatus*), and arroyo chub (*Gila orcutti*) occurred together at high densities in the shrinking pools. Adult bullfrogs were collected using an air rifle, and were preserved in formalin within 3 hours of the time of

collection. Only bullfrogs snout urostyle length ≥ 95 mm were used in the analysis because bullfrogs < 95 mm may be too small to consume adult California red-legged frogs. Stomach contents were identified to order for invertebrates, and vertebrates were identified to the lowest possible taxonomic level. The number of individuals of each prey type and the number of bullfrogs with each prey type were counted. The volume of each prey item was measured as the volume of water displaced by the item in a graduated cylinder.

Experiment I: Predation on Metamorphs

Although some authors have suggested that bullfrogs are “sit-and-wait” predators with a diet based on what is available (Dickerson 1906, Frost 1935, Cohen and Howard 1958, Bury and Whelan 1984), others have suggested that bullfrogs actively pursue small ranid frogs (Stewart and Sandison 1972, Smith 1977), and that bullfrogs preferentially feed on crayfish (Corse and Metter 1980). The results of Study 4 revealed a high proportion of crayfish and fish in the stomachs of bullfrogs collected from the field, even though California red-legged frogs were abundant at the collection site. Artificial ponds were used to determine: 1) whether bullfrogs would consume California red-legged frog metamorphs, and 2) whether bullfrogs displayed a preference among California red-legged frog metamorphs, red swamp crayfish (*Procambarus clarkii*), and goldfish (*Carassius auratus*). Goldfish were used because they were the only fish species available that were about the same size and mass as the other prey types (see below). In addition, goldfish were introduced

to California prior to 1900 (Moyle 1976), and they presently occur in the wild at localities throughout the state (Swift et al. 1993, Moyle 2002). A simplified experimental arena was used to examine bullfrog prey preference without prey refuge use or spatial avoidance.

Artificial ponds were galvanized steel stock tanks (circular, 1.5 m diameter, 0.57 m high). Each of 5 artificial ponds was set at approximately 20° slope by placing one brick under the southwestern-most side. Each pond was filled with untreated, aged water (from the State Water Project) to produce a maximum water depth of 7 cm, with 75% of the tank bottom covered by water and 25% of the tank bottom exposed. Phytoplankton and zooplankton were collected from 3 natural ponds at VAFB. One liter of pond water was filtered through 1 paper coffee filter, and this was repeated 10 times for each pond. Coffee filters were placed in a bucket, and plankton on the filters were suspended by adding 10 liters of untreated, aged water and stirring vigorously. Ten milliliters of the plankton suspension were added to each artificial pond at least 3 weeks prior to the experiment. Tank covers were made from tan-colored plastic shade cloth (mesh size 1 X 2 mm, 65% light blockage), and plastic strapping with adjustable buckles secured the covers tightly. The covers prevented the escape of experimental animals, permitted natural photoperiod, kept water temperatures below the thermal maxima of the experimental animals, and excluded other predators.

Adult bullfrogs (snout-urostyle length 139 - 174 mm) were collected from VAFB in mid-August 1998 and maintained in plastic tubs (78 X 46 X 40 cm) with

water and lids outside in full shade. Bullfrogs were fed crickets and mice ad libitum until 24 September 1998, and then starved for about 1 week to standardize hunger. California red-legged frog metamorphs (Gosner stage ≥ 46 ; snout-urostyle length: range 39 - 43 mm, mean 41.5 mm) were obtained from a pond at VAFB on 15 - 20 August 1998 using unbaited funnel traps (described in Studies 2 and 3). Crayfish were caught at various locations at VAFB using hoop net traps (described in Study 1). Metamorphs and crayfish were held in plastic barrels (each: 50 cm diameter, 74 cm high) with several centimeters of water and lids (hardware cloth, 6 mm mesh) outside in full shade. Goldfish were obtained from a commercial vendor. Excess water was blotted from prey animals, and mass was measured using an Acculab Pocket Pro Model #PP-250B Electronic Balance (Newton, Pennsylvania) for crayfish and fish, and Pesola Micro-Line Spring Scales for frogs.

Individual prey of similar mass were selected from the holding tanks for predation trials (wet weight: metamorphs - range 5.5 - 7.4 g, mean 6.4 g; crayfish - range 5.6 - 7.5 g, mean 6.6 g; fish - range 5.0 - 8.2 g, mean 6.5 g). Two individuals of each prey type (metamorph, crayfish, fish) were added to each pond. A small number of prey was used because bullfrog feeding rates were low. One adult bullfrog was added to each pond on 2 October 1998 at 1300 hours. Control ponds lacking bullfrogs were not used because prey could not escape from the mesocosms, and the only source of mortality was from predation. All missing prey items were assumed to have been consumed by bullfrogs. Survivorship was determined at 1700 hours on 2 October 1998, and at 1300 hours on 1, 2, 3, 4, 5, 6, 7, 8, 10, 12, 14, 17,

and 21 days after the bullfrogs were added. Water temperature was measured during each survivorship count using a hand held thermometer, and maximum and minimum water temperatures between counts were measured using a mercury maximum/minimum thermometer (ERTCO).

Experiment II: Predation on Larvae

I assessed the effects of adult bullfrogs on the survival and microhabitat use of California red-legged frog larvae in artificial ponds. I used large larvae with well-developed hind limbs because they spend more time near the water's surface than smaller larvae, and would likely be encountered by bullfrogs in natural situations. Artificial ponds were the stock tanks described in Experiment I. There were 10 artificial ponds arranged in 2 rows. All ponds were placed directly on level ground, and received similar exposure to natural light. Each pond was filled to one-third capacity (approximately 315 L, 40 cm deep) with untreated, aged water (State Water Project). A plankton suspension was prepared as described in Experiment I, and one liter of this suspension was added to each pond. The ponds were left uncovered during the pre-experimental period to facilitate colonization by invertebrates. The water in the ponds became turbid from phytoplankton growth within one week, but cleared after about 2.5 weeks, and algae and detritus settled to the bottom providing organic substrata 1-2 cm deep. The insides of the tanks had previously been painted white, but attached algae quickly stained the surfaces of the tanks. One cement block (19.5 X 19.5 X 40.0 cm) was added to each artificial pond

within a few centimeters of the southwest side to provide a potential resting spot for the bullfrog.

Two microhabitats that could serve as potential refugia for California red-legged frog larvae were added to each pond: a pack of dried cattail (*Typha* sp.) leaves on the pond bottom and a floating vascular plant, marsh pennywort (*Hydrocotyle* sp.). In California central coast ponds the leaves of cattail plants die in the winter, so the cattail leaves simulated the natural structure of pond bottoms. Fifty grams of dried cattail leaves were placed in an envelope of chicken wire (60 cm long X 40 cm wide X 4 cm deep, 3.5 X 2.5 cm mesh), which was positioned opposite from the cement block and anchored to the tank bottom with a rock. The tadpoles could easily swim through the chicken wire mesh to hide among the cattail leaves. Marsh pennywort was used as the second refugium because large, metamorphosing red-legged frog tadpoles frequently occurred in this plant in natural ponds (Study 3). Marsh pennywort appeared to be a suitable refuge from some predators due to its complex physical structure both above and below the water surface. I collected marsh pennywort from a natural pond at VAFB. Using a 46 cm diameter quilting hoop as a guide, I cut 46 cm diameter mats of the pennywort with household scissors. The rhizomes of this plant are interwoven, and the mats remained intact throughout the experiment. The mats were thoroughly rinsed and shaken to remove leeches and invertebrates that feed on tadpoles. I tied a string from the corner of the cement block to the edge of the marsh pennywort mat to anchor the plant near the tank center.

California red-legged frog larvae were obtained using unbaited minnow traps from a bullfrog-free pond at Vandenberg Air Force Base on 15 August 1998. Larvae used in the experiment were selected haphazardly from holding tanks. All larvae used in the experiment had tails ≥ 20 mm long. Excess water was blotted from each tadpole, and mass was measured using an Acculab Pocket Pro Model #PP-250B Electronic Balance (Newton, Pennsylvania) and total length was measured using calipers. Four California red-legged frog larvae (Gosner stages 41-45, 7.2-12.4 g, 60.4-114.0 mm TL) were added to each artificial pond on 24 August 1998, after an acclimation period of approximately 20 minutes. Tadpoles were acclimated by placing them in 1 gallon resealable plastic bags, floating the bags in the artificial ponds, and gradually adding water from the ponds to the bags. The number of tadpoles added to each artificial pond resulted in a density that was within the range of densities observed in natural habitats (personal observation).

Bullfrogs were obtained as in Experiment I. Each bullfrog was fed one mouse on 19 August 1998, and then starved for six days to standardize hunger. A single adult bullfrog was added to each of five ponds on 25 August 1998. Allocation of the bullfrogs to individual ponds was random. Tanks were covered and water temperatures were measured as described in Experiment I.

Larval survivorship and microhabitat use (proportions of surviving tadpoles in the leaf pack, floating plant mat, and other areas) were recorded 24, 48, and 72 hours, and 16 days after the introduction of the bullfrogs. Tank covers were removed 1 hour prior to counting tadpoles. During this time, I sat motionless and

guarded for escaping bullfrogs, but was out of view of the animals in the ponds. The larvae could not jump out of the ponds, and 1 hour was sufficient for the larvae to readjust following the disturbance caused by removing the covers. To count surviving tadpoles, I placed a sieve (a 46 cm quilting hoop covered with 1 X 1 mm mesh aquarium netting) under the floating plant, gently lifted it out of the water, untied the string, and transferred the plant mat to a tub that contained clean water. Tadpoles were then shaken out of the plant mat and counted. The leaf pack was slowly tilted up, shaken, and removed. Tadpoles that were within or under the pack were counted as they fled. The cement block and bullfrog were removed, and then the ponds were dip netted repeatedly to remove all remaining tadpoles. The number of tadpoles that were seen fleeing the leaf pack was subtracted from the number collected by dip net to give the number of tadpoles in open areas of the tank. A direct visual count of tadpoles in the open areas could not be performed because glare on the water surface obstructed a clear view of the bottom. After a count was completed, the ponds were reassembled, and the bullfrogs and surviving tadpoles were placed back in the tanks from which they were taken. The tanks were covered until the next observation period.

The first null hypothesis was that bullfrogs would not affect the survivorship of large California red-legged frog larvae in artificial ponds (replicates were 5 ponds with and 5 ponds without bullfrogs). Larval survival in treatment and control ponds was analyzed using the arcsine square root transformed proportion of larvae surviving in each pond for each of the observation periods. The second null

hypothesis was that microhabitat use of large California red-legged frog larvae would be the same in ponds with and without bullfrogs. The proportions of surviving larvae in each microhabitat (leaf pack, floating plant mat, and open areas; dependent variables) were compared between ponds with and without bullfrogs (independent factor) using MANOVA (Zar 1996) on the data from the first observation period (24 hours after the introduction of the bullfrogs). Because univariate F tests showed that the proportions of tadpoles in the leaf pack microhabitat were similar in treatment and control ponds, leaf pack data were dropped from the final analysis to maintain independence of the remaining response variables. Untransformed data met the assumptions for normality and homoscedasticity (Lilliefors test and Levene's test, respectively) and analyses were performed using Systat 5.2.1 (Evanston, Illinois).

Experiment III: Larval Detection of Chemical Cues.

I tested whether large California red-legged frog larvae would respond to water borne chemical cues from two potential anuran predators (adult bullfrog and adult red-legged frog) by altering their activity levels or degree of refuge use. Adult California red-legged frogs are probably the only native anuran species in the California central coast large enough to be a potential predator of large California red-legged frog larvae. If larvae responded to the native predator but not the introduced predator (bullfrog), then it is possible that there has been inadequate time for selection to have resulted in red-legged frog tadpoles that perceive and respond

to bullfrog chemicals. Under similar experimental conditions, Kiesecker and Blaustein (1997) showed that northern red-legged frog larvae from populations that were sympatric with introduced bullfrogs altered their activity levels and degree of refuge use when exposed to chemical cues from adult bullfrogs, and red-legged frog larvae from populations without bullfrogs were similar to controls. For the first 4 larvae tested I added another treatment, chemical cues from 13 adult Pacific treefrogs (native non-predators of California red-legged frog larvae). This treatment was designed to determine whether larvae responded to chemical cues from anurans in general, or only responded to potential predators. Because these 4 trials suggested that there was no difference in larval response between any of the 3 treatments and the controls, I discontinued the treefrog treatment.

California red-legged frog larvae were collected using funnel traps (described in Studies 2 and 3) from a pond in the Santa Ynez River floodplain on VAFB (Pond 80, Appendix C-3). No bullfrogs were detected at the time of collection (late-July through mid-August 2001), but one adult bullfrog was found the following summer (4 August 2002). California red-legged frogs had become established at this pond some time after 1995 (personal observation). Each of the California red-legged frog localities nearest to this site also has bullfrogs (Christopher 1996). The lower Santa Ynez River (1.0 kilometer from the collection site) has probably supported California red-legged frogs and bullfrogs for several decades. Therefore, the larvae used in this experiment came from a population segment with a relatively long history of exposure to introduced bullfrogs. In

August 2001, I trapped 3 other ponds in the lower Santa Ynez River floodplain where California red-legged frogs and bullfrogs co-occur, but too few larvae were obtained, and by mid-August most larvae had metamorphosed. These factors limited the number of experimental animals.

Larvae were held 1 - 7 days in a plastic tub (102 X 54 X 40 cm, water depth 7 cm) before use in the experiment. Total length (including tail), wet mass (using an Acculab Pocket Pro Model #PP-250B Electronic Balance, Newton, Pennsylvania), and metamorphic (Gosner) stage were recorded for each tadpole. One adult bullfrog and one adult California red-legged frog were obtained from VAFB and held individually in aquaria. The bullfrog and the California red-legged frog were fed earthworms, and then were starved > 19 hours prior to the experimental trials to prevent contamination of the experimental water by fecal matter.

Larvae were tested in a gravitational flow-through system, modified from Petranka et al. (1987) and Kiesecker and Blaustein (1997), consisting of 3 plastic tubs at different heights. Water flowed from the uppermost reservoir through a tub that contained a predator, and then to a tub containing a California red-legged frog tadpole. Water flowed between the tubs via plastic aquarium tubing (4 mm inside diameter) at 0.55 L/minute. The uppermost tub (78 X 46 X 40 cm) contained approximately 40 L of untreated, aged well water. The middle tub (37.5 X 34 X 21.5 cm) was filled with 14 L (10 cm deep) of well water and received a caged predator (adult California red-legged frog, adult bullfrog, treefrogs, or nothing for control). The cage was a plastic bin (26.5 X 18 X 11 cm) with 12 X 8 mm openings

on three sides enclosed by a nylon mesh bag (mesh size 2 X 2 mm). The lowermost tub (37.5 X 34 X 21.5 cm) had a refuge constructed from an opaque plastic sheet (18.75 X 34 cm) placed horizontally on the output side of the tub and elevated 5 cm from the bottom. The water depth of the lowermost tub was maintained at 10 cm (total volume = 14 L) by drain holes in the far end of the tub. Tadpoles could swim above or below the refuge.

All trials were conducted outdoors between 1330 and 1900 hours on 31 July, and 3, 4, 5, and 25 August 2001. A total of 12 tadpoles was tested and individual tadpoles were tested once. A trial consisted of one California red-legged frog tadpole exposed to one of the predator treatments (bullfrog, adult California red-legged frog, treefrogs, control). I used a random numbers table to determine the sequence of predator treatments for each tadpole. Each tadpole was exposed to all 3 or 4 treatments before testing the next tadpole to minimize the effects of environmental variation (time of day, temperature, wind). The middle and lower tubs were thoroughly rinsed with well water following each predator treatment. The uppermost tub, which held enough water for the 3 trials per tadpole, was refilled after each tadpole was tested. The cage with a predator was placed in the middle tub for 30 - 60 minutes before flow was initiated to allow chemicals from the predator to condition the water.

Each tadpole was acclimated to the experimental tub's water temperature before each trial by floating it in a plastic bag, and then it was released to the non-refuge side of the lowermost tub. Water flowed through the system for 10 minutes

before recording data to allow the predator-conditioned water to concentrate in the lowermost tub and the larvae to adjust to experimental conditions (Petranka et al. 1987). To minimize disturbance, the observer stood behind a tinted window and used a mirror positioned above the lowermost tub that allowed all open areas in the tub to be observed. As a measure of activity level, I counted the number of times the tadpole crossed the centerline of the tub over 10 minutes. To measure refuge use, I scored whether the animal was concealed by the refuge at 30 second intervals, simultaneous to the collection of activity data. An animal was considered to be concealed if >50% of its body was under the refuge plate. The null hypotheses of no difference in tadpole activity level or refuge use among treatments was tested using a repeated measures analysis of variance (Zar 1996) on square-root transformed data, with individual tadpoles as subjects (Systat 5.2.1, Evanston, Illinois).

RESULTS

Study 1: Distribution Patterns

The proportion of sites with adult or juvenile California red-legged frogs was negatively associated with the presence of bullfrogs (Table 2.2; Fisher exact test $P = 0.01$). California red-legged frogs were recorded at 97% of the sites that lacked bullfrogs and 78% of the sites where bullfrogs were present. California red-legged frogs were common in the region studied, and were absent from only 6 of the 95

sites, and four of these had bullfrogs. California red-legged frogs co-occurred with bullfrogs more frequently in ponds (13) than in streams (1). Four of the 6 sites where California red-legged frogs were absent were in Ventura County (Appendix B), and were either historic localities of the California red-legged frog, or were within several kilometers of historic localities in the same drainage. Two of the Ventura County sites also had bullfrogs. The other two sites lacking red-legged frogs were ponds at VAFB that had bullfrogs. One was an abandoned wastewater pond, and the other was at the edge of an agricultural field and is cultivated during dry years. Bullfrogs were present at only 18 of the 95 (19%) sites.

At a pair of created ponds that were surveyed frequently between 1995 and 2001, California red-legged frogs colonized both sites and increased in numbers over time despite occupancy by bullfrogs, which were poor invaders of these sites (Christopher 2000; Appendix E). Bullfrogs colonized pond 48-05 shortly after the pond was created in 1995, but were eliminated when the pond dried that fall and never successfully re-established. This pond was colonized by California red-legged frogs in 1996, which remained present through the study and increased to > 40 adults. A second pond (48-04, in the same complex as 48-05) was colonized by California red-legged frogs in 1996, and they remained present through this study increasing to > 94 adults. Bullfrogs colonized Pond 48-04 in 1998, and remained in low numbers. In fact, bullfrogs appeared to decline over time at Pond 48-04, as > 8 were seen in 1999, 3 adults in 2000, 2 adults in 2001, and 1 adult in 2002. Bullfrog

metamorphs were not observed at these ponds, but California red-legged frog metamorphs were common annually (Appendix E).

Study 2: Reproduction in Ponds

The presence of bullfrogs was not correlated with differences in the numbers of California red-legged frog egg masses in ponds (Figure 2.3; Mann-Whitney U test, $P = 0.66$). Conversely, the number of California red-legged frog larvae trapped was significantly lower for sites with than without bullfrogs (Figure 2.4; Mann-Whitney U test, $P = 0.049$). No larvae were obtained from one bullfrog site (Pond 36). Drying of the bullfrog site Pond 30 concentrated the larvae and metamorphs in a smaller area, increasing their densities and probability of detection.

The densities of metamorphs found during surveys were lower at ponds with than without bullfrogs (Figure 2.5; Mann-Whitney U test, $P = 0.049$). No California red-legged frog metamorphs were found at one bullfrog site, Pond 36 (Appendix F). California red-legged frog metamorphs at Pond 91 may have been underrepresented by surveys because this bullfrog-free site still had tadpoles at the time surveys were conducted. Since the drying of Pond 30 and the late metamorphosis at Pond 91 both decreased the chance of finding an effect of bullfrog presence, the conclusion that the presence of bullfrogs was correlated with reduced red-legged frog reproduction remains robust.

Study 3: Microhabitat Use of Larvae in Ponds

The presence of bullfrogs did not affect the microhabitat use of California red-legged frog larvae in ponds (Table 2.3; $F_{4,1} = 10.23$, $P = 0.23$). Too few tadpoles were obtained from ponds with bullfrogs to draw conclusions about microhabitats favored by tadpoles at these sites. At sites without bullfrogs, most tadpoles were obtained from the benthic microhabitats (A, B, and D; Table 2.4). No bullfrog tadpoles were caught in the traps.

Study 4: Bullfrog Predation in the Field

California red-legged frogs were infrequent prey of bullfrogs collected in the field. Forty-seven adult bullfrogs were collected (snout-urostyle length range: 95 - 193 mm, mean: 144 mm; 33 females, 14 males) and three of these had empty stomachs. One bullfrog stomach contained a California red-legged frog, which was approximately 75 mm snout-urostyle length. This one California red-legged frog ranked second in volume of all prey types (Table 2.5). Crayfish (Order Decapoda) had the highest frequency, contributed the greatest volume of any prey type, and were found in 84% of the bullfrogs (Table 2.5). Fish ranked second in frequency among the prey types, third in volume, and third in the number of bullfrogs with that prey type (Table 2.5). The genera of fish consumed included *Gambusia*, *Gasterosteus*, *Lepomis*, and *Gila*. One bullfrog stomach contained a two-striped garter snake (*Thamnophis hammondi*), which is a California Department of Fish and Game Species of Special Concern.

Experiment I: Predation on Metamorphs

Bullfrogs reduced California red-legged frog metamorphs to 50% of their original numbers within 24 hours in artificial ponds (Table 2.6). One bullfrog did not eat any prey during the experiment, and data for this mesocosm were omitted. Bullfrog feeding rates on frogs and crayfish were slightly higher than for fish (Table 2.6). At the end of the 21 day experiment, there were 2 juvenile frogs, 0 crayfish, and 3 fish remaining of the 8 of each type added to the ponds at the start of the experiment. There were no non-predatory losses of prey. Water temperature varied from 5.5 - 28.5 °C during the experiment, and temperatures decreased slightly toward the end of the experiment (Table 2.6).

Experiment II: Predation on Larvae

Survivorship of California red-legged frog larvae was significantly lower in artificial ponds with than without bullfrogs after 24 hours (Table 2.7; One-tailed t -test, $P = 0.0478$). There was no mortality of control tadpoles over the duration of the experiment. Bullfrogs consumed 25% of the red-legged frog tadpoles within 24 hours and thereafter feeding rates were low. Each of the 5 bullfrogs had consumed at least 1 California red-legged frog tadpole after 72 hours. After 16 days, 0-1 tadpoles remained in each pond.

Microhabitat use by California red-legged frog larvae was significantly different between artificial ponds with and without bullfrogs at the first observation period (MANOVA, $F_{2,8} = 6.34$, $P = 0.02$). Significantly fewer tadpoles were found

in the floating plant microhabitat when bullfrogs were present (Table 2.8; Mann-Whitney U test, $P = 0.01$). Bullfrogs were frequently observed sitting on the floating plant, and rarely were seen resting on the cement block. The proportion of tadpoles in the leaf packs did not differ between ponds with and without bullfrogs (Mann-Whitney U test, $P = 0.12$).

Experiment III: Larval Detection of Chemical Cues

Large California red-legged frog tadpoles did not respond to chemical cues from potential anuran predators. Activity levels ($F = 1.5303$, $df = 2$, $P = 0.2386$) and refuge use of the tadpoles were not significantly different between the treatments ($F = 0.4632$, $df = 2$, $P = 0.6353$; Appendix G).

DISCUSSION

The role of predators in organizing communities has long been a key topic in ecology. Predators affect prey abundance and community structure through both direct and indirect pathways (Paine 1966, Connell 1975, Zaret 1980, Morin 1983, Sih et al. 1985, Thorp 1986). Identifying specific mechanisms that affect predator-prey interactions can indicate the factors responsible for community change. Since antipredator adaptations arise from strong selection pressures, antipredator behaviors may be lacking in species or populations when particular predators are absent (Grubb 1972, Woodward 1983, Kats et al. 1988, Ducey and Brodie 1991, Chivers

and Smith 1995, Gamradt and Kats 1996). Determining whether prey possess effective antipredator adaptations can be useful in predicting if prey will coexist with an introduced predator (Kats et al. 1988).

Distribution Patterns

California red-legged frogs were common in the area surveyed in Study 1, and were present at 89 of the 95 (94%) sites, whereas bullfrogs were present at only 18 (19%) of these sites. Similarly, surveys of historic California red-legged frog localities in California's Central Valley found that California red-legged frogs occurred at about 90 of 120 (75%) sites, and bullfrogs at 13 of 115 (11%) sites (Hayes and Jennings 1988). In contrast, Moyle (1973) detected California red-legged frogs at 0 and bullfrogs at 68 (52%) of 130 stream localities surveyed in the San Joaquin Valley. Fisher and Shaffer (1996) surveyed 315 ponds, marshlands, and vernal pools in the Central Valley and Central Coast Ranges, and detected California red-legged frogs at 4 (1%) and bullfrogs at 44 (14%) of the sites. Limitations of my study include non-random selection of sites, and non-independence due to linkage between some of the sites. Therefore, my results may not be interpreted as indicating a general pattern, but certainly California red-legged frogs were present at most sites with suitable habitat while bullfrogs were relatively less common in the area studied.

Although the occurrence of California red-legged frogs was significantly negatively associated with the presence of bullfrogs in Study 1, the presence of

bullfrogs is probably not a major factor regulating the distribution of adult and juvenile California red-legged frogs in the region studied since red-legged frogs were absent from only 4 (22%) of the bullfrog sites. Of these 4 sites, 1 had repeated human disturbance and 2 were isolated from other California red-legged frog populations. The 2 sites where both California red-legged frogs and bullfrogs were absent also were isolated from other California red-legged frog populations. These 4 isolated sites are located in Ventura County (Appendix B), which is the southern edge of the frog's current distribution (Jennings and Hayes 1994). Isolated populations are more vulnerable to extinction even in high quality habitats (Sjogren 1991). In contrast, bullfrogs have been suggested to be responsible for restricting the distribution of the California red-legged frog in other areas (Moyle 1973, Fisher and Shaffer 1996). In the Central Valley, bullfrogs were present at all ($N=10$) of the historic California red-legged frog sites where they have been extirpated (Hayes and Jennings 1988).

The distributional patterns of bullfrogs and native ranids in my study area may be similar to patterns found at more northerly latitudes. The presence of bullfrogs was not related to the relative abundance or presence of northern red-legged frogs in Washington (Adams 1999). Richter and Azous (1995) thought that bullfrogs were not responsible for decreasing anuran species richness in permanent wetlands in the Puget Sound Basin. Distribution patterns of the northern red-legged frog at 42 historical breeding sites in the Willamette Valley in Oregon were not

related to the presence of bullfrogs alone, but were related to habitat disturbance in combination with the presence of bullfrogs (Kiesecker et al. 2001).

An important difference between my study and others that examined California red-legged frog and bullfrog co-occurrence was that I excluded sites with introduced fish from my analysis but introduced fish probably were present at many of the sites in the other studies (Moyle 1973, Hayes and Jennings 1988, Fisher and Shaffer 1996). Introduced fish may negatively affect California red-legged frogs (Hayes and Jennings 1986; Chapter 3) and positively affect bullfrogs (Hambright et al. 1986, Werner and McPeck 1994, Adams et al. 2003). In fact, the occurrence of bullfrogs was positively associated with the presence of introduced fishes in the California central coast (Chapter 4).

The results of my study support the observation that California red-legged frogs remain common in the Coast Range of California (Fisher and Shaffer 1996, Davidson et al. 2001) where bullfrogs are rare compared to other areas in the state (Bury and Luckenbach 1976, Fisher and Shaffer 1996). In areas where California red-legged frog declines have been most severe, the Central Valley, foothills of the Sierra Nevada, and southern California (Davidson et al. 2001), bullfrogs tend to be relatively more common (Bury and Luckenbach 1976). Aquatic sites in these areas may be more suitable for bullfrogs due to higher summer water temperatures, increased anthropogenic disturbance, and increased water permanence as a result of agricultural and domestic water projects (see Moyle 1973, Hayes and Jennings 1988).

Effects of Environmental and Biotic Factors

The negative association between bullfrogs and California red-legged frogs in Study 1 could be due to subtle differences in habitat suitability for these species (see Hayes and Jennings 1986, 1988), with a greater proportion of sites surveyed that were suitable for California red-legged frogs than were suitable for bullfrogs. Most distances between bullfrog-free sites and bullfrog sites in this study were within the range of dispersal distances documented for bullfrogs in the eastern U. S. (Ingram and Raney 1943, Willis et al. 1956), suggesting that bullfrogs could have colonized many sites if environmental conditions were suitable. A high proportion of the sites surveyed were natural ponds and streams with minimal disturbance, and most of the sites were in areas that are managed as protected or semi-protected areas (such as VAFB, Los Padres National Forest, and other areas). Bullfrogs are often associated with man-made or disturbed habitats (Moyle 1973, Hammerson 1982, Hayes and Jennings 1986, Zampella and Bunnell 2000, Kiesecker et al. 2001, Batista 2002; but see Adams et al. 2003), and California red-legged frogs often inhabit sites with low levels of anthropogenic disturbance (Hayes and Jennings 1988).

Sixty-nine of the 77 (90%) sites where bullfrogs were absent were either within the coastal fog belt or were shaded streams at higher elevations, and low water temperatures may be unfavorable for bullfrogs (discussed in Chapter 4). In addition, dense emergent and shore vegetation that was present at most sites in this study can decrease encounter rates of predators and prey due to structural

complexity (Crowder and Cooper 1982, Gillinsky 1984, Axelsson et al. 1997), which may decrease predation effects of bullfrogs.

A large proportion of the ponds in my study area may dry in late summer or fall, especially in years with below-average rainfall. Bullfrogs are associated with permanent water because in most geographic regions their tadpoles must overwinter (Viparina and Just 1975, Cecil and Just 1977, Bury and Whelan 1984). In contrast, red-legged frog larvae usually complete metamorphosis by the fall after they hatch (Dickerson 1906, Storer 1925; but see Fellers et al. 2001). The seasonal drying of aquatic habitats can negatively affect bullfrog reproduction (Cook 1997), decrease bullfrog population sizes compared to those at permanent sites (Werner and McPeck 1994), and decrease introduced bullfrog effects on native frog populations (Rosen and Schwalbe 1995, Cook 1997).

Another possible explanation for the failure of bullfrogs to dominate the frog fauna in central coastal California in the absence of introduced fish is biotic resistance from native communities. Some authors have found that bullfrog tadpoles are competitively superior to native tadpoles because of the larger size of overwintered bullfrog tadpoles relative to hatchling native tadpoles (Kupferberg 1997, Kiesecker and Blaustein 2001). However, bullfrog eggs hatch in summer when California red-legged frog tadpoles are large. In addition, since bullfrog tadpoles select warm water (Brattstrom 1963, Lucas and Reynolds 1967, Crawshaw et al. 1992, Nie et al. 1999), bullfrog tadpoles may encounter the larvae of the Pacific treefrog (*Pseudacris regilla*) and western toad (*Bufo boreas*), which can

occur in high densities along warm pond margins and would typically be larger than bullfrog hatchlings. Because adult California red-legged frogs consume small frogs (Hayes and Tennant 1985), they also may prey on juvenile bullfrogs.

Bullfrog effects are probably directly related to bullfrog densities, due to a density effect on encounter rates, and bullfrog densities in the sites studied were low. In fact, adult California red-legged frogs often outnumbered bullfrogs when introduced fish were absent (Appendix E). For example, at Pond 48-04 only 8 adult bullfrogs were observed during any one survey, whereas more than 51 adult and juvenile California red-legged frogs have been found at this site. A 2001 survey of Pond 30 detected 9 adults and 1 juvenile California red-legged frogs and no bullfrogs (Appendix E). At Pond 39 only 1 adult bullfrog had been seen prior to the establishment of introduced fish, and during this time period the maximum number of California red-legged frogs seen was about 75 (see detailed account in Chapter 4). Bullfrogs outnumbered California red-legged frogs only at one fishless site and this site was frequently disturbed by human activities. This site had a high count for bullfrogs of 21 adults/juveniles and 24 metamorphs, while only 2 adult and 17 metamorph California red-legged frogs were seen (Appendix E). Pond 36 also had the greatest reduction in California red-legged frog larvae and metamorphs in Study 2. In an 11 ha Sonoma County, California marsh that lacked introduced fish the population size estimate for bullfrogs was 27 - 39 adults and California red-legged frogs was 127-179 adults (Cook 1997).

When introduced fish and crayfish are present, bullfrog densities on the central coast are within the range found for other areas of California. Bullfrog densities in the lower Santa Ynez River at VAFB on 24 July 2001 were 7.5/km for bullfrogs > 100 mm snout vent length, and 25.7/km for bullfrogs < 100 mm snout vent length (unpublished data). Clarkson and DeVos (1986) reported bullfrog densities (>100 mm snout-vent length) in the lower Colorado River as 9.1/km. In the Central Valley of California, unmanipulated bullfrog densities in canals ranged from 16.3 to 87.3/km for bullfrogs > 100 mm snout vent length and 0.4 to 25.5/km for bullfrogs < 100 mm snout vent length (Treanor 1975). Therefore, bullfrogs may have greater effects on California red-legged frog populations when introduced fish are present because fish may indirectly facilitate bullfrog populations (Werner and McPeck 1994, Adams et al. 2003) thereby increasing bullfrog densities.

Bullfrog Predation

An adult California red-legged frog was consumed by a bullfrog under field conditions (Study 4) and bullfrogs consumed California red-legged frog metamorphs (Experiment I) and large tadpoles (Experiment II) in artificial ponds. Although predation rates estimated from mesocosm studies cannot be extrapolated to the field, bullfrog feeding rates were lower in artificial ponds than I expected based on bullfrog voracity implied in the literature. Low temperatures in the covered tanks may have reduced bullfrog predation rates.

The mesocosm design used in Experiment II may have decreased the rate of bullfrog predation on tadpoles because ponds lacked shallow water. Since most California red-legged frog larvae are associated with benthic microhabitats (Study 3), bullfrog predation on tadpoles occupying the tank bottoms would have been unlikely due to water depth. Bullfrogs may have only captured tadpoles when they swam to the surface or were within the floating plant. Therefore, artificial conditions in Experiment II should have decreased the chance of finding a bullfrog effect.

Bullfrog predation rates on frogs and tadpoles in nature probably vary with several factors, including habitat structural complexity, the potential for microhabitat separation, temperature, and the availability of alternative prey. Of 47 adult bullfrogs collected from the field, all apparently having ample access to California red-legged frogs as potential prey, only 1 had consumed a California red-legged frog (Study 4). Introduced bullfrogs have been found to consume California red-legged frog tadpoles, metamorphs (Cook and Jennings 2001) and adults (Cook 2002) in other field studies, but it appears that feeding rates are low even when all lifestages of California red-legged frogs were abundant. Of 156 bullfrogs collected from a 0.3 ha pond over 1.5 years, only 2 had California red-legged frogs (metamorphs) in their stomachs (Cook and Jennings 2001). Doubledee's (1999) model of bullfrog predation effects on California red-legged frogs predicted that individual bullfrog consumption rates of 2 juvenile red-legged frogs each day would be sufficient for an adult bullfrog population of 20 individuals to completely

eliminate the annual recruitment of a California red-legged frog population of 50 individuals, resulting in the extinction of the red-legged frog population within 9 years. Further study of bullfrog predation rates on California red-legged frogs in the field is needed to determine population effects on red-legged frogs.

Reproduction in Ponds

California red-legged frog tadpole and metamorph abundances were reduced in ponds with bullfrogs compared to ponds without bullfrogs even though the numbers of egg masses observed were not different (Study 2). While the results of Study 4 and Experiments I & II suggest these reductions may be due to bullfrog predation, I cannot rule out that differences in physical or structural attributes of the pond habitats may also have had an effect (see Appendix D). I failed to detect any California red-legged frog tadpoles or metamorphs at Pond 36 even though 5 California red-legged frog egg masses were observed at this pond. Pond 36 had the highest degree of habitat disturbance as it was periodically excavated for the removal of clay substrate (personal observation). Emergent vegetation, which appears to be a preferred microhabitat of California red-legged frog larvae (Study 3), was absent in this pond. The presence of emergent vegetation may be important for California red-legged frog tadpoles if they feed on algae that is attached to the emergent vegetation, or if they use the vegetation as refugia from predators. Water clarity in this pond was poor due to mud suspended in the water column, and this may have decreased light penetration and algal growth. Pond 36 was adjacent to

abandoned wastewater treatment ponds, and contamination from toxic materials was possible.

The bullfrog site Pond 30 had the highest number of egg masses detected of all 6 ponds in Study 2, but the second lowest number of tadpoles and density of metamorphs. Even though California red-legged frog tadpoles appeared to have increased rates of development at this site, with metamorphs appearing earlier than at the other sites, pond drying could have decreased survivorship if not all tadpoles could reach metamorphosis before the pond dried up. In addition, pond drying may have increased encounters of tadpoles and metamorphs with predators (bullfrogs, birds, raccoons, invertebrates), and may have increased intraspecific competition.

At the other end of the spectrum was a relatively small bullfrog-free site (Pond 79) that had more than 282 California red-legged frog metamorphs in 1997 (Study 2), and relatively high numbers of metamorphs in each year that it did not dry (Appendix E). About 1/3 of this pond was a shallow marsh with moderate densities of cattails, and at least another 1/3 of the pond was covered with dense mats of marsh pennywort. Metamorphs were found at greater densities in the shallow marsh and marsh pennywort microhabitats compared to areas with open water and shores with steep slopes (personal observation). The high availability of these favorable microhabitats may be responsible for the high densities of metamorphs detected at this site. These microhabitats were absent from the bullfrog sites (Appendix D).

One of the bullfrog-free sites (Pond 91) differed from the other sites because it lacked shallow areas along the margin. This site had low densities of California red-legged frog metamorphs in 1997, even though the number of tadpoles trapped in this pond was moderate. Warm water present in shallow areas may increase rates of tadpole development (Duellman and Trueb 1986), and the presence of these microhabitats may influence food resources.

The reliability of sampling in Study 2 can be evaluated by a Spearman rank correlation of the rank order for all 6 ponds (Zar 1996). The number of larvae trapped in ponds was highly correlated with the density of observed metamorphs (Spearman's $r_s = 0.94$). Adams (1999) also found a significant correlation between trap data for tadpoles and visual surveys for recently metamorphosed northern red-legged frogs.

Additional visual encounter surveys conducted from 1995 - 2002 at these sites also indicated California red-legged frogs (especially metamorphs) tended to be reduced at ponds with bullfrogs (Appendix E). At the bullfrog site Pond 36, the largest number of adult and juvenile California red-legged frogs found during any one survey was 3, and only 1 or 2 adult frogs were observed during surveys conducted between 1997 and 2002. The low numbers of adults at this pond could reflect the poor recruitment found in Study 2. Although no California red-legged frog metamorphs were detected at Pond 36 in Study 2, 17 metamorphs were observed in 2002 while adult bullfrogs remained present (Appendix E). These metamorphs were all found hiding in deep cracks in the mud along the shore

(personal observation), and these cracks probably were effective refugia from bullfrogs. The maximum count of adult and juvenile California red-legged frogs within a year at the bullfrog site Pond 30 was 4 (in 1995) and 10 (in 2001) (Appendix E). Metamorphs (maximum count 9 and 1 tadpole) were detected only in 1997 at Pond 30, but this pond was surveyed less frequently than the other sites because it often dries in summer/fall when metamorph surveys were conducted. California red-legged frog abundance at the bullfrog site Pond 39 was probably affected by the 2002 introduction of predatory fish (Chapter 4), but prior to the establishment of fish there were up to 75 adult and juvenile California red-legged frogs while metamorphs remained quite rare (1 to 6 seen during metamorph surveys). In comparison, at the bullfrog-free site Pond 79 the annual maximum count for adult and juvenile California red-legged frogs ranged between 4 and 31, and metamorph counts were 282, 23, and 16 (Appendix E). Similarly, the bullfrog-free site Pond 77 had between 4 to 30 adults and juveniles, and 112, 19, and 165 metamorphs (Appendix E). At the bullfrog-free site Pond 91, the annual maximum count of adult and juvenile California red-legged frogs ranged between 17 and 64, while counts for metamorphs were 15, 14, and 169 (Appendix E).

An unexpected result of Studies 2 and 3 was that no bullfrog tadpoles were captured in traps. This could be due to several factors: 1) bullfrog larvae may not be readily caught in funnel traps, 2) bullfrog larvae may inhabit the middle of the ponds, 3) the previous year's larvae may have already metamorphosed and the present year's larvae may have been small enough to pass through the trap mesh,

4) the present year's larvae may have metamorphosed prior to trapping, and 5) bullfrog reproduction may have been nonexistent or low. In the latter case, sampling effort may not have been adequate to detect the presence of bullfrog larvae. Using the same type of funnel traps, Adams et al. (1998) reported capturing bullfrog tadpoles, whereas Adams et al. (1999) failed to detect bullfrog tadpoles using this method. A survey of Pond 36 on 10 September 1997 revealed bullfrog tadpoles undergoing metamorphosis (personal observation). Although these individuals were small (35-40 mm snout-urostyle length), they were most likely present as tadpoles when this pond was trapped (5 July, 20 July, & 4 August 1997), and possibly originated from eggs laid in the spring of that year (see Chapter 4).

Reduced densities of California red-legged frog tadpoles and metamorphs at ponds with bullfrogs, whether the result of direct or indirect effects of bullfrogs on red-legged frogs or due to differences in environmental conditions between ponds, may indicate that these sites are population "sinks" (Pulliam 1988, Dias 1996). Adjacent sites lacking bullfrogs and other introduced aquatic predators may be the main sources of California red-legged frog recruitment, and metamorphosed frogs immigrate to sites that have bullfrogs (see Appendices C & E). This would result in a landscape pattern with a limited proportion of sites where bullfrogs and red-legged frogs co-occur, as seen in Study 1. High connectivity among California red-legged frog subpopulations may be important for maintaining coexistence of California red-legged frogs and bullfrogs (see Chapter 4).

Bullfrog Prey Preference

Bullfrogs showed a slight preference for metamorphosed California red-legged frogs and crayfish over fish (Experiment I). Bullfrogs collected from a river habitat had consumed crayfish and fish with the highest frequency, and crayfish were the most important prey type in adult bullfrog diets (Study 4). Other studies of bullfrog diet in the field revealed that crayfish (Penn 1950, Bush 1959, Korschgen and Baskett 1963, McKamie and Heidt 1974, Corse and Metter 1980, Clarkson and DeVos 1986, Platt and Fontenot 1993) and fish (Cross and Gerstenberger 2002) dominated prey volumes. Some authors have suggested that bullfrogs preferentially feed on crayfish (Korschgen and Baskett 1963), and bullfrogs may move into areas with high densities of crayfish in order to exploit this prey resource (Corse and Metter 1980). Bullfrogs actively pursue juvenile frogs by responding to distress calls given by the juvenile frogs (Smith 1977; see also Stuart and Sandison 1972). Analyses of the stomach contents of bullfrogs caught in the wild have shown that juvenile frogs can comprise more than 80% of the volume of prey items (Smith 1977, Stuart and Painter 1993, Werner et al. 1995), and can be the type of prey most frequently consumed (Stewart and Sandison 1972). Variation in the seasonal availability of frogs probably influences the rate in which they are consumed by bullfrogs (Korschgen and Baskett 1963). Because California red-legged frogs were abundant at the collection site in Study 4, and only 1 of 47 adult bullfrogs had consumed a red-legged frog, predation rates on frogs in the field may be quite low when other prey are available. The presence of crayfish and small fish may

indirectly facilitate the survival of red-legged frogs when bullfrogs are present by acting as alternative prey, or bullfrog densities may increase when crayfish and fish are available due to providing an abundant food source (see Chapter 4).

Antipredator Adaptations

California red-legged frogs do not appear to possess defenses that decrease predation by bullfrogs. Although microhabitat use by California red-legged frog larvae in artificial ponds was affected by the presence of bullfrogs (Experiment II), this result could be due to factors other than red-legged frog antipredator responses. Since bullfrogs often occupied the microhabitat preferred by red-legged frog tadpoles in artificial ponds (floating plant mat), physical disturbance caused by the bullfrogs may have caused the tadpoles to flee. If tadpoles increased refuge use in response to free-ranging bullfrogs, the proportion of tadpoles in the leaf pack microhabitat should have been significantly greater in ponds with than without bullfrogs. Tadpoles did not alter activity levels or their degree of refuge use in response to chemical cues from bullfrogs (Experiment III), and microhabitat use by California red-legged frog larvae in natural ponds was not affected by the presence of bullfrogs (Study 3). However, the analysis of pond-scale microhabitat use would have been improved if more tadpoles were obtained from ponds with bullfrogs. Differences in microhabitat use between metamorph California red-legged frogs and bullfrogs at the river site in Study 4 could have decreased the proportion of metamorphs in bullfrog diet, and would explain the absence of metamorphs in the

47 bullfrog stomachs examined. At this site, all of the adult bullfrogs were found within 1 m of the isolated stream pools, whereas most California red-legged frog metamorphs were seen moving around in the dry riverbed >1 m away from the pools (personal observation). The tendency for California red-legged frog metamorphs to move into terrestrial habitats following metamorphosis (Chapter 4) may be an adaptation that decreases predation rates by adult red-legged frogs.

The results of this study are not in agreement with those reported by Kiesecker and Blaustein (1997, 1998) for the northern red-legged frog. Northern red-legged frog larvae altered microhabitat use when introduced bullfrogs were present in experimental enclosures (Kiesecker and Blaustein 1998), and red-legged frog tadpoles from populations with bullfrogs had higher survivorship in enclosures than tadpoles from populations lacking bullfrogs, suggesting the effectiveness of these behaviors (Kiesecker and Blaustein 1997). Using a gravitational flow-through system similar to that in Experiment III, Kiesecker and Blaustein (1997) found that northern red-legged frog tadpoles from populations sympatric with bullfrogs reduced their activity and increased their refuge use when exposed to chemical cues from bullfrog tadpoles and adults, whereas tadpoles from sites lacking bullfrogs did not differ from controls. Northern red-legged frog tadpoles from sites without bullfrogs, however, responded to chemical cues from native predators (Wilson and Lefcort 1993, Kiesecker and Blaustein 1997). In contrast, California red-legged frog tadpoles in Experiment III did not respond to chemical cues from a bullfrog or a native anuran predator.

Any of the following could be responsible for the failure to detect a significant response in Experiment III: 1) chemically-mediated predator avoidance is not exhibited by California red-legged larvae or is not exhibited in response to the particular types of predators in this study, 2) individual predators can differ in the amount and type of chemicals produced, and this study would have been improved by increasing the number of individual predators tested (more individuals of each predator type were not available at the time of the study), 3) California red-legged frog tadpoles respond to chemical cues other than by decreasing activity and/or increasing refuge use, and 4) the tadpoles didn't recognize the experimental refuge as an appropriate refuge. In addition, some anuran larvae only respond to aquatic predators when those predators have recently consumed conspecific prey (Wilson and Lefcort 1993, Laurila et al. 1998). Both the bullfrogs used in Experiment III and those used by Kiesecker and Blaustein (1997) were fed earthworms prior to use in experiments. Because bullfrogs were not present at the site where tadpoles were collected for Experiment III, it is possible that antipredator defenses were not present in the population from which the tadpoles were collected. However, this would not account for the lack of response to a native anuran predator. Responses of larvae in Experiment III were similar to those reported for the streamside salamander, *Ambystoma barbouri*, in which activity levels for individual larvae were correlated across treatments (Sih 1992, Sih et al. 2000). In Experiment III, some individuals showed higher activity than others across all treatments (Appendix G).

The tendency of prey to respond to chemical cues of aquatic predators varies within and among species, and has been correlated with the frequency of encounters with those predators (Kats et al. 1988). Antipredator responses may have both a learned (Klopfer 1957, Curio et al. 1978, Conover 1987, Maloney and McLean 1995) and genetic (Kats et al. 1988, Ducey and Brodie 1991, Sih and Kats 1994, Kiesecker and Blaustein 1997) basis. Some prey can learn to recognize and respond to chemical cues from novel predators after field experience with those predators (Chivers and Smith 1995). In the absence of evolutionary constraints, natural selection should result in the evolution of antipredator behaviors for prey that frequently encounter predators; however, conflicting selection pressures may be responsible for a species' inability to respond to current predation pressures (see Sih et al. 2000). Because the costs of refuge use and decreased activity include decreases in feeding, growth, and developmental rates (Werner et al. 1983, Holomuzki 1986, Sih 1987, Skelly 1992), these antipredator behaviors can result in decreased reproductive rates (Berven and Gill 1983, Sih 1987, Smith 1987). If the costs of antipredator behaviors are too high, responses that would otherwise increase survival rates may not become predominant in a population (Sih et al. 2000). Finally, the time required for populations or species to develop antipredator behaviors in response to introduced predators has been little studied. The strength of selection for antipredator behaviors and the effectiveness of the behaviors also probably influence the speed at which these behaviors become generalized.

In summary, this study demonstrated that adult bullfrogs consume small adult California red-legged frogs in the field, and tadpoles and metamorphs in experimental situations. Antipredator behaviors of California red-legged frog larvae to introduced bullfrogs were found in only 1 of 3 studies, and could have been due to the experimental conditions. Recruitment of California red-legged frogs was dramatically reduced at ponds with bullfrogs in comparison to ponds without bullfrogs. However, on a landscape scale bullfrogs alone were probably not responsible for restricting the distribution of California red-legged frogs in the California central coast. The degree to which predation by introduced bullfrogs reduces California red-legged frog population sizes or recruitment probably varies with several factors, including environmental conditions and interactions with other native and introduced species.

CONCLUSIONS

1. This study demonstrated a negative association between California red-legged frog presence and bullfrog presence across 95 sites in central coastal California. California red-legged frogs were present at 94% and bullfrogs at 19% of the sites.
2. The abundances of California red-legged frog larvae and metamorphs were significantly reduced at ponds with bullfrogs, even though the numbers of egg masses observed were not significantly different.

3. Bullfrogs consumed large California red-legged frog larvae and recently metamorphosed frogs in artificial ponds. An adult bullfrog consumed a small adult California red-legged frog at a river site, but frogs were not important in bullfrog diet at this site. Bullfrogs preyed on slightly more California red-legged frog metamorphs and crayfish than fish in a simplified experimental arena.
4. California red-legged frog larvae did not appear to display antipredator behaviors to introduced bullfrogs. California red-legged frog metamorphs may often select microhabitats different from those used by bullfrogs.
5. In the central coast of California, predation by bullfrogs alone does not appear to be responsible for occupancy patterns of California red-legged frogs. However, reduced densities of California red-legged frog tadpoles and metamorphs at bullfrog ponds suggest that these sites are population sinks. Immigration from predator-free sites may be responsible for maintaining coexistence of California red-legged frogs with bullfrogs at many sites.

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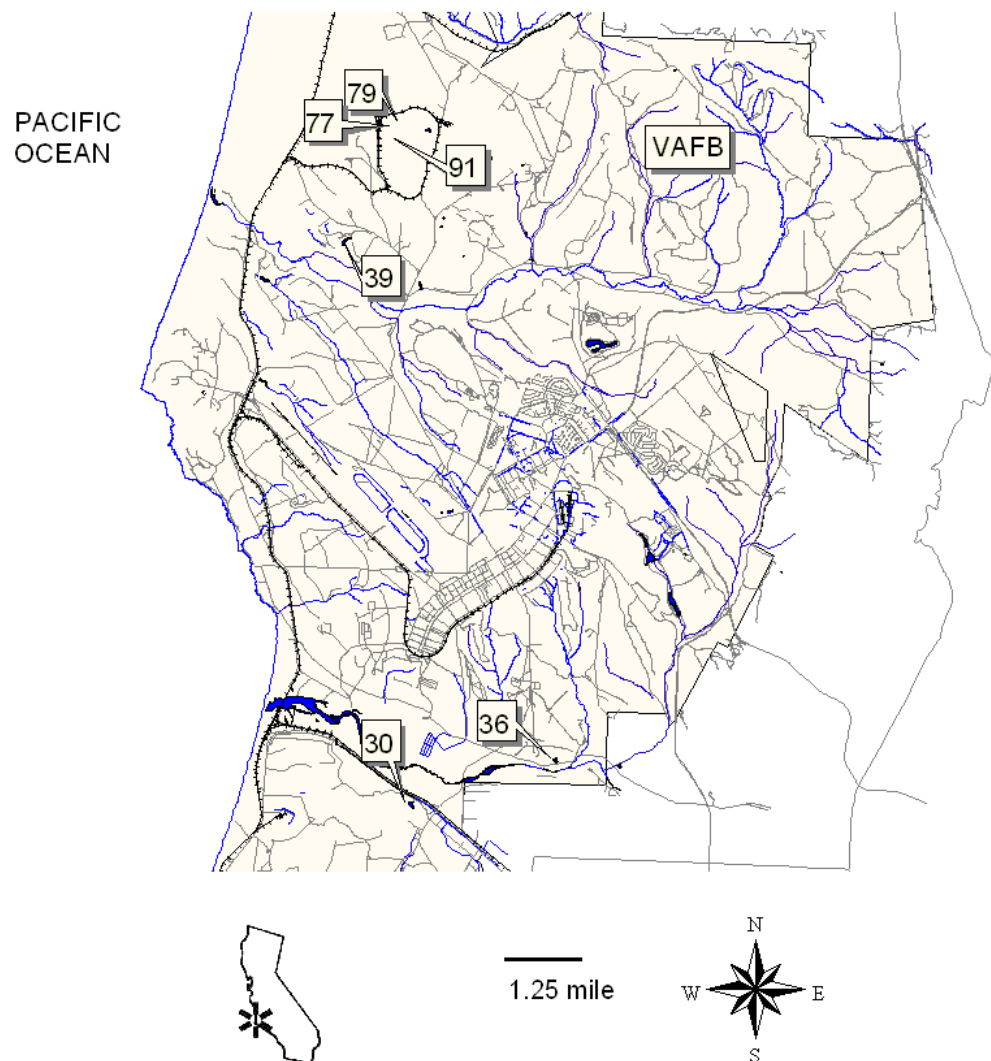


Figure 2.1. Location of sites sampled for California red-legged frog eggs, tadpoles and metamorphs in Studies 2 and 3 on Vandenberg Air Force Base, California.



Figure 2.2. Cross-section of pond shoreline showing one example transect for sampling tadpoles using funnel traps (dark ovals) in different microhabitats (letters) used in Studies 2 and 3. Traps at microhabitats A, B, and D were placed on the bottom of the pond. The trap at microhabitat C was suspended from the emergent vegetation, except for Pond 36 where emergent vegetation was absent and the trap was suspended just below the surface of the water from a post 0.5 m from shore. A post (vertical lines) was used to mark the transect and suspend a trap just below the water surface at microhabitat E.

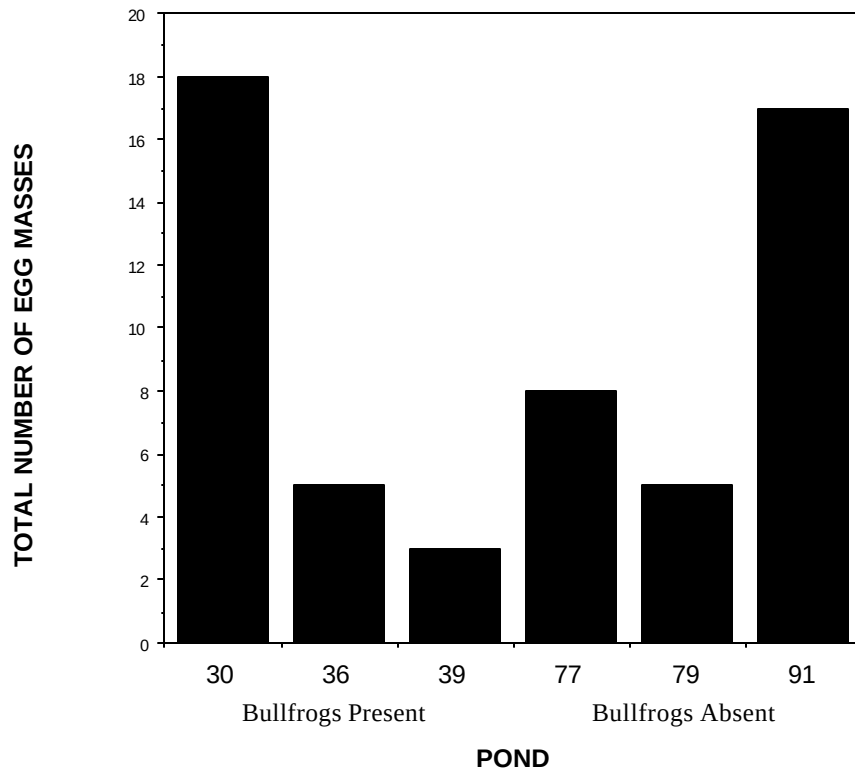


Figure 2.3. Total numbers of California red-legged frog egg masses observed during visual encounter surveys in Study 2. Each pond was surveyed in its entirety twice during the peak breeding season. The number of egg masses in ponds with bullfrogs was not significantly different from ponds without bullfrogs (Mann-Whitney U test, $P = 0.66$).

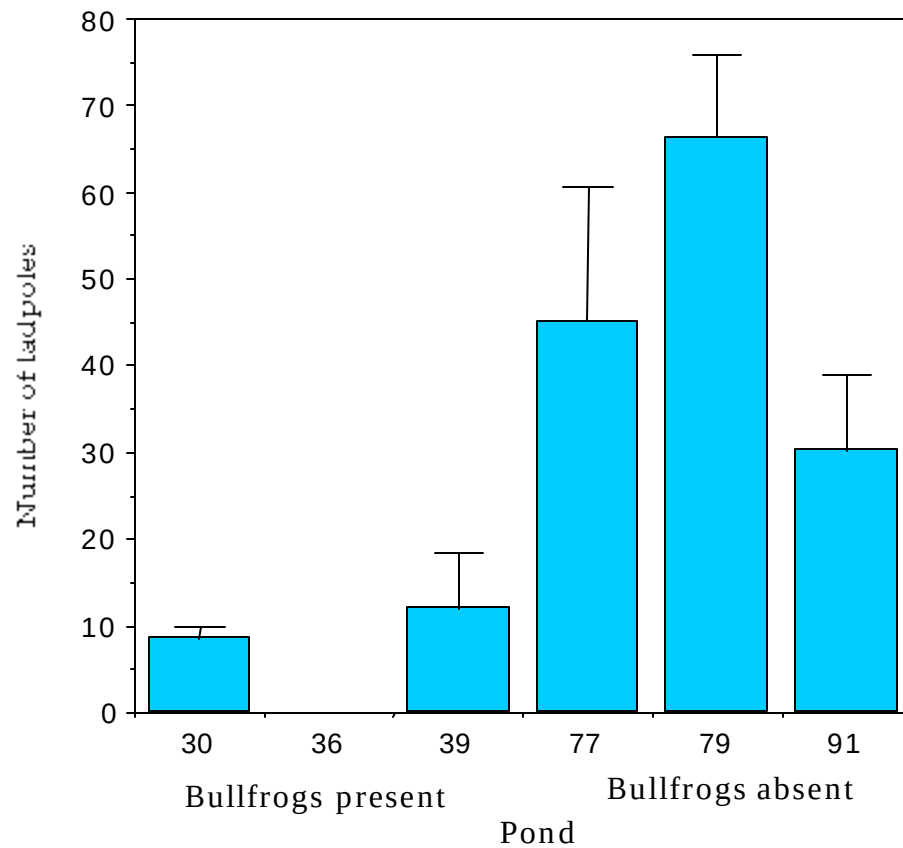


Figure 2.4. Numbers of California red-legged frog tadpoles trapped in ponds (mean $\pm$ 1 SE) in Study 2. Each pond was sampled 3 times (except Pond 30 which was sampled only twice because it dried up) when tadpoles were at late larval stages. Recently metamorphosed frogs were also counted for Pond 30 because pond drying accelerated larval development. Tadpole abundance in ponds with and without bullfrogs was significantly different (Mann-Whitney U test, $P = 0.049$).

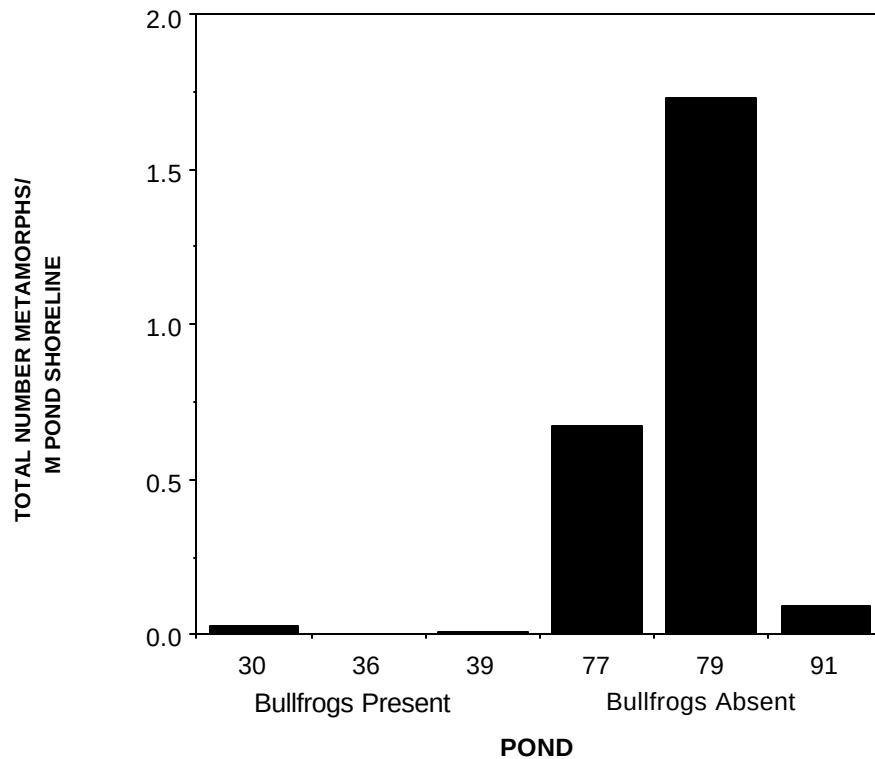


Figure 2.5. Densities of California red-legged frog metamorphs observed during visual encounter surveys in Study 2. Each pond was surveyed in its entirety 3 times during the peak of metamorph activity, except Pond 91 that still had some untransformed tadpoles at the end of the study. Pond 30 dried up earlier than the other ponds, which increased the chance of detecting metamorphs relative to the other ponds. Densities are the cumulative number of metamorphs seen at each site across the surveys divided by pond shoreline (m). Metamorph density at ponds with and without bullfrogs was significantly different (Mann-Whitney U test, $P = 0.049$).

Table 2.1. Study design for Chapter 2: Interactions of introduced bullfrogs (BF) and California red-legged frogs (RLF).

Name	Type of Study	Question	Scale
Study 1: Distribution Patterns	Correlational	Is the presence of BF correlated with the presence of RLF?	Landscape
Study 2: RLF Reproduction in Ponds	Field	Is the presence of BF correlated with decreased abundance of RLF eggs, tadpoles, and metamorphs?	Pond
Study 3: Microhabitat Use of Larvae in Ponds	Field	Does the presence of BF affect microhabitat use of RLF larvae?	Pond
Study 4: Bullfrog Predation in the Field	Field	Do BF eat RLF in nature when alternate prey are available? What life stages of RLF are eaten?	Stream Reach
Experiment I: Predation on Metamorphs	Controlled Experiment	Will BF eat RLF metamorphs when alternative prey are available, and prey have no refugia?	Mesocosm
Experiment II: Predation on Larvae	Controlled Experiment	Will BF eat RLF larvae? Do RLF larvae effectively use refugia to escape predation from BF?	Mesocosm
Experiment III: Larval Detection of Chemical Cues	Controlled Experiment	Do RLF respond to chemical cues of BF by altering activity levels and refuge use?	Microcosm

Table 2.2. Occurrence of the California red-legged frog and bullfrog at sites with suitable habitat for both species in coastal central California in Study 1. Sites with introduced fish species, and sites in which the absence of introduced fish was not confirmed, were excluded. Numbers are total sites per category (ponds, stream reaches). A significant association between California red-legged frogs and bullfrogs was tested using a Fisher exact test (df=1, a=0.5).

	Bullfrogs present	Bullfrogs absent	<i>P</i>
Red-legged frogs present	14 (13, 1)	75 (48, 27)	0.01
Red-legged frogs absent	4 (2, 2)	2 (0, 2)	

Table 2.3. MANOVA results for effects of the presence of bullfrogs on microhabitat use of California red-legged frog tadpoles in Study 3. Microhabitats (A, C, D, E) are described in Figure 2.2, and data are in Table 2.4.

Source	df	MS	<i>F</i>	<i>P</i>
A	1	0.11	0.45	0.54
Error	4	0.24		
C	1	0.79	0.62	0.47
Error	4	0.13		
D	1	0.24	0.11	0.76
Error	4	0.23		
E	1	0.19	0.14	0.72
Error	4	0.15		

Table 2.4. Numbers of California red-legged frog tadpoles trapped in five microhabitats at ponds with and without bullfrogs in Studies 2 and 3. Numbers are means of 3 trapping sessions (except for Pond 30 which was trapped only twice because it dried up), with mean proportion in each microhabitat for each pond in parentheses. Total is the number of tadpoles trapped from all microhabitats averaged across trapping sessions. Microhabitats are depicted in Figure 2.2.

Micro-habitat	Bullfrog status					
	Ponds With Bullfrogs			Ponds Without Bullfrogs		
	30	36	39	77	79	91
A	1.0 (0.12)	0	2.0 (0.16)	18.7 (0.34)	10.0 (0.12)	9.3 (0.30)
B	2.0 (0.26)	0	5.0 (0.50)	27.3 (0.46)	31.0 (0.31)	9.7 (0.34)
C	1.0 (0.10)	0	1.0 (0.04)	6.7 (0.10)	13.3 (0.14)	7.7 (0.20)
D	1.5 (0.17)	0	3.0 (0.22)	5.7 (0.10)	33.7 (0.36)	2.3 (0.10)
E	3.0 (0.34)	0	1.0 (0.08)	0.3 (0.01)	6.0 (0.07)	1.3 (0.06)
TOTAL	8.5	0	12.0	45.3	66.3	30.3

Table 2.5. Stomach contents of bullfrogs ($n=44$) from Study 4. Bullfrogs were collected in the late summers of 1996 and 1997 from the Santa Ynez River between Gibraltar Reservoir and the confluence of Mono Creek, Santa Barbara County, California. Number of prey items is the total number of individuals of each prey type for all bullfrogs (% of total prey items). Plants, rocks, and sand were not included in the calculation number of prey items. Volume is the total volume of each prey type for all bullfrogs (% of total volume). Number of bullfrogs is the number of bullfrog stomachs that contained each prey item (% of total bullfrogs).

Prey group	No. of Prey Items (%)	Volume ¹ (%)	No. of Bullfrogs (%)
Plant		8.7 (1.6)	16 (36.4)
Rock		2.5 (0.5)	8 (18.2)
Sand		1.3 (0.2)	4 (9.1)
Anura	1 (1.1)	49.0 (9.0)	1 (2.3)
Squamata	1 (1.1)	4.0 (0.7)	1 (2.3)
Fish	20 (21.7)	30.8 (5.7)	11 (25.0)
Decapoda	34 (37.0)	433.3 (79.9)	37 (84.1)
Gastropoda	2 (2.2)	0.4 (0.1)	1 (2.3)
Isopoda	8 (8.7)	0.7 (0.1)	3 (6.8)
Araneida	9 (9.8)	2.8 (0.5)	7 (15.9)
Coleoptera	9 (9.8)	4.0 (0.7)	6 (13.6)
Trichoptera	1 (1.1)	0.1 (<0.1)	1 (2.3)
Lepidoptera	4 (4.3)	3.1 (0.6)	3 (6.8)
Diptera (adult)	1 (1.1)	0.1 (<0.1)	1 (2.3)
Diptera (larvae)	1 (1.1)	1.2 (0.2)	1 (2.3)
Unidentified	1 (1.1)	0.2 (<0.1)	1 (2.3)

¹in ml.

Table 2.6. Numbers of prey surviving over time in artificial ponds with bullfrogs (*Rana catesbeiana*) in Experiment I. Prey are recently metamorphosed California red-legged frogs (*R. aurora draytonii*), crayfish (*Procambarus* sp.), and goldfish (*Carassius auratus*). One bullfrog did not eat any prey during the experiment and data from this mesocosm were omitted. Data are from 4 artificial ponds, and each received one adult bullfrog and two individuals of each prey species. Numbers are total surviving (percent of original number) across all tanks. Water temperature (in °C) is given as temperature at 1300 hours (Temp), and maximum and minimum values recorded since the previous survivorship count.

	Days from start						
	0.2	1	2	3	4	5	6
Frog	5 (63)	4 (50)	3 (38)	3 (38)	3 (38)	3 (38)	3 (38)
Crayfish	6 (75)	6 (75)	4 (50)	3 (38)	2 (25)	2 (25)	2 (25)
Fish	8 (100)	7 (88)	6 (75)	5 (63)	5 (63)	4 (50)	4 (50)
Temp	NA	23.0	25.0	28.5	28.5	28.0	26.0
Max	NA	27.5	25.0	28.5	28.5	28.0	28.0
Min	NA	9.5	10.0	10.0	11.0	9.5	10.0

Table 2.6. Extended.

	Days from start						
	7	8	10	12	14	17	21
Frog	3 (38)	2 (25)	2 (25)	2 (25)	2 (25)	2 (25)	2 (25)
Crayfish	2 (25)	2 (25)	1 (13)	1 (13)	1 (13)	1 (13)	1 (13)
Fish	4 (50)	4 (50)	4 (50)	4 (50)	3 (38)	3 (38)	3 (38)
Temp	24.0	23.5	22.5	22.5	19.5	25.0	22.5
Max	26.0	25.0	26.5	25.0	20.0	25.0	26.0
Min	10.0	10.5	7.0	10.0	6.0	5.5	7.0

Table 2.7. Numbers of California red-legged frog larvae surviving in artificial ponds with ($N=5$) and without ($N=5$) bullfrogs over successive observation periods in Experiment II. Survivorship between ponds with and without bullfrogs was significantly different ($P < 0.05$) at all observation periods.

Time	Bullfrog	Mean	% of original	Range per pond
24 h	Present	3.0	75	2 - 4
	Absent	4.0	100	4
48 h	Present	3.0	75	2 - 4
	Absent	4.0	100	4
72 h	Present	2.6	65	2 - 3
	Absent	4.0	100	4
16 d	Present	0.2	5	0 - 1
	Absent	4.0	100	4

Table 2.8. Total numbers (mean proportion) of surviving California red-legged frog larvae in each microhabitat type in artificial ponds with and without bullfrogs in Experiment II. Data are from the first observation period (24 hours after the introduction of the bullfrog). The effect of bullfrogs on the distribution of tadpoles among microhabitats was significant (MANOVA, $P = 0.02$).

Bullfrog	Microhabitat		
	Floating Plant	Leaf Pack	Open areas
Absent	18 (0.90)	1 (0.05)	1 (0.05)
Present	5 (0.28)	5 (0.40)	5 (0.32)

CHAPTER 3

**INTERACTIONS OF INTRODUCED FISHES AND AN INTRODUCED
CRAYFISH WITH CALIFORNIA RED-LEGGED FROGS:
PREDATION EFFECTS ON RECRUITMENT AND
ANTIPREDATOR DEFENSES**

ABSTRACT

I studied the effects of introduced fishes and a crayfish on the federally threatened California red-legged frog (*Rana aurora draytonii*) in coastal central California. At a landscape scale, a survey of 95 sites revealed that adult California red-legged frogs were common in this region, and their occurrence was related to the presence or absence of introduced fishes. Adult California red-legged frogs were present at 94% of the sites that lacked introduced fish and 52% of the sites where fish were present. Of the 20 sites where California red-legged frogs were absent, 16 (80%) had introduced fishes. The frog was more likely to be absent from ponds than streams when introduced fish were present.

At a pond scale, I compared measures of the recruitment of California red-legged frogs at sites with and without introduced fish species. California red-legged frog larvae and metamorphs (frogs which had metamorphosed that season) were

significantly more abundant in ponds lacking fish than in fish ponds. No California red-legged frog egg masses were detected in two of the fish ponds even though adult frogs were present. High densities of frog egg masses were observed at one fish site, but larvae and metamorph abundances were greatly reduced in comparison to fishless sites.

Western mosquitofish (*Gambusia affinis*), bluegill (*Lepomis macrochirus*), and largemouth bass (*Micropterus salmoides*) did not consume California red-legged frog eggs, and red swamp crayfish (*Procambarus clarkii*) did not consume small red-legged frog tadpoles, in artificial ponds (mesocosm scale). However, bluegill, largemouth bass, brown bullhead (*Ameiurus nebulosus*), and mosquitofish significantly decreased the survivorship of California red-legged frog tadpoles in artificial ponds. Predation rates by largemouth bass were higher for small than large tadpoles.

The presence of free-ranging introduced fish and crayfish in artificial ponds affected the microhabitat use and activity of small California red-legged frog tadpoles, but the behavior of large tadpoles was not significantly different from controls. Small California red-legged frog tadpoles did not respond to caged mosquitofish or bluegill by significantly altering activity levels or refuge use. Small tadpoles decreased activity and increased refuge use during the day regardless of whether caged mosquitofish were present. There was a non-significant tendency for tadpoles to decrease activity and increase refuge use when caged bluegill were

present compared to when they were absent, and these responses were detected only during the day but not at night.

Evidence presented here indicates that several species of introduced fish can reduce the densities of California red-legged frog larvae through predation, and consequently reduce recruitment levels to near zero. Coexistence of adult California red-legged frogs with introduced fishes appears to be due to immigration from adjacent fishless sites. Predation by introduced fishes may be responsible for excluding California red-legged frogs from habitat patches that are otherwise suitable if immigration rates of adult or juvenile frogs from sites without introduced predators to sites with non-native fishes are sufficiently low.

INTRODUCTION

Introductions of non-native species have caused the decline and extinction of many native species worldwide (Simberloff 1981, Williamson 1996). Some of the most profound cases of non-native species effects are caused by predators introduced outside of their native ranges (Simberloff 1981). Aquatic predator introductions have especially strong effects on freshwater communities (Thorp 1986). Pond- and stream-breeding amphibians have undergone extensive declines in recent decades, and introduced aquatic predators are thought to be at least partially responsible (Moyle 1973, Hayes and Jennings 1986, Bradford et al. 1993, Jennings and Hayes 1994, Stebbins and Cohen 1995, Knapp and Matthews 2000, Gillespie

2001, Pilliod and Peterson 2001). While amphibians may be negatively affected by non-native crayfish (Gamradt and Kats 1996, Gamradt et al. 1997) and non-native amphibians including bullfrogs (Moyle 1973, Kiesecker and Blaustein 1998), fish introductions appear to have the greatest ecological effects on amphibian populations (Drost and Fellers 1995). Even species of amphibians that can coexist with native fish species may be vulnerable to introduced fishes (Gillespie 2001). In California, fish introductions are of particular concern since about half of the fish species occupying freshwater habitats are non-native (Moyle 1976b, 2002; Hobbs and Mooney 1998, Moyle and Davis 2000). Below I present field and experimental studies that examine the effects of several non-native fishes and a crayfish on a threatened frog species.

The Effects of Native Fish on Amphibian Communities

Fish predation often regulates the species composition and richness of amphibian larval assemblages (Heyer et al. 1975, Woodward 1983, Petranks 1983, Hayes and Jennings 1986, Hecnar and M'Closkey 1997, Azevedo-Ramos et al. 1999, Hero et al. 2001). Only a subset of amphibian species can breed successfully in habitats occupied by fish (Grubb 1972, Ireland 1989, Bronmark and Edenhamn 1994, Hecnar and M'Closkey 1997, Azevedo-Ramos et al. 1999, Smith et al. 1999). These amphibian species have larvae that use microhabitats which are inaccessible to fish (Macan 1966, Cooper 1988, Holomuzki 1995) or they may possess antipredator adaptations against fish predation (see below). Because only those

amphibian species that possess appropriate antipredator defenses can persist with fish, fish distributions combined with prey defenses often determine the composition of tadpole assemblages at local scales (Hero et al. 2001).

Antipredator Adaptations

Predation can be a strong selective agent, resulting in the evolution of antipredator adaptations (Lima and Dill 1990, Endler 1991). While some antipredator adaptations are generalized, and reduce predation rates from several types of predators, responses may instead be specific to particular predators. In the latter case, antipredator adaptations that are effective defenses against one predator may not be effective against other predators (Gascon 1992, Hero et al. 2001). Larval amphibians display both fixed and plastic antipredator adaptations. Fixed antipredator adaptations are expected to be more common in populations that evolved under relatively constant predation pressures and when there is a cost to plasticity (Lardner 1998). Plastic responses, or predator-induced defenses, are only expressed when predator cues are present (Harvell 1990, Lardner 1998). Plastic responses probably evolved under conditions with fluctuating predator populations (Lardner 1998). Many antipredator adaptations carry costs such as decreased rates of resource acquisition (Mittelbach 1981, Sih 1987, Lima and Dill 1990, Werner 1992, Scheffer 1997, Nystrom and Abjornsson 2000). Therefore, prey often face a trade-off between reducing predation risk and foraging possibilities (Lima and Dill 1990, Werner and Anholt 1993, Skelly 1995, Scheffer 1997, Lewis 2001). Plastic

antipredator responses allow prey to alter their behavior in response to changing predation risk (Ives and Dobson 1987, Relyea 2001b).

Fixed antipredator adaptations displayed by larval amphibians include toxicity, cryptic coloration, and low baseline levels of activity (Voris and Bacon 1966, Wassersug 1971, Kruse and Francis 1977, Duellman and Trueb 1986, Kats et al. 1988, Sih et al. 1992, Crossland and Alford 1998, Hero et al. 2001). Amphibian eggs may be protected from predators through toxicity (Licht 1969, Denton and Beebee 1991, Punzo and Lindstrom 2001) or by the jelly that envelops amphibian embryos (see below). Some larval amphibians are unpalatable to certain predators due to noxious skin secretions (Voris and Bacon 1966, Kruse and Francis 1977, Kats et al. 1988, Rundio and Olson 2001). Unpalatability is probably the most efficient and widespread adaptation that allows some larval amphibians to coexist with fish (Hero et al. 2001), and fixed antipredator adaptations are absent in many amphibian species that typically breed in fishless habitats (Kruse and Francis 1977, Kats et al. 1988, Azevedo-Ramos and Magnusson 1999, Gillespie and Hero 1999).

Plastic antipredator adaptations include prey behavioral responses to predators that reduce prey encounter, detection, or capture rates (Lima 1998). Plastic responses of larval amphibians to predators include reductions in activity (Petranka et al. 1987, Semlitsch 1987, Lawler 1989, Figiel and Semlitsch 1990, Holomuzki 1995, Laurila 2000), spatial avoidance of predators and/or increased refuge use (Macan 1966, Holomuzki 1986, Petranka et al. 1987, Semlitsch 1987, Cooper 1988, Kats et al. 1988, Sih et al. 1988, 1992; Fauth 1990, Tyler et al. 1998b,

Nystrom and Abjornsson 2000), aggregation (Watt et al. 1997), and alteration of diel activity patterns (Petranka et al. 1987, Semlitsch 1987, Sih et al. 1992). Some larval amphibians can alter their morphology to better escape capture when particular predators are present (Lardner 1998, 2000; Laurila et al. 2001, Relyea 2001a). Plastic antipredator responses displayed by amphibian embryos include delayed time to hatching, which can result in larger hatchling size (Sih and Moore 1993, Schalk et al. 2002), and altered morphology at hatching (Laurila et al. 2001; but see Anderson and Petranka 2003). Other amphibian species avoid breeding at sites that have particularly dangerous predators (Petranka 1983, Woodward 1983, Kats et al. 1988, Semlitsch 1988, Resetarits and Wilbur 1989, Kats and Sih 1992, Hopey and Petranka 1994, Bronmark and Edenhamm 1994, Holomuzki 1995). Antipredator behaviors tend to reduce prey population fluctuations in model predator-prey systems (Ives and Dobson 1987, Sih 1987, Krivan 1998; but see Ramos-Jiliberto et al. 2002).

Larval amphibians can distinguish between different predators and modify their responses accordingly (Kiesecker et al. 1996, Schmidt and Amezcuita 2001, Pearl et al. 2003). Amphibian larvae and embryos can recognize water borne chemical stimuli from many types of predators (Petranka et al. 1987, Kats et al. 1988, Sih and Kats 1991, Sih et al. 1992, Wilson and Lefcort 1993, Sih and Moore 1993, Kiesecker et al. 1996) and larval responses may be strongest when predators have recently consumed conspecific prey (Wilson and Lefcort 1993, Laurila et al. 1998; but see Leftcort 1996). Recognition of predator chemical cues by amphibian

larvae appears to be a result of natural selection (Kats et al. 1988, Sih and Kats 1994, Gallie et al. 2001).

The types of adaptations displayed by amphibian larvae vary with the types of predators encountered throughout their evolutionary history (Kruse and Francis 1977, Kats et al. 1988). A particular amphibian species may only respond to predators with which they coevolved (Grubb 1972, Woodward 1983, Kats et al. 1988, Gamradt and Kats 1996, Schmidt and Amezcuita 2001, Pearl et al. 2003). Antipredator adaptations that are effective against native predators may not be sufficient to allow coexistence with introduced predators (Gamradt and Kats 1996, Gillespie 2001). Native amphibians that recognize and respond to novel predators in ways that decrease predation risk may be better able to persist with introduced predators (Pearl et al. 2003).

Effects of Fish Introductions on Amphibian Communities

Fish introductions may be one of the factors responsible for observed declines in several amphibian species (Macan 1966, Bradford et al. 1993, Fellers and Drost 1993, Stebbins and Cohen 1995, Gamradt and Kats 1996, Knapp 1996, Jennings 1996, Gillespie 2001, Pilliod and Peterson 2001, Matthews et al. 2001). A negative correlation between the presence of introduced fishes and the abundance of native amphibians has been observed in many cases worldwide (Grinnell and Storer 1924, Moyle 1973, Hayes and Jennings 1986, 1989; Bradford 1989, Bradford et al. 1993, Jennings and Hayes 1994, Brana et al. 1996, Fisher and Shaffer 1996, Tyler et

al. 1998a, Funk and Dunlap 1999, Goodsell and Kats 1999, Knapp and Matthews 2000, Pilliod and Peterson 2001, Welsh and Boiano 2001, Matthews et al. 2001, Knapp et al. 2001). Long-term population monitoring of native amphibians has revealed dramatic declines following the introduction of non-native fish (Meyer et al. 1998; see Fellers and Drost 1993) and increases following the eradication of non-native fish (Funk and Dunlap 1999, Knapp et al. 2001).

While there are several ways that introduced fish interact with amphibians, fish predation on amphibian larvae probably has the strongest effect on amphibian populations (Macan 1966, Ireland 1989, Jennings 1996, Gillespie and Hero 1999). Larvae may be vulnerable if they fail to recognize fish as predators or if they lack appropriate antipredator adaptations (Gamradt and Kats 1996, Gillespie 2001; reviewed above). Freshwater fish species that prey on amphibian larvae include sunfish (Kruse and Francis 1977, Werschkul and Christensen 1977, Kats et al. 1988, Ireland 1989, Figiel and Semlitsch 1990, Smith et al. 1999), bass (Kruse and Francis 1977, Ireland 1989), mosquitofish (Gamradt and Kats 1996, Goodsell and Kats 1999, Komak and Crossland 2000), trout (Macan 1966, Cooper 1988, Bradford et al. 1993, Tyler et al. 1998b, Gillespie 2001), catfish (Kruse and Francis 1977), and goldfish (Glandt 1985, Moneillo and Wright 2001). Hatchling amphibian larvae are probably the most vulnerable stage because of their small size and immobility (Macan 1966, Calef 1973, Lawler 1989; see Licht 1974), but larger larvae are also consumed by many fish species (Gillespie 2001).

It is unclear whether fish consume amphibian eggs in natural habitats. Mosquitofish (Grubb 1972), trout (Licht 1969), and sticklebacks (Licht 1969) consumed amphibian eggs in laboratory experiments. Some fish species may not recognize amphibian eggs as prey since eggs are immobile (Werschkul and Christensen 1977). Amphibian eggs were rejected by fish possibly due to unpalatability (Licht 1969, Magnusson and Hero 1991) or the sticky gelatinous coating that envelops the embryos (Werschkul and Christensen 1977, Ward and Sexton 1981, Semlitsch 1988, Gamradt and Kats 1996, Azevedo-Ramos and Magnusson 1999). When the outer jelly coat from amphibian egg masses was removed, fish consumed individual eggs (Werschkul and Christensen 1977, Ward and Sexton 1981, Semlitsch 1988). Damage to the outer jelly coating by freezing, drying, or physical disturbance by predators, can increase predation on eggs (Walters 1975). Eggs of amphibian species that are laid singly, instead of in a mass, were consumed by bluegill (Semlitsch 1988).

The presence of non-native fish causes many freshwater habitats to be ecological sinks (see Danielson et al. 1992) for some amphibian species (Bradford et al. 1993, Gillespie and Hero 1999, Knapp and Matthews 2000). Since non-native fish have been introduced to most permanent aquatic habitats (Maret et al. 1995, Gillespie and Hero 1999; see Fisher and Shaffer 1996), and many ephemeral aquatic sites that cannot support fish have been eliminated by agricultural and urban development (Gillespie and Hero 1999, Semlitsch 2002), amphibian source populations have been reduced in many regions. Introduced fish also contribute to

the fragmentation and isolation of remaining amphibian populations by eliminating populations or reducing immigration rates due to decreased population sizes (Bradford et al. 1993, Knapp and Matthews 2000). Since many anuran species may exist as metapopulations that depend on immigration between nearby sites (Alford and Richards 1999), reduced movement among populations can increase the chance of extinction due to stochastic processes (Hayes and Jennings 1986, Sjogren 1991, Gulve 1994, Green 1997; see Marsh and Trenham 2001).

Effects of Crayfish Introductions on Amphibian Communities

The introduction of red swamp crayfish (*Procambarus clarkii*) may have contributed to the decline of native amphibian species in California (Gamradt and Kats 1996). Several species of crayfish, including the red swamp crayfish, prey on amphibian larvae (Reynolds 1978, Formanowicz and Brodie 1982, Holomuzki 1989, Fauth 1990, Gamradt and Kats 1996, Axelsson et al. 1997, Nystrom and Abjornsson 2000). Crayfish may also cause sublethal injuries to tadpoles (Fauth 1990, Axelsson et al. 1997, Nystrom et al. 2001), which can subsequently result in increased predation rates on tadpoles due to decreased swimming efficiency (Morin 1985, Semlitsch 1990, Figiel and Semlitsch 1991). The edibility of amphibian eggs by crayfish is not well understood. Ward and Sexton (1981) reported that the outer jelly coating prevented amphibian eggs from being eaten by crayfish, whereas other researchers observed crayfish eating intact eggs in experimental situations (Gamradt and Kats 1996, Axelsson et al. 1997, Punzo and Lindstrom 2001). Gamradt et al.

(1997) found that aggressive attacks from introduced red swamp crayfish deterred breeding in California newts (*Taricha torosa*). The abundances of some amphibian larvae increased following the elimination of crayfish (Abrahamsson 1966, Gamradt and Kats 1996).

Crayfish can have indirect effects on amphibian larvae by eliminating or decreasing cover by aquatic macrophytes (Abrahamsson 1966, Lodge and Lorman 1987, Lodge et al. 1994, Lodge et al. 2000b, Nystrom et al. 2001). Decreased aquatic plant densities can increase fish (Crowder and Cooper 1982, Gillinsky 1984) and crayfish (Axelsson et al. 1997) predation rates on tadpoles due to decreases in refugia. Crayfish can act as vectors for fungal diseases, parasites, and other potential pathogens (Sogandares-Bernal 1965, Lodge et al. 2000a), but it is not known whether these organisms also affect amphibians.

Introduced Fish and Crayfish Effects on the California Red-legged Frog

The California red-legged frog (*Rana aurora draytonii*) historically occurred throughout most of the lowland areas of California (Storer 1925), and was formerly one of the most abundant amphibians in the state (see Jennings and Hayes 1985). Today it is absent from approximately 70% of its historical range and is listed as a federally threatened species (U. S. Fish and Wildlife Service 2002). The decline of this subspecies is thought to be due in part to the establishment of a diverse fauna of non-native aquatic predators, including several species of introduced fish, crayfish and bullfrogs (Moyle 1973, Hayes and Jennings 1986, Jennings and Hayes 1994,

Stebbins and Cohen 1995, Jennings 1996). There appears to be an inverse relationship between the presence of introduced fish and California red-legged frogs at a landscape scale (Hayes and Jennings 1986, 1989; Fisher and Shaffer 1996), and frog populations tend to be small where frogs and introduced fishes co-occur (Hayes and Jennings 1986). The effects of crayfish introductions on the California red-legged frog are not well understood (but see Jennings et al. 1992), but introduced red swamp crayfish have negatively affected other California amphibians (Gamradt and Kats 1996, Gamradt et al. 1997).

At least 53 non-native species of fish occur in freshwater habitats in the California, and additional species are becoming established at a rate of about 1 every 3 years (Dill and Cordone 1997, Moyle 2000). Of these, at least 36 fish species were introduced to California from other parts of North America (Moyle 2002). In the 1880s, fish were transported from the East Coast of the United States to California in railroad cars that were built specifically for transporting fish (Moyle 2002). Most deliberate introductions of freshwater fish to California were conducted by the California Fish Commission, and were sponsored by the U. S. Fish Commission, to “improve” California fisheries by introducing species that were “superior” to native species (Moyle 2002). Authorized introductions of fish species ceased in 1972, but illegal and accidental introductions continue (Moyle 2002). Non-native fishes and crayfish continue to become established in new areas of the state by dispersal through aqueducts that connect drainage systems (Hayes and Jennings 1989, Lodge et al. 2000b, Moyle 2002).

California red-legged frogs may have evolved under limited fish predation because they breed in areas with relatively depauperate native fish communities (Hayes and Jennings 1986, Swift et al. 1993, Dill and Cordone 1997). The California red-legged frog may be vulnerable to introduced species of fish due to a lack of appropriate antipredator adaptations, and because foraging modes of non-native fishes differ from those of many native fish species (see Hayes and Jennings 1986). Jennings (1988) suggested that the benthic habits of California red-legged frog larvae predispose them to predation by benthos-foraging fish species, such as ictalurids and some centrarchids. Like other amphibians, California red-legged frog larvae may be most vulnerable to predation immediately after hatching, when they are relatively immobile and remain in aggregations near the hatched egg mass (Calef 1973, Licht 1974, Hayes and Jennings 1986). California red-legged frog eggs may also be vulnerable to fish predators (Jennings 1988).

Field studies of California red-legged frog and aquatic predator interactions are difficult due to limited co-occurrence of the frog with each potential predator, and direct responses to habitat degradation (Moyle 1973, Hayes and Jennings 1989). Habitat loss and degradation are among the primary causes responsible for this subspecies' decline (Jennings 1988, Davidson et al. 2001). Introduced fishes and crayfish are particularly abundant in habitats that have been altered by human activities (Moyle 1976b, 2002, Hayes and Jennings 1986, Swift et al. 1993; see Lindqvist and Huner 1999). Habitat alterations could also increase encounters between amphibian larvae and aquatic predators due to reductions in the availability

of potential refugia (Hayes and Jennings 1986). Teasing apart the relative contributions of habitat alterations and direct effects of introduced predators to frog declines requires manipulative studies (Moyle 1973, Hayes and Jennings 1986).

Prior to the present study, little research had been conducted on the palatability of California red-legged frog larvae and eggs to the non-native fish species now found throughout the frog's historic range. Lawler et al. (1999) used experimental ponds to examine interactions between western mosquitofish and California red-legged frog tadpoles. While the presence of mosquitofish did not affect the survivorship of tadpoles, tadpoles raised with mosquitofish had reduced growth rates and increased time to metamorphosis compared to tadpoles in ponds lacking mosquitofish (Lawler et al. 1999). Larvae of the northern red-legged frog (*R. a. aurora*), which is a closely related but probably separate species (Hayes and Miyamoto 1984, Green 1985, Hayes and Kremples 1986), were palatable to bluegill (*Lepomis macrochirus*) (Adams 2000, Pearl et al. 2003) and smallmouth bass (*Micropterus dolomieu*) (Kiesecker and Blaustein 1998).

I used field studies and experimental manipulations to determine the role several non-native fish species and one non-native crayfish species (see species descriptions below) may have played in the decline of the California red-legged frog (Table 3.1). I surveyed 95 sites in coastal central California to determine if there was a relationship between the presence of introduced fishes and California red-legged frogs on a landscape scale. I compared the abundances of California red-legged frog egg masses, larvae, and metamorphs (recently-transformed frogs) at

ponds with and without introduced fishes to determine if non-native fish affected California red-legged frog recruitment at a pond scale. I also sampled California red-legged frog tadpole densities in five pond microhabitats to determine if tadpoles used different microhabitats in the presence versus absence of introduced fishes. At mesocosm and microcosm scales, I used artificial ponds to determine if several species of introduced fishes and one introduced crayfish species would consume California red-legged frog eggs and larvae. I tested whether California red-legged frog larvae displayed antipredator behaviors in the presence of free-ranging and caged non-native fishes. Examination of the distributions, abundance, and interactions of California red-legged frogs and introduced fishes and crayfish should provide predictions about the coexistence and persistence of California red-legged frogs with introduced predators, with implications for introduced predator effects on other native anuran species.

STUDY SPECIES

California Red-legged Frog

Breeding habitats of California red-legged frogs include ponds, marshes, sloughs, lakes, reservoirs, and slow-moving areas in streams (Storer 1925, Wright and Wright 1949, McKeown 1974, Stebbins 1985). Breeding occurs during the rainy season, from November through April (Storer 1925, Wright and Wright 1949, Stebbins 1985, Hayes and Jennings 1986, Christopher 1996, 2000). Most California

red-legged frogs spawn when ponds are at peak water levels (Storer 1925; personal observation). Egg masses are usually deposited in emergent vegetation at the margins of ponds or stream pools (Dickerson 1906, Storer 1925, Wright and Wright 1949, Jennings et al. 1992). California red-legged frog tadpoles are 8 - 10.5 mm total length at hatching and grow quickly, reaching total lengths of 83 mm (Storer 1925) to 120 mm (unpublished data) prior to transformation. Larvae inhabit the margins of aquatic habitats, especially areas with grasses or aquatic vegetation (Storer 1925; unpublished data). Most larvae metamorphose after 3.5 to 7 months (Dickerson 1906, Storer 1925, Jennings and Hayes 1989), but in some cases larvae may overwinter (Storer 1925, Fellers et al. 2001). Additional information on the natural history of the California red-legged frog is given in Chapter 2 and the Introduced Fish and Crayfish Effects on the California Red-legged Frog section above.

Largemouth Bass

The native range of the largemouth bass, *Micropterus salmoides*, is the Mississippi River basin from Ontario and Quebec to northeastern Mexico (Carlander 1977, Moyle 2002). This species has been introduced worldwide and is now widespread across most of North America (Carlander 1977, Moyle 2002). Carlander (1977) calls largemouth bass one of the most important sport fish in the United States. The first introductions of largemouth bass to California took place between 1888 and 1891 (Smith 1896, Shebley 1917, Moyle 2002). Largemouth

bass presently occur throughout the state, except at high elevations and in the deserts (Moyle 2002). Largemouth bass inhabit farm ponds, lakes, reservoirs, sloughs, river backwaters, and foothill streams (Moyle 1976b). They appear to favor habitats with anthropogenic disturbance, warm water, and beds of aquatic plants (Moyle 1976b). Largemouth bass forage mainly during the day in littoral zones less than 6 m deep (Moyle 1976b, 2002; Hickley et al. 1994). They have a large gape, and capture prey through pursuit or ambush (Moyle 2002). The diet of adult largemouth bass is comprised mainly of crayfish, fish, larval salamanders, tadpoles, and frogs (Espinosa and Deacon 1973, Moyle 1976b, 2002; Hickley et al. 1994, Godinho et al. 1997, Garcia-Berthou 2002).

Bluegill

Bluegill, *Lepomis macrochirus*, are a sunfish native to most of eastern North America, from Ontario and the Great Lakes to northeastern Mexico (Moyle 1976b, 2002). They have been introduced throughout western North America and to several regions throughout the world (Moyle 1976b, Carlander 1977). Bluegill were first introduced to California in 1908 and became widely distributed throughout the state within 10 – 20 years (Moyle 1976b, 2002). Bluegill can tolerate a wide range of aquatic conditions, and optimal habitats appear to be warm reservoirs, ponds, sloughs, and sluggish streams at low altitudes (Carlander 1977, Moyle 1976b, 2002). They are most often found near aquatic macrophytes in water less than 5 m deep (Moyle 1976b, 2002). Bluegill feed throughout the water column, including

the water surface, benthos, shallow water, and among aquatic plants (Baumann and Kitchell 1974, Moyle 1976b). Bluegill are omnivorous and opportunistic feeders, and their prey include aquatic and terrestrial insects, snails, small fish, fish eggs, crayfish, algae, and aquatic plants (Kitchell and Windell 1970, Moyle 1976b, 2002). Bluegill reduced the survivorship of amphibian larvae in experimental situations (Semlitsch 1988, Werner and McPeck 1994, Adams 2000).

Brown Bullhead

The brown bullhead, *Ameiurus nebulosus*, is a catfish native to the eastern United States and southeastern Canada (Lee et al. 1980, Moyle 2002). This species has been introduced throughout the western United States (Moyle 2002) and was introduced to central California in 1874 (Curtis 1949). Brown bullhead occur in California throughout the Central Valley and most large coastal drainages (Moyle 2002). Brown bullhead are one of the most abundant warmwater gamefishes in California (Moyle 1976b). They are widespread in the state because they can persist in a wide range of habitats, but prefer sloughs, foothill reservoirs, and sluggish rivers (Moyle 1976b, 2002). They are usually found in beds of aquatic plants with mud substrata (Moyle 2002). Adult brown bullhead school and are mainly nocturnal (Moyle 1976b). The adults are omnivores that search for benthic food (Keast and Webb 1966, Scott and Crossman 1973, Moyle 1976b). A similar non-native species, the black bullhead (*A. melas*), is also very common in California (Moyle 2002). In one account, the introduction of this species to a Louisiana pond

resulted in the elimination of formerly well-established populations of bullfrog tadpoles, crayfish, and *Gambusia patruelis* (Viosca 1931).

Western Mosquitofish

Western mosquitofish, *Gambusia affinis*, are small (to 60 mm TL) live-bearing fish native to central North America, from Illinois south to Texas, Alabama and eastern Mexico (Moyle 1976b, 2002). Western mosquitofish have been introduced worldwide for mosquito control (Krumholz 1948, Moyle 1976b, 2002). They were first introduced to California in 1922, and are still planted for mosquito control (Moyle 2002). Western mosquitofish are currently present throughout the state (Moyle 1976b, Swift et al. 1993). Western mosquitofish occur in a wide range of aquatic habitats, and withstand low dissolved oxygen levels and brackish water (Moyle 1976b, 2002). This species does especially well in disturbed habitats (Moyle 1976b, 2002). Western mosquitofish prefer the shallow edges of lakes and streams that are inaccessible to predatory fish and have high water temperatures (Moyle 1976b, 2002). They are usually found near the edge of beds of aquatic plants (Moyle 1976b, 2002).

Population growth in the western mosquitofish can be rapid in the warmer regions of California because individual females can produce 4 broods per season (Moyle 1976b). Western mosquitofish are omnivorous and opportunistic feeders, and will eat algae or invertebrates depending on their relative abundances (Moyle 1976b, 2002). This species can be cannibalistic (Dionne 1985, Moyle 2002), and

also consumes amphibian larvae (Gamradt and Kats 1996, Goodsell and Kats 1999, Komak and Crossland 2000; but see Lawler et al. 1999). Since the mosquitofish is a small, gape-limited species, it may only be able to consume small amphibian larvae (Webb and Joss 1997). However, mosquitofish may nip off the edges of the fins of large tadpoles (Lawler et al. 1999, Komak and Crossland 2000), which can be lethal to the tadpoles (Komak and Crossland 2000).

Red Swamp Crayfish

The red swamp crayfish, *Procambarus clarkii*, is native to the south central United States and northeastern Mexico (Hobbs 1972), but has been introduced to many areas throughout the world (Huner and Avault 1978, Huner and Barr 1983, Hobbs et al. 1989, Barbaresi and Gherardi 2000). Red swamp crayfish were introduced to California in the early 1900s (Reigel 1959). They can withstand a wide range of aquatic conditions (Huner and Avault 1978, Huner and Barr 1983, Hobbs et al. 1989), and persist in areas with drastic, seasonal fluctuations in water levels (Huner and Barr 1983). Red swamp crayfish can survive out of water in moist conditions for at least three months (Hobbs et al. 1989). High fecundity and rapid growth rates influence the invasibility of the red swamp crayfish. They can reach sexual maturity in as little as three months, and multiple broods in one year are possible in warm climates (Huner and Barr 1983, Huner and Lindqvist 1995). Large females can produce over 600 young at a time (Hobbs et al. 1989).

Red swamp crayfish have stationary periods when they hide in their burrows during the day and forage locally at night, as well as periods with bursts of nomadic movement (Gherardi et al. 2000, Gherardi and Barbaresi 2000). During their nomadic periods, they can cover up to 20 km² in an aquatic habitat over 4 days, and they can move overland between aquatic sites (Gherardi et al. 2000). The diet of red swamp crayfish includes plants, organic sediment, detritus, insects, other crustaceans, fish (Huner and Lindqvist 1995, Gutierrez-Yurrita et al. 1998), and amphibian eggs and larvae (Gamradt and Kats 1996, Gherardi et al. 2001). Red swamp crayfish are aggressive and will attack adult amphibians, causing injuries and excluding some amphibians from potential aquatic breeding sites (Huner and Barr 1983, Gamradt et al. 1997).

STUDY DESIGN

I performed 6 studies that examined interactions between introduced fish or crayfish and California red-legged frogs at 4 scales (Table 3.1). The rationale for using a variety of approaches was described in Chapter 2. Each of the studies I performed has subheadings in the Study Sites, Methods, and Results sections. The Discussion section synthesizes the results from these and other investigations. Interactions among introduced fish, crayfish, bullfrogs, environmental factors, and California red-legged frogs, are examined in Chapter 4.

Study Sites

Study 1

Distribution patterns of introduced fishes and California red-legged frogs were analyzed using data I collected in central coastal California. These data resulted from various other projects that had the common goal of determining the status of the California red-legged frog at each site. All 95 sites included in this study met the habitat requirements for California red-legged frogs (see Chapter 2) and were within the geographical range of this species. Ephemeral and semi-permanent sites that could not support fish populations were excluded to minimize the influence of differences in habitat type between fish and fishless sites. Sites with only native fish species, or in which the only introduced fishes were western mosquitofish or translocated native fish species, were classified as introduced predatory fish “absent” instead of “present” sites. Sites were divided into two groups: ponds and reservoirs (40 sites), and river and stream reaches (55 sites). The number of sites per county was: Santa Barbara = 64, Santa Cruz = 1, San Luis Obispo = 22, and Ventura = 8 (Appendix H).

Vandenberg Air Force Base (VAFB), in Santa Barbara County, California was the primary study area, encompassing 48 sites in the study (Appendices C and H). The geography and aquatic habitats of VAFB were described in Chapter 2. Game fish stocking at VAFB was conducted from the mid-1960s through 1980 at 5 ponds totaling 49 acres (California Department of Fish and Game 1969, 1972;

Young 1972, Coulombe and Mahrtdt 1976, Coulombe and Cooper 1976, Cudd 1986). The U.S. Fish and Wildlife Service stocked fish purchased from the California Department of Fish and Game, in cooperation with the U. S. Air Force (California Department of Fish and Game 1969, 1972; Young 1972). “Unknown sources” also contributed to fish introductions in the past (Young 1972), and continue today (personal observation). Species introduced were largemouth bass, channel catfish (*Ictalurus punctatus*), bluegill, western mosquitofish, carp (*Cyprinus carpio*), redear sunfish (*Lepomis microlophus*), Sacramento perch (*Archoplites interruptus*), black crappie (*Pomoxis nigromaculatus*), translocated rainbow trout (*Oncorhynchus mykiss*), and translocated three-spine sticklebacks (*Gasterosteus aculeatus*) (California Department of Fish and Game 1969, 1972; Young 1972, Coulombe and Mahrtdt 1976, Coulombe and Cooper 1976, Soil Conservation Service 1977). Management of the fisheries in these ponds included rotenone treatment to remove undesirable species, dredging, enlargement of pond basins, mechanical vegetation removal, herbicide applications, and pumping water into a pond from an adjacent stream to maintain water levels in the summer (Young 1972, Coulombe and Cooper 1976). After stocking was discontinued, redear sunfish, largemouth bass, channel catfish, bluegill, and western mosquitofish have maintained self-sustaining populations in Vandenberg ponds (California Department of Fish and Game 1977, Watkins 1986; personal observation).

The portion of the Santa Ynez River on VAFB contains bluegill, fathead minnow (*Pimephales promelas*), western mosquitofish (Coulombe and Cooper

1976, Coulombe and Mahrt 1976), green sunfish (*Lepomis cyanellus*), black bullhead (*Ictalurus melas*), and largemouth bass (Swift et al. 1997). The river also has native fishes such as tidewater goby (*Eucyclogobius newberryi*), three-spine stickleback, Pacific staghorn sculpin (*Leptocottus armatus*), prickly sculpin (*Cottus asper*), starry flounder (*Platichthys stellatus*), topsmelt (*Atherinops affinis*), and steelhead (*Oncorhynchus mykiss*) (Coulombe and Cooper 1976, Coulombe and Mahrt 1976, Swift et al. 1997). Catfish, carp, largemouth bass, and sunfish were stocked in San Antonio Creek (Coulombe and Cooper 1976), and recently western mosquitofish, arroyo chub (*Gila orcutti*), fathead minnow, green sunfish, and brown bullhead were observed (unpublished data). Native species in San Antonio Creek include tidewater goby, prickly sculpin, staghorn sculpin, threespine stickleback, and starry flounder (Swift et al. 1997). In summary, there are at least 5 ponds and two stream systems on VAFB that currently support introduced fish species, and all of these sites also have introduced bullfrogs and red swamp crayfish (unpublished data). Crayfish were reported from 3 VAFB ponds in the 1970s (Coulombe and Mahrdt 1976, Coulombe and Cooper 1976), and I detected them from a total of 7 ponds and 5 drainages (unpublished data).

Study 2

I studied the effects of introduced fish on the recruitment of California red-legged frogs and microhabitat use of larvae at 6 permanent ponds on VAFB (Figure 3.1). Three ponds (37, 38, 46) contained introduced fish and adult California red-

legged frogs, and three ponds (77, 79, 91) contained only California red-legged frogs. The former 3 sites were the only ponds on VAFB where predatory introduced fish species and California red-legged frogs co-occurred. Ponds 38 and 46 contained centrarchids and ictalurids (Appendix H). Ictalurids probably were present at Pond 37 because this site is an impoundment in a drainage where brown bullhead were abundant, but the only fish captured during trapping for this study were western mosquitofish (introduced) and prickly sculpin (native). Introduced bullfrogs and crayfish also were present at the fish sites, and were absent at the fishless sites. Habitat suitable for California red-legged frogs was present at all six sites (e.g., structurally complex shore and emergent vegetation, presence of shallow and moderately deep water, low levels of human modification; See Appendix I).

Studies 3, 4, 5 & 6: Predation on Eggs and Tadpoles

In Mesocosms, and Antipredator Behavior of Tadpoles

Artificial pond (described in Methods) experiments were conducted at a level open field at VAFB. There were no structures or trees that shaded the ponds; however, overcast conditions were common during the experiments. Artificial ponds were subject to natural light and climate.

METHODS

Study 1: Distribution Patterns

Survey data were used to examine the frequency of co-occurrence of California red-legged frogs and predatory introduced fish species to determine whether California red-legged frogs tended to be absent from sites with fish. The presence of fish was determined using existing data (California Department of Fish and Game 1969, 1972; Coulombe and Mahrdrdt 1976, Cudd 1986, U. S. Forest Service 1993, 1994; Swift et al. 1997), visual surveys (shallow, clear streams), and sampling (sites without existing data, those suspected to have fish based on connectivity to other fish sites, and sites likely to have been stocked due to location). Fish were sampled using hoop net traps (fiberglass hoop diameter 50.8 centimeters, 4 hoops and 2 throats per trap, mesh size 3.2 centimeters, netcoated black nylon #15 knotted netting; “The Shorty” Miniature Hoop Net, Nylon Net Company, Memphis, Tennessee) to determine species composition.

Visual encounter surveys (Crump and Scott 1994, Crisafulli 1997) for California red-legged frogs were conducted between 1994 and 1999. Surveys were conducted at night using high-intensity focused-beam lights (Wheat Cap Lamps, Model 5800-H, Koehler Manufacturing Company, Marlborough, Massachusetts) to detect frog eyeshine. All potential habitats at each site were thoroughly searched while wading or using float tubes. Numbers of California red-legged frogs were categorized by age class (adult, juvenile, metamorph; See appendix E for size

categories). Each site was surveyed 1 – 15 times, and California red-legged frogs were considered absent only if they were not observed after 2 - 4 surveys. The numbers of bullfrogs observed during the surveys were also recorded. Crayfish were not sampled, but were often observed during visual surveys or trapped during fish sampling.

Ninety-five sites had water throughout the study period and received enough surveys to detect all frog species present (Appendix H). More than 89% of the surveys took place between April 1 and September 30, which is the peak period to detect California red-legged frogs in this region. The null hypothesis that the presence of adult California red-legged frogs was independent of the presence of introduced predatory fish was tested using a Chi-square contingency table analysis (Systat 5.2.1, Evanston, Illinois).

Study 2: Reproduction in Ponds

I compared the relative abundances of California red-legged frog egg masses, larvae, and recently-metamorphosed frogs (metamorphs) at three ponds with and three ponds without introduced fish. The purpose of this study was to determine whether the presence of introduced predatory fish affected the recruitment (reproductive success) of California red-legged frogs in ponds through direct or indirect effects.

Visual surveys for California red-legged frog egg masses were conducted from 19 January 1997 through 9 March 1997. Each site was surveyed twice, and the

order of surveys was haphazard. All areas were thoroughly searched by wading or float tube. A flag was tied near each egg mass with an identifying number to prevent recounting egg masses during the subsequent survey.

The abundance and microhabitat use of larvae at each site was determined using unbaited, galvanized hardware-cloth two-funnel traps (Gee's minnow traps, 42 cm long, 19 cm diameter at ends, 21.5 cm maximum diameter, funnel openings 3 – 3.5 cm, mesh 5 mm; Model MT2, Nylon Net Company, Memphis, Tennessee) (Adams et al. 1997). Each pond received 30 traps during each of 3 sampling sessions. Traps were arrayed along 6 transects per pond, with transects perpendicular to shore and 5 traps per transect. Transects locations were determined by mapping the sites, numbering potential transect locations (34 - 48 per site) on the maps, and randomly selecting 6 locations per site. Transects were marked by placing a post (PVC pipe) into the pond substrate, which extended at least 20 cm above the water surface. Posts were positioned in the open water 1 m away from the perimeter band of emergent vegetation. Each transect had one trap placed in each of 5 microhabitats in the littoral zone, which sampled three lateral zones (shore, emergent vegetation, open water) and two heights within the water column (near surface, benthic; Figure 3.2). Traps were set at 1400 hours and checked at 2200 hours, encompassing both day and night hours. Traps were not deployed overnight because some of the traps were completely submerged to sample deeper microhabitats and anoxic conditions lethal to tadpoles may occur overnight in some ponds (unpublished data). Each pond was sampled three times from 23 May –

3 August 1997. The order in which the ponds were sampled during the first session was haphazard. Sampling was repeated over two more sessions with the order of the ponds the same as the first session. Tadpoles of all developmental stages were counted.

Because the number of larvae captured by traps may be affected by larval activity, which in turn may be affected by the presence of predators, surveys for metamorphs were also conducted. The numbers of metamorphs present at the 6 ponds were estimated from visual encounter surveys conducted during the period of peak metamorphosis. Estimating the peak of metamorphosis at each site was complicated by high variation in the timing of metamorphosis among individuals and sites (unpublished data). In addition, a large proportion of California red-legged frogs emigrate into upland habitats within a few weeks of metamorphosis (Chapter 4), and thus cannot be found during visual surveys of aquatic habitats. Peaks of metamorph activity were estimated based on the developmental stages of tadpoles caught in traps (described above), and observations of metamorph abundance at these sites during previous years (Appendix E). Ponds where water levels dropped seasonally tended to have tadpoles with increased rates of development, and these ponds were surveyed earlier in the survey period. One pond (Pond 91) still had untransformed tadpoles until the end of September, since transforming frogs with tails could be seen resting on aquatic vegetation during the metamorph surveys. Surveys could not be performed after late September 1997 because low nighttime air temperatures greatly reduced the number of frogs active at or near the water's

surface, thus reducing the number that could be found during visual surveys (personal observation). As a consequence, Pond 91 was surveyed late within the sampling period (13 - 23 September 1997), whereas the other ponds were surveyed from 15 August - 23 September 1997. Three surveys were conducted at each pond, separated by 3 - 16 days (Appendix J). Visual encounter surveys for metamorphs began immediately after total darkness and followed the methods described in Study 1.

The null hypotheses were: 1) the numbers of California red-legged frog egg masses, tadpoles, and metamorphs are not different between sites with and without introduced fish, and 2) the proportions of California red-legged frog tadpoles trapped in each of the 5 microhabitats would be similar for ponds with and without fish, indicating that larvae did not alter microhabitat use in the presence of fish. Because other factors (habitat suitability, presence of crayfish and bullfrogs, etc.) might contribute to any observed differences between ponds with and without fish, fish predation alone could not be considered to be entirely responsible for any observed differences. The object of this study, however, was to determine if sites where California red-legged frogs coexist with introduced fishes were sources or sinks for red-legged frog populations (Pulliam 1988, Dias 1996), when all pond-scale factors are included.

The total number of egg masses found at each pond was used for analysis. The number of tadpoles captured during each sampling session was calculated, and the mean number of tadpoles per pond was used for analysis. It was not possible to

identify individual metamorphs in this study, but it was unlikely that the same individuals were counted more than once during consecutive surveys due to the length of time between surveys and the emigration of metamorphs into upland habitats shortly after metamorphosis (Chapter 4, Appendix E). Therefore, cumulative numbers of metamorphs observed at each site were used for analysis. Because ponds differed in size (Appendix I) and metamorphs were observed only in the littoral zones of ponds, the cumulative number of metamorphs observed per pond was divided by pond perimeter (obtained from the VAFB geographic information system, BTG, Santa Maria, California) to give metamorph density. Mann-Whitney U tests (Systat 5.2.1, Evanston, Illinois) were used to determine whether the total numbers of egg masses, mean number of tadpoles trapped, and density of metamorphs differed between ponds with and without fish. The replicates were the 3 ponds in each category (fish/no fish). Statistical analysis of tadpole microhabitat use in ponds with and without fish could not be performed because too few tadpoles were obtained from ponds with fish.

Study 3: Fish Predation on Eggs

I assessed whether individuals of three introduced fish species would consume California red-legged frog eggs in artificial ponds. Egg masses of the red-legged frog are globular clusters about the size of a grapefruit, and are deposited on vegetation near the surface of the water. Therefore, benthic predators such as crayfish and ictalurids were not tested. Artificial ponds were galvanized steel stock

tanks (circular, 1.5 m diameter, 0.57 m high). There were 10 unshaded tanks arranged in 2 rows on level ground outside for each trial (western mosquitofish, bluegill, and largemouth bass). Each pond was filled with untreated, aged water (from the State Water Project) to a depth of 55 cm (approximately 900 L). Equivalent, small aliquots of plankton collected from 3 natural ponds at VAFB were added to each artificial pond. The water in the ponds became turbid from phytoplankton growth within one week, and cleared after about 2.5 weeks. Algae and detritus settled to the bottom providing organic substrata 1-2 cm deep and attached algae colonized the tank surfaces. Two cement blocks (each: 19.5 X 19.5 X 40.0 cm) were stacked lengthwise, 6 cm away from the tank edge on the southwest side of the tanks, creating a hiding place for fish between the wall of the tank and the blocks.

In natural ponds at VAFB, California red-legged frog egg masses often are attached to marsh pennywort (*Hydrocotyle* sp.), a floating vascular plant with interwoven rhizomes. I collected marsh pennywort from a natural pond on VAFB. Using a 46 cm diameter quilting hoop as a guide, I cut 46 cm diameter mats of the pennywort with household scissors. The mats were thoroughly rinsed and shaken to remove leeches and invertebrates that feed on frog eggs, and then attached with a string to the topmost cement block to anchor the plant near the tank center. Plant mats remained intact throughout the experiment.

One California red-legged frog egg mass was collected on 23 January 1998 from a VAFB pond that dried up before tadpoles could have metamorphosed.

Additional egg masses could not be collected due to U.S. Fish and Wildlife Service Collecting Permit Special Terms and Conditions. As a consequence, I split up the egg mass and used 10 individual eggs (with embryos Gosner Stages 18 and 19) in each of the artificial ponds per trial. The jelly coating of the eggs was dried slightly and allowed to adhere by the stickiness of the jelly to a thin piece of cardboard (5 X 5 cm). The cardboard with the eggs was then tied to the marsh pennywort near the water surface, and positioned vertically with the eggs facing away from the plant. This manipulation probably increased the exposure of the eggs to fish.

Fish were captured from sites on VAFB. Western mosquitofish and bluegill were maintained in tubs (mosquitofish - wading pool 3 m diameter; bluegill - plastic bins 78 X 46 X 40 cm) and fed commercial flake fish food prior to the experiments. Largemouth bass were maintained in the stock tanks and were fed mosquitofish, goldfish, commercial pellet fish food, and aquatic invertebrates. Fish were starved for 48 hours prior to the experiment to standardize hunger.

There were three trials, each using a different species of fish. In each trial, 5 randomly selected ponds received fish (treatment) and 5 did not (control). Fish were added to ponds at least 24 hours prior to the addition of frog eggs to allow for acclimation. The mosquitofish trial used 35 adult fish (mean 20.5 mm TL, range 14 - 27 mm TL) in each pond that received fish. The bluegill (mean 13.2 cm TL, range 11.0 - 17.0 cm TL) and largemouth bass (mean 23.1 cm TL, range 21.0 - 26.0 cm TL) trials used one fish in each pond that received fish. California red-legged frog eggs were added to each pond as described above. A mercury

maximum/minimum thermometer was added to one pond in each trial to record water temperature extremes. The tanks were covered with tight-fitting lids made from 65% light-blocking shade cloth. The survivorship of eggs was determined as the number of eggs remaining in each artificial pond after a 72 hour trial period. The mosquitofish trial was conducted 25 - 28 February 1998, and water temperature ranged 12.5 - 18.0° C. The bluegill trial was conducted 8 - 11 March 1998, and water temperature ranged from 13.0 - 20.0 °C. The largemouth bass trial was conducted 25 - 28 January 1998, and water temperature ranged from 13.0 - 19.0 °C.

The null hypothesis was that each of the three species of fish would not affect the survivorship of California red-legged frog eggs in artificial ponds. Proportions of eggs remaining from the original number in each pond were used in the analyses. Transformations were not successful in meeting the assumption of normality, so nonparametric analyses were performed using Systat 5.2.1 (Evanston, Illinois).

Study 4: Fish and Crayfish Predation on Tadpoles

And Antipredator Behavior of Tadpoles

I assessed whether several species of aquatic predators that have been introduced to California red-legged frog habitats (red swamp crayfish, bluegill, largemouth bass, brown bullhead) would consume California red-legged frog tadpoles, and whether tadpoles displayed antipredator responses to these predators, in artificial ponds. Each trial tested one free-ranging fish or crayfish species and

either small or large tadpoles (Table 3.2). The artificial ponds were set up as in Study 3. Two microhabitats that could serve as refugia for California red-legged frog larvae were added to each pond: a pack of dried cattail (*Typha* sp.) leaves on the pond bottom and a floating plant, marsh pennywort. In California central coast ponds the leaves of cattail plants die in the winter, so the cattail leaves simulated the natural structure of pond bottoms. Fifty grams of dried cattail leaves were placed in an envelope of chicken wire (60 cm long X 40 cm wide X 4 cm deep, 3.5 X 2.5 cm mesh), which was positioned opposite from the cement block stack and anchored to the tank bottom with a rock. The tadpoles could easily swim through the chicken wire mesh to hide among the cattail leaves. Marsh pennywort was used as a second refugium because California red-legged frog tadpoles frequently occurred in this plant in the field. Marsh pennywort was added to the ponds as in Study 3.

Tadpoles used in the small tadpole trials were raised from eggs collected for, but not used in, Study 3. Tadpoles were maintained in plastic buckets (50 cm diameter, 74 cm high) outside in partial sun, and fed boiled lettuce and commercial flake fish food ad libitum. Large tadpoles and crayfish were collected from ponds at VAFB using unbaited traps < 2 days prior to being used in experiments, and were held in plastic tubs (78 X 46 X 40 cm) with lids and water 10 cm deep. The fish used in the small tadpole trials (Table 3.2) were collected and maintained as in Study 3. Different individual fish were used for the largemouth bass/small tadpole and largemouth bass/large tadpole trials. Largemouth bass and brown bullhead used

in the large tadpole trials were collected from ponds at VAFB 27 July - 9 August 1998, and maintained in stock tanks.

The crayfish and fish were not fed for 48 hours to standardize hunger, and were added to the artificial ponds at least 24 hours prior to the addition of tadpoles to allow for acclimation. In each trial, 5 ponds were randomly chosen to receive one individual predator (treatment) and 5 did not receive a predator (control). Each artificial pond received either 20 small tadpoles (mean 17.1 mm TL, range 14 - 23 mm TL, Gosner stage 25) or 5 large tadpoles (bass trial: body length - mean 31.5 mm, range 26.3 - 38.9 mm; tail length - mean 52.0 mm, range 10.6 - 74.8 mm; wet mass - mean 5.9 g, range 3.0 - 11.4 g, Gosner stage 39 - 45; bullhead trial: body length - mean 32.8 mm, range 26.3 - 41.8 mm; tail length - mean 49.7 mm, range 10.5 - 78.3 mm; wet mass - mean 6.7 g, range 3.0 - 12.4 g; Gosner stage 39 - 45). Tadpoles were acclimated by placing the larvae in 1 gallon resealable plastic bags, floating the bags in the artificial ponds, and gradually adding water from the ponds to the bags over approximately 20 minutes. Tadpoles that swam abnormally while being released from the bags were replaced. The number of tadpoles added to each artificial pond resulted in a density that was within the range of densities observed in natural habitats (personal observation). The tanks were tightly covered with 65% light-blocking shade cloth, and the trials ran for 24 hours.

To assess tadpole survivorship and behavior, the covers were removed and tanks left undisturbed for ≥ 1 hour prior to recording tadpole behavior, which was sufficient for the larvae to readjust following the disturbance caused by removing

the covers. Tadpole activity was estimated as the proportion of surviving tadpoles moving (swimming, feeding, or moving their tails) over 1 minute of quiet observation. Larval survivorship and microhabitat use (proportions of surviving tadpoles in the leaf pack, floating plant mat, and other areas) were recorded as follows. I placed a sieve (a 46 cm quilting hoop covered with 1 X 1 mm mesh aquarium netting) under the floating plant, gently lifted it out of the water, untied the string, and transferred the plant mat to a tub of clean water. Tadpoles were then shaken out of the plant mat and counted. The leaf pack was slowly tilted up, shaken, and removed. Tadpoles that were within or under the pack were counted as they fled. The cement block and fish or crayfish were removed, and then the ponds were dip netted repeatedly to remove all remaining tadpoles. The number of tadpoles that were seen fleeing the leaf pack was subtracted from the number collected by dip net to give the number of tadpoles in open areas of the tank. A direct visual count of tadpoles in the open areas could not be performed because glare on the water surface obstructed a clear view of the bottom.

The first null hypothesis was that predators would not affect the survivorship of California red-legged frog tadpoles (dependent variables) in artificial ponds (replicates were 5 ponds with and 5 ponds without predators). Larval survivorship in treatment and control ponds was analyzed using the proportion of larvae surviving in each pond for each of the trials. Transformations were not successful in meeting parametric assumptions, so nonparametric methods were used. The second null hypothesis was that the activity of tadpoles would be the same in ponds with

and without predators, and the proportion of surviving tadpoles that were active was used as the dependent variable in this analysis. Nonparametric methods were used when transformations were unsuccessful in meeting parametric assumptions. The third null hypothesis was that the microhabitat use of small California red-legged frog larvae would be the same in ponds with and without predators. The proportions of surviving larvae in each microhabitat (leaf pack, floating plant mat, and open areas; dependent variables) were compared between ponds with and without predators (independent factor) using MANOVA (Zar 1996). Because univariate F tests showed that the proportions of tadpoles in the leaf pack microhabitat were similar in treatment and control ponds, leaf pack data were dropped from the final analysis to maintain independence of the remaining response variables. Untransformed data met assumptions of normality and homoscedasticity (Lilliefors test and Levene's test, respectively) and analyses were performed using Systat 5.2.1 (Evanston, Illinois).

Study 5: Mosquitofish Predation on Small Tadpoles

And Antipredator Behavior of Tadpoles

I tested whether free-ranging western mosquitofish would consume small California red-legged frog tadpoles in microcosms and whether tadpoles displayed antipredator behaviors in response to mosquitofish. Experiments were conducted using microcosms because preliminary studies indicated that injured and partially eaten small tadpoles were difficult to detect in larger experimental arenas. Unlike

the larger fish species studied, the gape of mosquitofish was too small to consume whole tadpoles. Since mosquitofish usually feed in shallow water and California red-legged frog tadpoles often occur in these habitats (see Chapter 2, Study 3), microcosms provided a compromise between realistic conditions and the degree of control needed to observe interactions between these species. Microcosms were circular, flat-bottomed, green plastic tubs (20.5 cm high, 38 cm diameter). The trial used ten tubs and each tub was filled with 15 liters of a 50:50 mixture of aged tap water conditioned with StartRight (Jungle Laboratories Corp.) and rainwater. Refugia for tadpoles were cardboard squares (10.5 X 10.5 cm) anchored to the bottoms of tubs with cobbles. The corrugated bottom of the tubs permitted all 6 tadpoles to hide under the cardboard squares.

Small tadpoles were obtained from stock as described in Study 4. Mosquitofish were obtained and maintained as in Study 3. The total lengths (snout to tail tip) of the experimental animals was measured by photographing the animals together next to a ruler, projecting the slide image on a screen, and comparing the animal images to that of the ruler.

Five randomly chosen tubs received 4 mosquitofish each on 28 March 1998, with the other 5 tubs acting as controls without mosquitofish. Mosquitofish (mean 21 mm TL, range 15 - 30 mm TL) were starved for 24 hours prior to the experiment to standardize hunger. On 5 April 1998, tadpoles (mean 15 mm TL, range 12 - 18 mm TL, Gosner stage 25) were acclimated to the water temperature in the tubs by floating them in plastic bags for 10 minutes, and then 6 tadpoles were introduced

into each of the tubs. This resulted in natural densities of tadpoles and mosquitofish observed in the margins of aquatic habitats (personal observation). Data on tadpole survivorship and behavior were taken 4 times (5, 9, 32, 48 hrs after the introduction of the tadpoles; the 5 and 48 hour observation periods were during daylight, and the 9 and 32 hour observation periods were at night). The experiment was terminated after 48 hours. The behavioral data recorded were the number of tadpoles in open areas and refugia. For survivorship, tadpoles counted as “dead” were those whose remains were found and those that were missing from the original number added. Since I was able to find all 6 tadpoles in the control tubs, I assumed that fish had eaten missing tadpoles in fish tubs. Water temperature was recorded at the start of the trial and during each observation period.

The first null hypothesis was that free-ranging mosquitofish would not affect the survivorship of small California red-legged frog tadpoles in microcosms. The proportions of tadpoles remaining from the original number were used in the analyses. The second null hypothesis was that refuge use by small tadpoles was the same in microcosms with and without mosquitofish. The proportions of surviving larvae in refugia were compared between microcosms with and without fish using data from the first observation period (5 hours after the start of the experiment). Transformations were not successful in meeting parametric assumptions, so nonparametric analyses were performed using Systat 5.2.1 (Evanston, Illinois).

Study 6: Nonlethal Predator Effects on Small

California Red-legged Frog Tadpole Behavior

Antipredator responses of small California red-legged frog tadpoles to nonlethal (caged) mosquitofish and bluegill examined whether tadpoles responded to chemical, visual and/or tactile cues of potential fish predators. Behavioral responses of tadpoles to caged fish could strengthen inferences based on the free-ranging predator trials in Studies 4 and 5. A decrease in the proportion of active, exposed tadpoles in the free-ranging fish trials could be due to either tadpole behavioral shifts into refugia, or by predation on exposed tadpoles. An increase in refuge use or a decrease in activity in response to visual and chemical cues of fish but in the absence of predation can only be due to a behavioral response.

The mosquitofish trial was conducted using microcosms as in Study 5. Prior to the caged mosquitofish trial, each tub was emptied, scrubbed, and refilled with 15 L tap water. Water was conditioned with StartRight and aged outside for 11 days. Each tub received an enclosure for the mosquitofish. The enclosures were 1 liter clear plastic containers with many small holes that allowed circulation of water and chemical cues from the predators. Possible tadpole refugia (the cardboard plates described in Study 5) were placed in each tub. Eight small tadpoles (mean 15 mm TL, range 12 - 18 mm TL, Gosner stage 25) were added to each tub on 18 April 1998. Three mosquitofish (mean 21 mm TL, range 15 - 30 mm TL) were added to the enclosure in each of 5 randomly assigned tubs on 21 April 1998, with the other 5 tubs acting as fishless controls.

Tadpole antipredator behavior (reduced activity and increased refuge use) was measured during 4 observation periods before and 4 observation periods after the addition of mosquitofish to the enclosures. For both control and experimental tubs, I refer to time periods as “before” and “after” fish addition, even though fish were not actually added to control tubs, and I refer to “fish” tubs as those that were to but had not yet received fish in the before observations and those that did receive fish in the after observations. Time of day, water temperature, and sunlight (partial sun, full sun, shade, or night) were recorded during each observation period. The before and after observation periods were matched for time of day so that results with similar environmental conditions could be compared. I recorded the number of tadpoles outside and under refugia at 44, 39, 37, and 27 hours before fish were added, and 4, 9, 11, and 21 hours after fish were added. During each observation period, I counted tadpoles under refugia 3 times separated by 5 minutes, and the mean for each tub was used in the analysis. I used a repeated-measures ANOVA on log-transformed (before fish) or arcsine square root-transformed (after fish) proportions of tadpoles under refugia to examine fish, time, and fish X time effects on refuge use (Systat 5.2.1, Evanston, Illinois). Activity was assessed as the proportion of tadpoles in each tub swimming during 1 minute of observation. I recorded activity 20, 15, 13, and 3 hours before fish were added, and 4, 9, 11, and 21 hours after fish were added. The experiment was terminated 21 hours after fish were added. Transformations were not necessary to meet assumptions of normality and homogeneity of variances. I used a repeated-measures ANOVA treating the

untransformed proportions of tadpoles swimming as the response variable to examine fish, time, and fish X time effects on activity (Systat 5.2.1, Evanston, Illinois).

The bluegill trial was conducted in the stock tanks that were set up as in Studies 3 and 4. Tanks were scrubbed and refilled with aged water and plankton suspension on 19 June 1998, and left uncovered. The water in the ponds became clouded with algae, and then cleared on 12 July 1998. A fish enclosure made from aluminum window screening (diameter 60 cm, height 40 cm, mesh 2 mm) was placed in the center of each mesocosm. Tadpoles were raised from eggs collected in Study 2. Each pond received 10 small tadpoles (total length: mean 45.7 mm, range 26.9 - 75.5 mm; wet mass: mean 0.8 g, range 0.1 - 2.7 g; Gosner stage 25) on 13 July 1998. Dead or abnormal tadpoles were replaced with new individuals from the rearing tank over the experiment to maintain 10 tadpoles in each pond. The mortality of tadpoles attributable to causes other than predation was higher in this experiment than in other studies and may have been related to an elevated pH in experimental ponds (which was 9.4 - 9.8, and the pH of the water used to fill the tanks was 8.3).

Bluegill were trapped in Franklin Lakes, Paso Robles, San Luis Obispo County, California (035° 35' 26.98" N, 120° 38' 54.86 W) on 6 March 1998 and maintained in a black fiberglass stock tank (1.5 m long X 0.7 m high X 0.9 m high). Fish were fed commercial flake fish food and then were starved for 72 hours prior to the experiment. The enclosure in each of 5 randomly chosen ponds received 1

bluegill (fork length mean 109.4 mm, range 96.7 - 115.0 mm) on 17 July 1998, with the other five tanks acting as controls without fish. The tanks were not covered to minimize disturbance during lid manipulation. The study was terminated on 20 July 1998.

Behavioral observations were made once during the day and once at night with a dim light, with observations were separated by 12 hours, on each of three days before and three days after the addition of fish. In both control and experimental ponds, I refer to time periods as “before” and “after” and the ponds as “fish” or “no fish” as in the nonlethal mosquitofish trial. Activity was measured as the proportion of tadpoles moving during 1 minute, as in Study 4. Transformations were not necessary to meet assumptions of normality and homogeneity of variances for activity data. I used a repeated-measures ANOVA on the untransformed proportions of tadpoles swimming to examine fish, time of day, and fish X time of day effects on activity (Systat 5.2.1, Evanston, Illinois). Microhabitat use was measured as the proportion of tadpoles found in the floating plant, leaf pack, and open areas as in Study 4. The proportion of tadpoles in leaf packs was used in the statistical analysis since tadpoles increased use of leaf packs with free-ranging bluegill in Study 4. This response variable did not need to be transformed to meet assumptions of normality and homogeneity of variances. I used a repeated measures ANOVA that examined fish, time of day, and fish X time of day effects on the proportions of tadpoles in leaf packs (Systat 5.2.1, Evanston, Illinois). Water temperature was measured during each observation period using a hand-held

mercury thermometer, and maximum/minimum water temperatures also were recorded between observation periods.

RESULTS

Study 1: Distribution Patterns

The proportion of sites with adult and juvenile California red-legged frogs was negatively associated with the presence of introduced predatory fish (Table 3.3; Chi-square contingency table analysis $\chi^2 = 22.89$, $P < 0.0001$). California red-legged frogs were recorded at 94% of the sites that lacked fish and 52% of the sites with fish. California red-legged frogs were absent from 20 of the 95 sites, and 16 (80%) of these had fish. Negative associations between fish and frogs appeared to be more pronounced in ponds than in streams. At sites without fish, California red-legged frogs occupied 100% (27) of the ponds and 89% (31) of the stream reaches surveyed. When fish were present, California red-legged frogs occupied 22% (2) of the ponds and 63% (15) of the stream reaches sampled.

Centrarchids (bass and/or sunfish species) and ictalurids (catfish species) were recorded at approximately 100% and 38%, respectively, of the sites where California red-legged frogs were absent (Appendix H). Introduced bullfrogs and crayfish were more commonly observed at sites with than without introduced fish (see Chapter 4). Seventy-nine percent of the fish sites had bullfrogs and 55% had crayfish. In contrast, 16% of the fishless sites had bullfrogs and 6% had crayfish.

Study 2: Reproduction in Ponds

No California red-legged frog egg masses were found at two of the fish sites (Ponds 38 and 46); however, because high numbers were found at the third fish site there was no significant difference in the number of egg masses found in ponds with and without fish (Figure 3.3; Mann-Whitney U test, $P = 0.51$). Conversely, the number of California red-legged frog larvae trapped was significantly lower at sites with than sites without introduced fish (Figure 3.4; Mann-Whitney U test, $P = 0.046$). No larvae were obtained from two of the fish sites (Ponds 38 and 46). The low number of California red-legged frog larvae obtained at sites with fish prevented a comparison of tadpole microhabitat use between sites with and without fish.

The densities of metamorphs found during surveys were lower at ponds with than without introduced fish (Figure 3.5; Mann-Whitney U test, $P = 0.046$). No California red-legged frog metamorphs were observed in two of the fish sites (Ponds 38 and 46), and only 1 was seen in Pond 37 over 3 surveys.

Study 3: Fish Predation on Eggs

The proportions of surviving California red-legged frog eggs were similar in artificial ponds with and without mosquitofish (Mann-Whitney U test, $P = 0.32$), bluegill (Mann-Whitney U test, $P = 0.32$), and largemouth bass (Mann-Whitney U test, $P = 1.00$). Eggs were not lost from control and largemouth bass ponds, one egg

was missing from one pond with mosquitofish, and two eggs were missing from one pond with bluegill (Table 3.4).

Study 4: Fish and Crayfish Predation on Tadpoles

And Antipredator Behavior of Tadpoles

The proportions of small California red-legged frog tadpoles surviving were similar in artificial ponds with and without crayfish (Mann-Whitney U test, $P = 0.50$). In contrast, the survivorship of small tadpoles was significantly lower in ponds with bluegill (Mann-Whitney U test, $P = 0.008$) and largemouth bass (Mann-Whitney U test, $P = 0.004$) than ponds without these predators. In the bluegill trial, survivorship of tadpoles was 96% in control ponds and 23% in fish ponds. In the largemouth bass trial, survivorship was 99% in control ponds and 0% in all of the fish ponds (Table 3.5). Survivorship of large tadpoles also was significantly reduced in ponds with largemouth bass (Mann-Whitney U test, $P = 0.034$) and brown bullhead (Mann-Whitney U test, $P = 0.004$) compared to controls (Table 3.5). The effect of largemouth bass on tadpole survivorship was greater for small than large tadpoles (Table 3.5), even though the starting number of small tadpoles (20/tank) was greater than for large tadpoles (5/tank). One of the control tadpoles from the largemouth bass/large tadpole trial was missing at the termination of the experiment. The large tadpoles had well-developed hind legs, and it is possible that the missing one could have jumped out of the pond during the 1 hour period between the removal of the lids and the survivorship count. The only tadpoles that

were found dead or damaged were in ponds with brown bullhead, including two that were killed and partially eaten, one that was killed and damaged, and one that was injured but still alive (counted as a surviving tadpole).

The activity of small tadpoles was similar in ponds with and without crayfish (Independent *t*-test, $P = 0.52$), but microhabitat use differed between ponds with and without crayfish (MANOVA, $F_{2,8} = 4.36$, $P = 0.052$; Table 3.6). When crayfish were present there were slightly more tadpoles in open areas and fewer in the floating plant (Table 3.6). Small tadpole activity (Mann-Whitney U test, $P = 0.010$) and microhabitat use (MANOVA, $F_{2,7} = 13.01$, $P = 0.004$) were significantly different between ponds with and without bluegill (Table 3.7). Twenty-one percent of control tadpoles were active but no tadpoles were active when bluegill were present. Significantly more tadpoles were in the leaf packs (Mann-Whitney U test, $P = 0.012$), and significantly fewer were in open areas (Mann-Whitney U test, $P = 0.014$) and the floating plant (Mann-Whitney U test, $P = 0.011$) in ponds with versus without bluegill (Table 3.7). Behavior was analyzed using 4 of the 5 ponds with bluegill because no tadpoles survived in one of the ponds.

Small tadpole behavior could not be examined in the largemouth bass trial because no tadpoles survived in ponds with fish. There was no activity of large tadpoles in control or predator treatments. The microhabitat use of large tadpoles was not significantly different in the presence versus absence of largemouth bass (MANOVA, $F_{2,8} = 1.00$, $P = 0.4$; Table 3.8) or bullhead (MANOVA, $F_{2,8} = 2.64$,

$P = 0.13$; Table 3.9). Slightly fewer tadpoles were in open areas when bass (Mann-Whitney U test, $P = 0.190$) and bullhead (Mann-Whitney U test, $P = 0.0935$) were present. The small number of tadpoles used in large tadpole trials, and the reduced number surviving in fish ponds, probably reduced statistical power for these analyses.

Study 5: Mosquitofish Predation on Small Tadpoles

And Antipredator Behavior of Tadpoles

In the free-ranging mosquitofish trial, the proportions of surviving small tadpoles differed between microcosms with and without mosquitofish (Mann-Whitney U test, $P = 0.018$) by the first observation period. There was no mortality of control tadpoles during the experiment. Mean survivorship of tadpoles in microcosms with mosquitofish was 3.4 at the first observation period and 1.4 at the last observation period (Figure 3.6). Tadpoles with fragments of their tails missing were observed in microcosms with fish, and most of these died and then were eaten by the fish. The proportion of surviving tadpoles under refugia was higher in microcosms with than without mosquitofish (Mann-Whitney U test, $P = 0.016$, Figure 3.7).

Study 6: Nonlethal Predator Effects on Small

California Red-legged Frog Tadpole Behavior

Tadpoles did not respond to chemical or visual cues of caged mosquitofish. Refuge use did not differ between fish and fishless microcosms both before (repeated measures ANOVA, $F = 2.66$, $df = 1, 5$, $P = 0.181$), and after (repeated measures ANOVA, $F = 0.01$, $df = 1, 5$, $P = 0.937$) mosquitofish addition. There was a significant time of day effect before ($F = 5.41$, $df = 3, 15$, $P = 0.014$) and after ($F = 44.35$, $df = 3, 15$, $P < 0.0001$) fish addition. The fish X time interaction effect was significant before ($F = 3.41$, $df = 3, 15$, $P = 0.019$) but not after fish addition ($F = 1.29$, $df = 3, 15$, $P = 0.300$). Tadpoles increased refuge use with increased water temperature and sun exposure, and almost all tadpoles were in open areas at night (Figure 3.8). Similarly, there was no difference in tadpole activity in fish versus fishless microcosms both before (repeated measures ANOVA, $F = 0.20$, $df = 1, 5$, $P = 0.660$) and after (repeated measures ANOVA, $F = 0.25$, $df = 1, 5$, $P = 0.633$) fish were added. There was a significant time of day effect before ($F = 9.77$, $df = 3, 15$, $P = 0.0002$) and after ($F = 11.75$, $df = 3, 15$, $P = 0.0001$) fish addition. The fish X time interaction effect was significant before ($F = 3.33$, $df = 3, 15$, $P = 0.036$) but not after fish addition ($F = 0.40$, $df = 3, 15$, $P = 0.753$). More tadpoles were active at night regardless of the presence of caged mosquitofish.

Both before and after bluegill were added to cages, tadpoles in control and caged bluegill treatments did not differ in activity levels (Figure 3.9; repeated-measures ANOVA, before: $F = 0.52$, $df = 1, 8$, $P = 0.491$; after: $F = 0.68$, $df = 1$,

8, $P = 0.433$). There was a significant time effect on tadpole activity before ($F = 2.86$, $df = 5, 40$, $P = 0.027$) but not after ($F = 1.21$, $df = 5, 40$, $P = 0.321$) fish were added. The fish X time interaction was not significant before ($F = 0.51$, $df = 5, 40$, $P = 0.763$) or after ($F = 2.01$, $df = 5, 40$, $P = 0.085$) fish addition. However, tadpoles without caged fish (both before treatments and the no fish after treatment) increased activity over time (regression, $F_{1,16} = 6.89$, $r^2 = 0.30$, $P = 0.018$). When the fish treatment was included in the regression, the increase in activity over time was not significant ($F_{1,22} = 3.35$, $r^2 = 0.13$, $P = 0.081$). The proportion of tadpoles active was similar in daytime versus nighttime before fish were added (repeated measures ANOVA, $P > 0.05$), but activity tended to be reduced during the day when fish were present compared to ponds without fish (repeated measures ANOVA, $F = 4.62$, $df = 1, 8$, $P = 0.0639$; Figure 3.9). Thus tadpoles appeared to respond to caged bluegill by slight reductions in activity levels, but fish effects were not strong enough to override the effects of time alone and time of day effects on tadpole activity.

Both before and after bluegill were added to cages, the proportion of tadpoles in leaf packs microhabitats did not differ between control and caged bluegill treatments (Figure 3.10; repeated measures ANOVA, before: $F = 1.42$, $df = 1, 8$, $P = 0.268$; after: $F = 2.53$, $df = 1, 8$, $P = 0.150$). There was a significant time effect both before ($F = 3.98$, $df = 5, 40$, $P = 0.005$) and after ($F = 11.41$, $df = 5, 40$, $P < 0.0001$) fish were added. The fish X time interaction was not significant before ($F = 0.66$, $df = 5, 40$, $P = 0.658$) or after ($F = 2.28$, $df = 5, 40$, $P = 0.064$) fish

were added. The proportion of tadpoles in leaf packs during the day was similar in treatment and control ponds before fish were added (repeated measures ANOVA, $F = 3.31$, $df = 1, 18$, $P = 0.1064$) but there was a slight difference after fish were added ($F = 3.68$, $df = 1, 8$, $P = 0.091$). Tadpoles tended to increase use of leaf packs when fish were present during the day but not at night (Figure 3.10).

DISCUSSION

Distribution Patterns

The occurrence of adult and juvenile California red-legged frogs in coastal central California was correlated with the presence or absence of introduced fishes (Study 1). Adult California red-legged frogs were present at 94% of the sites that lacked introduced fish and 52% of the sites where fish were present. Of the 20 sites where California red-legged frogs were absent, 16 (80%) had introduced fishes. Centrarchids (bass and sunfish species) may have the strongest effects on frogs since they were present at 100% of the sites with no frogs, and because they preyed voraciously on tadpoles in artificial pond experiments (Study 4). Western mosquitofish were present at almost all of the fish sites surveyed, but may have smaller effects on California red-legged frog occupancy patterns due to their small size and feeding behavior (discussed below). Ictalurids (catfish species) were present at 38% of the sites lacking California red-legged frogs and 47% of the sites where California red-legged frogs co-occurred with fish. Hayes and Jennings

(1986) noted that ictalurid and centrarchid fishes, in particular, appeared to be responsible for excluding native frogs from otherwise suitable habitats in California. Introduced trout species also have been found to affect the distribution of native frogs (Bradford 1989, Bradford et al. 1993, Knapp and Matthews 2000, Matthews et al. 2001, Gillespie 2001), but were uncommon in my study area.

Fish effects appeared to be greater in pond habitats than in streams, because California red-legged frogs occupied 100% of the fishless ponds but only 22% of the ponds with fish, and 89% of the fishless stream reaches versus 63% of the reaches with fish. In this study, introduced fishes were slightly more common in streams (present in 40% of the reaches surveyed) than in ponds (33%). Most ponds in this study were on VAFB and are more protected from fish introductions than ponds on private or National Forest lands. Introduced fish were present in all 4 of the river or stream systems in this study that had reservoirs (which also contained non-native fish) and the distribution of introduced fish in North America is generally positively related to the presence of impoundments (Gido and Brown 1999). Tadpoles may be more likely to coexist with fish in streams than in ponds if streams provide better refugia from fish (see Effects of Habitat below).

In this study, adult and juvenile California red-legged frogs were recorded at 52% of the sites where introduced fish were present. Ninety-four percent of these sites were close to fishless ponds or stream reaches; consequently, it is possible that dispersal from fishless to fish sites could be maintaining frog presence at sites with introduced fish (discussed below). Bulger et al. (2003) found that California red-

legged frogs moved at least 3.6 km between sites during breeding migrations. Therefore, the coexistence of adult frogs and fish at some sites could result from frog emigration from fishless sites where California red-legged frog reproduction is high, even if fish reduce or eliminate the frog's reproductive effort at sites where they are sympatric.

The results of similar studies are mixed. In the Central Valley of California, Hayes and Jennings (1989) detected California red-legged frogs at 56% of the sites where introduced fish were absent and 44% of the sites where fish were present; however, frog densities were lower at sites with fish (Hayes and Jennings 1986). Fisher and Shaffer (1996) found that native amphibian species (including California red-legged frogs) in California's Central Valley and Coast Ranges were found primarily in sites lacking introduced fishes. In contrast, the abundance of northern red-legged frogs was not correlated with the presence of introduced fishes in Washington (Adams 1999).

Effects of Habitat

The higher frequency of co-occurrence of California red-legged frogs with introduced fish in streams versus ponds could be due in part to the greater availability of refugia in streams. It may be easier for tadpoles to avoid fish in streams due to the presence of better types of refugia such as crevasses in banks and spaces under rocks. Large predatory fish are usually restricted to large pools in streams, so amphibian larvae could persist in pools that do not support fish such as

off-channel or shallow pools. In ponds, there are probably not enough refugia from fish to allow substantial proportions of California red-legged frog tadpoles to avoid fish predators throughout their relatively long larval period. I conducted trapping at VAFB ponds using unbaited hoop net traps and found that centrarchid and ictalurid fish species were common in the emergent vegetation around pond perimeters where California red-legged frogs frequently occur (unpublished data).

Periodic flooding is another factor that could facilitate the coexistence of frogs and introduced fish in streams. Many introduced fish species are not adapted to withstand the high, flashy flows characteristic of western U.S. rivers. High flow events have been followed by decreases in the abundance of non-native, but not native, fishes (Meffe 1984, Marchetti and Moyle 2001). Largemouth bass often do not sustain populations in streams, and their populations are maintained by stocking or immigration from reservoirs and farm ponds (Moyle 2002). As a consequence, densities of introduced fish may be lower in streams than in ponds.

A high proportion of the sites surveyed in Study 1 were natural ponds and streams with minimal disturbance, and most of the sites were in areas that are managed as protected or semi-protected areas (such as VAFB, Los Padres National Forest, and other areas). Complex vegetative structure in aquatic habitats has been positively correlated with larval amphibian survival because of increased cover for amphibian prey and a decreased foraging efficiency of their predators (Werner et al. 1983, Stenhouse 1984, Holomuzki 1989), and human-modified habitats often have decreased availability of refugia for tadpoles. Habitat alterations that increase water

temperature (e.g. reduced vegetative cover) and decrease flashy flood flows (e.g. impoundments) enhance populations of many introduced fishes (Moyle 1976a, Baltz and Moyle 1993). Therefore, the conditions present in my study area should have decreased fish effects relative to those in areas with a higher degree of habitat modification.

Pond Scale Effects of Introduced Fish

Reproductive success of the California red-legged frog was greatly reduced at sites with introduced fishes (Study 2), even though metamorph density in the fishless site Pond 91 was probably underestimated because there were still untransformed tadpoles present in this pond at the time the surveys were conducted. California red-legged frog tadpole and metamorph abundances were reduced in Pond 37, which contained fish, compared to ponds without fish even though the number of egg masses observed was higher in Pond 37 than the other ponds. Because no egg masses were found at the other two fish sites, however, it is difficult to pinpoint the frog life history stage that is most affected by the presence of introduced fish. There probably were some egg masses laid in each of the fish ponds, but egg densities were too low to be detected during surveys. The abundance of adult frogs varied greatly between years (Appendix E), and adult frogs were not more abundant at the fishless (77, 79, 91) than fish sites (37, 38, 46). The number of egg masses found in Study 2, however, was correlated with the maximum number of adult frogs observed in 1997 (Pearson correlation, $X^2 = 8.414$, $P = 0.004$). Tadpole

and metamorph abundances were certainly lower in fish than fishless ponds, regardless of the mechanism.

California red-legged frog tadpoles and metamorphs apparently were extremely low in abundance at the fish sites Ponds 38 and 46 over at least 7 years, because trapping and surveys have almost always failed to detect them at these sites (Appendix E). Similarly, California red-legged frogs and their tadpoles have never been detected at another VAFB site where there are three ponds with introduced predatory fish (Pine Canyon Lakes, Site 45), even though frogs are present in the drainage immediately below the lakes.

The results of this study are in agreement with studies of introduced trout and native mountain yellow-legged frogs (*Rana muscosa*). In surveys of >1700 sites, Knapp and Matthews (2000) found that frogs and trout were generally allopatric, but did co-occur at some sites, and the abundance of frog larvae was lower at sites with trout than at sites lacking trout. Pilliod and Peterson (2001) also found that native amphibian recruitment was reduced in lakes containing introduced trout compared to lakes without trout.

Reduced densities of California red-legged frog tadpoles and metamorphs at ponds with introduced fish, whether due to direct or indirect effects of fish on frogs or due to some other differences between ponds indicate that these areas are population “sinks” (Pulliam 1988, Dias 1996). In fish sites, frog population growth rates are probably negative in the absence of immigration. Adjacent sites lacking introduced aquatic predators may be the main sources of frog recruitment, via

immigration of metamorphosed frogs, to fish sites (see Appendices C & E). This would result in a landscape pattern with a limited proportion of sites where introduced fish and red-legged frogs co-occur, as seen in Study 1. Therefore the persistence of populations where California red-legged frogs co-occur with introduced fish is likely dependent on frog dispersal.

Frog Lifestages Vulnerable To Predation

Even though the experimental manipulations performed in Study 3 probably increased the vulnerability of California red-legged frog eggs to fish predators, the survivorship of eggs was not affected by the presence of western mosquitofish, bluegill or largemouth bass. This finding conflicts with studies that found some sunfish species consume the eggs of aquatic vertebrates (Huish 1957, Goodson 1965, Hayes and Jennings 1986). In contrast, bluegill, largemouth bass, western mosquitofish and brown bullhead fed readily on California red-legged frog tadpoles in artificial ponds (Studies 4 and 5), suggesting that predation on small tadpoles is likely to be the primary mechanism for introduced fish species effects on California red-legged frog populations.

California red-legged frog tadpoles grow quickly and reach a relatively large size prior to metamorphosis. For gape-limited fish predators such as mosquitofish and some sunfish species, it is possible that some tadpoles can reach a size refugium. Semlitsch (1987) noted that bluegill preyed only on the smallest amphibian larvae. Laboratory experiments conducted by Lawler et al. (1999)

showed that mosquitofish attack rates decreased as the size of California red-legged frog tadpoles increased, and that large tadpoles were never consumed. Using small experimental containers Komak and Crossland (2000) found that western mosquitofish repeatedly nipped the ends of tadpole tails until entire tails were eaten and tadpoles were immobilized, then they consumed the rest of the tadpoles. Mosquitofish in Study 5 inflicted injuries on tadpoles by nipping at their tail fins and these injuries were always fatal. In natural ponds, however, large California red-legged frog tadpoles have been observed to reach metamorphosis after sustaining tail and tailfin injuries and many even appeared to have regrown parts of their tails following injuries (unpublished data). California red-legged frog tadpoles that grew from hatchlings to 160 day-old larvae in the presence of mosquitofish in earthen artificial ponds sustained tail injuries, but did not have decreased survivorship compared to ponds lacking mosquitofish (Lawler et al. 1999). Attacks by mosquitofish on larval California newts (*Taricha torosa*) may be the cause of a high frequency of limb and digit truncations found in wild populations (Johnson et al. 2001).

The effects of western mosquitofish predation on California red-legged frog tadpoles are probably significant only with small tadpoles and in situations where there is little microhabitat separation between fish and tadpoles. The stomachs of mosquitofish collected in the wild have contained the small tadpoles of Pacific treefrogs (*Pseudacris regilla*) (Goodsell and Kats 1999), and those consumed by mosquitofish in experimental situations were only 8 mm TL (Goodsell and Kats

1999). Refugia present in Lawler et al.'s (1999) artificial ponds that may have increased California red-legged frog tadpole survivorship when mosquitofish were present were deep water, cobbles, and dense vegetation. The presence of alternate prey in natural ponds may also decrease predation on tadpoles, because tadpoles apparently are not a preferred prey item of mosquitofish (Lawler et al. 1999).

In contrast, largemouth bass and brown bullhead were able to consume even the largest California red-legged frog tadpoles. Injuries inflicted by brown bullhead on large California red-legged frog tadpoles in Study 4 probably resulted from bullhead difficulties in consuming large tadpoles. Since injuries inflicted on tadpoles by brown bullhead were more severe than those caused by mosquitofish, tadpole mortality would probably result in natural situations, as under experimental conditions. Largemouth bass consumed California red-legged frog tadpoles up to 100 mm total length in artificial ponds, and probably also consume California red-legged frog metamorphs since bass are known to consume frogs (Moyle 2002).

Red Swamp Crayfish

There was no effect of red swamp crayfish on the survivorship of California red-legged frog tadpoles in Study 4. Observations suggested that the approach velocities of foraging crayfish were much lower than the escape velocities of tadpoles. Crayfish cannot float and can only swim backward; therefore they only pursue prey that they can overtake by walking or capture from ambush (Gutierrez-Yurrita et al. 1998). Other studies have indicated that crayfish rarely capture

tadpoles that are large enough to be capable swimmers (Holomuzki 1989, Lefcort 1996). Indirect effects of crayfish on amphibian larvae may be more important than their direct effects because crayfish can reduce the abundance of aquatic macrophytes that may be used by larvae as refugia from other predators (e.g., fish) (Lodge et al. 1994).

In some situations crayfish have been shown to consume amphibian eggs and larvae (Gamradt and Kats 1996, Gherardi et al. 2001) and exclude amphibians from aquatic breeding sites through their aggressive behavior (Huner and Barr 1983, Gamradt et al. 1997). The ability of amphibian larvae to escape from crayfish is probably related to the degree to which the larvae are confined. Studies that demonstrated red swamp crayfish captures of amphibian larvae used smaller experimental arenas than those used in this study. The ability of amphibian larvae to escape from crayfish is probably reduced in natural pools or ponds that shrink to a small size in the summer (see Gamradt and Kats 1996).

Antipredator Behaviors

California red-legged frog tadpoles appeared to lack fixed antipredator adaptations (e.g., toxicity, unpalatability, cryptic coloration, and low baseline levels of activity) to the introduced fish species studied. In fact, tadpoles were palatable to bluegill, largemouth bass, western mosquitofish, and brown bullhead. Tadpoles displayed some plastic behavioral responses (increased refuge use and decreased activity) to free-ranging fish and crayfish, although it is unclear whether these were

actually antipredator responses. When free-ranging blue gill were present, no small tadpoles were active, the proportion of tadpoles in leaf packs significantly increased, and the proportions in the floating plant and open areas significantly decreased. Bluegill feed in aquatic vegetation and throughout the water column (Moyle 1976b); therefore, the leaf pack microhabitat was probably the “safest” area in ponds with bluegill. Decreased tadpole activity may have decreased the risk of predation (see Skelly 1994) because bluegill feed using visual cues. Similarly, significantly more small tadpoles were in refugia when free-ranging mosquitofish were present than when they were absent. Even though there was no significant effect of crayfish on tadpole survivorship, tadpoles altered microhabitat use when crayfish were present. Responses to crayfish could be related to physical disturbance caused by the active crayfish, although it is unclear why tadpoles did not increase use of the floating plant when crayfish were present since this microhabitat was inaccessible to the crayfish. Small tadpole responses to largemouth bass could not be determined since no tadpoles survived when bass were present, which could suggest that even if tadpoles displayed antipredator responses they were ineffective against bass in a confined situation.

In contrast, there was no significant behavioral response of large tadpoles to largemouth bass or brown bullhead even though these fishes were dangerous predators. However, the probability of finding an effect if there was one was reduced by low statistical power. For example, since the number of large tadpoles surviving in largemouth bass ponds ranged from 1 to 5 (Table 3.5), the proportions

found the three microhabitats varied greatly among the fish ponds. In fact, there was a tendency for tadpoles to avoid open areas in the presence of bass and bullhead, and tadpoles were probably the most vulnerable to fish in open areas. Responses via activity levels were not detected in part because large tadpoles were not active during the day in both control and predator ponds. In natural habitats, California red-legged frog tadpoles appear to increase nocturnal activity and decrease daytime activity as they begin transformation (personal observation). Lawler et al. (1999) also found that small California red-legged frog tadpoles decreased activity in the presence of introduced fish, but that large tadpoles did not. Decreased antipredator behavior with increased size or developmental stage has been noted for other amphibian species as well (Anholt et al. 1996).

Small tadpoles had strong behavioral responses when mosquitofish and bluegill were free-ranging (Studies 4 and 5), but did not respond significantly to visual, chemical, or tactile cues produced by mosquitofish and bluegill (Study 6). Many species of amphibians that coevolved with particular species of predators recognize and respond to chemical cues from these predators in the absence of actual predation risk (Kats et al. 1988, Sih and Kats 1994, Holomuzki 1995, Gallie et al. 2001). It appears that California red-legged frog tadpoles may recognize the presence of introduced fish as a potential threat in general, but they do not recognize introduced fish species as predators per se. Alterations in the activity levels and microhabitat use of tadpoles in response to predators in Studies 4 and 5 could have been due to physical disturbance by active predators. In Study 6 the slight decrease

in tadpole activity during the day when bluegill were present could have been due to increased bluegill activity in the enclosures during the day.

Surprisingly, more tadpoles were in leaf packs during the day in “fish” ponds than in fishless ponds both *before* and after bluegill were added to enclosures in Study 6 (Figure 3.10). Tanks had been scrubbed and refilled with water, and fresh floating plants and leaf packs were added prior to this experiment, so no explanation is known for a possible tank effect. This study could have been improved by extending the sampling period after fish were added. Tadpole refuge use in the caged mosquitofish trial in Study 6 was affected by time of day, and since the manipulation exposed tadpoles to temperature fluctuations that were greater than would be selected by tadpoles in natural systems, it is possible that responses to fish were masked. Since no tadpoles died it is unclear whether tadpoles were stressed by these thermal conditions. In some studies prey responded to predator chemical cues only after predators had been fed conspecific prey (see Chivers and Smith 1995, Chivers et al. 1996), but in this study fish were not fed tadpoles prior to experiments.

Amphibian larvae were not expected to display antipredator responses to types of predators with which they have no recent evolutionary experience. For example, amphibian species that breed in temporary pools and have never encountered fish predators generally do not exhibit antipredator adaptations to fish (Kats et al. 1988). While Kiesecker and Blaustein (1998) found that microhabitat use by northern red-legged frog tadpoles was similar in enclosures with and without

introduced smallmouth bass (*Micropterus dolomieu*), Pearl et al. (2003) found that northern red-legged frog larvae increased refuge use in response to chemical cues from native fish, introduced blue gill, and introduced red swamp crayfish. California red-legged frogs often inhabit permanent aquatic habitats, and thus like the northern red-legged frog have evolved with fishes that may prey on amphibians. In central California, native potential fish predators of tadpoles include salmonids, cottids, two cyprinids, and one centrarchid (Hayes and Jennings 1986; see also Swift et al. 1993, Moyle 2002). Responses of tadpoles to introduced fishes in this study could represent generalized adaptations to native fishes. Even though the frog eggs and tadpoles used in my study were from populations that were allopatric with native predatory fish, gene flow from populations exposed to native fishes could explain antipredator responses. In addition, large tadpoles appeared to show lower levels of antipredator responses to fish than small tadpoles, and this may be related to the inability of many small species of native fish to consume large tadpoles.

In this study, introduced fish significantly decreased survivorship of tadpoles although tadpoles displayed “characteristic” antipredator behaviors, and these behaviors may not decrease predation rates enough to allow some larvae to survive to adulthood in natural situations. Even though my experimental manipulations probably increased the chance of predation, reduced frog recruitment in the pond scale study suggests that tadpoles cannot survive in ponds with introduced fishes. If native fish were not important predators on California red-legged frog larvae due to habitat segregation, microhabitat preferences, or feeding modes, red-legged frogs

may not have developed strong antipredator adaptations. Many studies of larval amphibians that demonstrated strong antipredator responses to fish predation are species that are native to the eastern United States. Eastern and western North American ranid frogs are different lineages: eastern species were probably derived from western European groups, and the ancestral stock of the western group may have entered North America via the Bering land bridge or once may have been widespread throughout the Holarctic region (Case 1978; see also Duellman and Sweet 1999). Predatory fish communities are generally more diverse in eastern versus western North America (see Hayes and Jennings 1986). Therefore, antipredator responses to fish may not be expressed as strongly or be as common in western versus eastern ranid frogs.

Some researchers have observed that amphibian antipredator behaviors alone are relatively ineffective against predatory fish (Hero et al. 2001). Amphibian species that breed in habitats with strong predation pressure from fish mainly rely on unpalatability instead of plastic behavioral responses (Kats et al. 1988, Lawler and Hero 1997, Hero et al. 2001). The results of Studies 4 and 5 suggest that California red-legged frog larvae are palatable to several introduced species of fish, which strengthens the assumption that native fishes may have not presented strong selection pressures on California red-legged frogs. Whether native fishes consume California red-legged frog larvae, however, has not been studied.

Another possible explanation for the apparent tadpole antipredator behaviors observed in this study is that these are relict behaviors that arose during former

historic periods of natural selection or were inherited from a remote ancestor. Retained traits that no longer have use can persist for at least 70,000 to 300,000 years (Coss 1998) and can continue through speciation events (Bolen et al. 2000). For example, California ground squirrels (*Spermophilus beecheyi*) exhibited antisnake behavior to rattlesnakes (*Crotalus* sp.) even though their populations have experienced a prolonged period of relaxed selection (Coss 1993, 1998). Several bird species that are hosts to obligate brood parasites retain defenses against parasitism after they are no longer parasitized (McLean and Rhodes 1991, Rothstein 2001) or display host defenses that were probably inherited from an ancestral taxon (Bolen et al. 2000). The retention of adaptations in the absence of selection is probably related to the length of time needed for loss through genetic drift, as well as the costs of maintaining them, such as would occur if tadpoles responded to non-predatory fishes in a way that decreased tadpole feeding rates (Skelly 1992; see Lima and Dill 1990). However, the costs of chemical predator induced defenses were not found to affect growth or development rates western toads, *Bufo boreas* (Benard and Fordyce 2003) and antipredator behaviors or alterations in morphology in response to predators were not found to affect tadpole growth rates in pool frogs, *Rana lessonae* (Van Buskirk and Arioli 2002) and western chorus frogs, *Pseudacris triseriata* (Bridges 2002).

The antipredator behaviors exhibited by California red-legged frog tadpoles may be ineffective against the foraging modes of introduced fish. Native fish feed primarily by sight in the water column or on organisms exposed on surfaces, and

rarely disturb aquatic vegetation or benthic sediment. In contrast, many introduced centrarchids search vegetation and benthic sediment for prey (see Hayes and Jennings 1986, Moyle 2002). Since California red-legged frog tadpoles frequently use aquatic vegetation and benthic areas (Chapter 2), they may be more vulnerable to introduced than native fishes. Similarly, California newt larvae have antipredator adaptations for native predators that are not adequate to allow coexistence with introduced red swamp crayfish or mosquitofish (Gamradt and Kats 1996). Gillespie (2001) also found that amphibian larvae possessed antipredator adaptations that were effective in promoting co-existence with native but not introduced species of fish.

California red-legged frog tadpoles responded to the presence of introduced crayfish, even though crayfish did not affect their survivorship, similar to the findings of Fauth (1990). Some amphibian species that evolved with crayfish display antipredator behaviors in the presence of crayfish (Holomuzki 1989, Fauth 1990, Nystrom and Abjornsson 2000) and some native amphibian species respond to chemical cues of introduced crayfish (Pearl et al. 2003), whereas other amphibian species do not display these behaviors (Nystrom and Abjornsson 2000). It is unlikely that California red-legged frogs encountered native crayfish during their recent evolutionary history (see Reigel 1959). Only 5 of the 390 species of crayfish native to North America occur naturally west of the Rocky Mountains (Lodge et al. 2000b). Other California amphibian species that have not coevolved with crayfish do not display adaptations that deter crayfish predation (Gamradt and Kats 1996). It

is likely that tadpole responses found in this study were due to physical disturbance rather than actual antipredator behavior. Conversely, responses to physical disturbance could be considered generalized antipredator responses if these responses decrease predation rates to multiple types of predators.

Introduced fish may not directly eliminate adult and juvenile California red-legged frogs from aquatic habitats, but this study indicates that they drastically reduce frog recruitment thereby eliminating some source sites and increasing population fragmentation. Small, fragmented populations are more vulnerable to stochastic disturbances and have higher extinction probabilities. Reductions in recruitment and isolation of populations can lead to regional population declines. Pressures from introduced fishes are probably one of the most important factors affecting the persistence of remaining California red-legged frog metapopulations, and may be second only to habitat loss and degradation.

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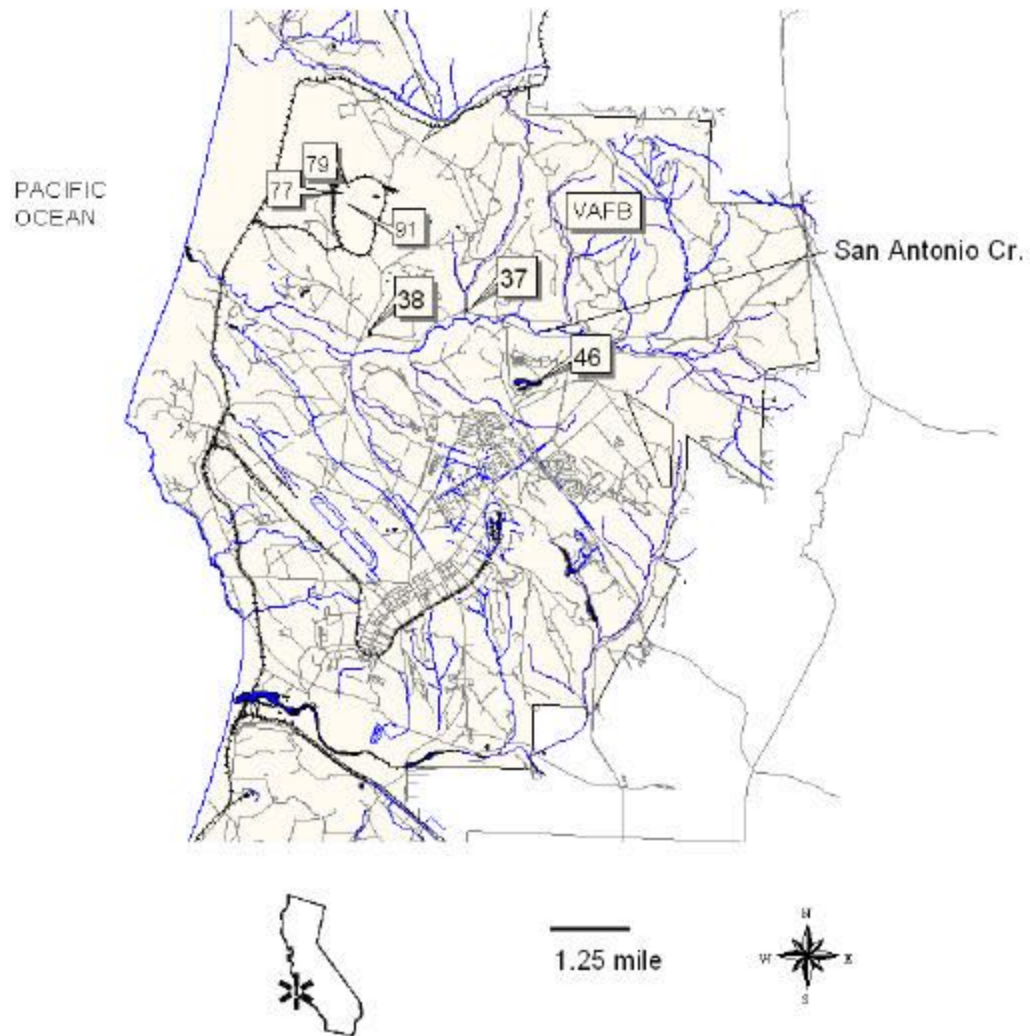


Figure 3.1. Location of sites sampled for California red-legged frog eggs, tadpoles and metamorphs in Study 2 on Vandenberg Air Force Base, California.

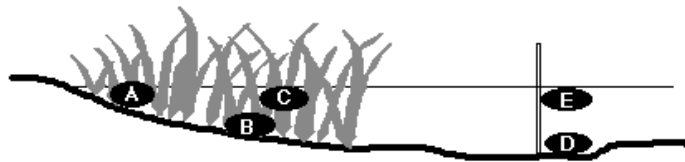


Figure 3.2. Cross-section of pond shoreline showing one example of a transect for sampling tadpoles using funnel traps (dark ovals) in different microhabitats (letters) used in Study 2. Traps at microhabitats A, B, and D were placed on the bottom of the pond. The trap at microhabitat C was suspended from the emergent vegetation. A post (vertical lines) was used to mark the transect and suspend a trap just below the water surface at microhabitat E.

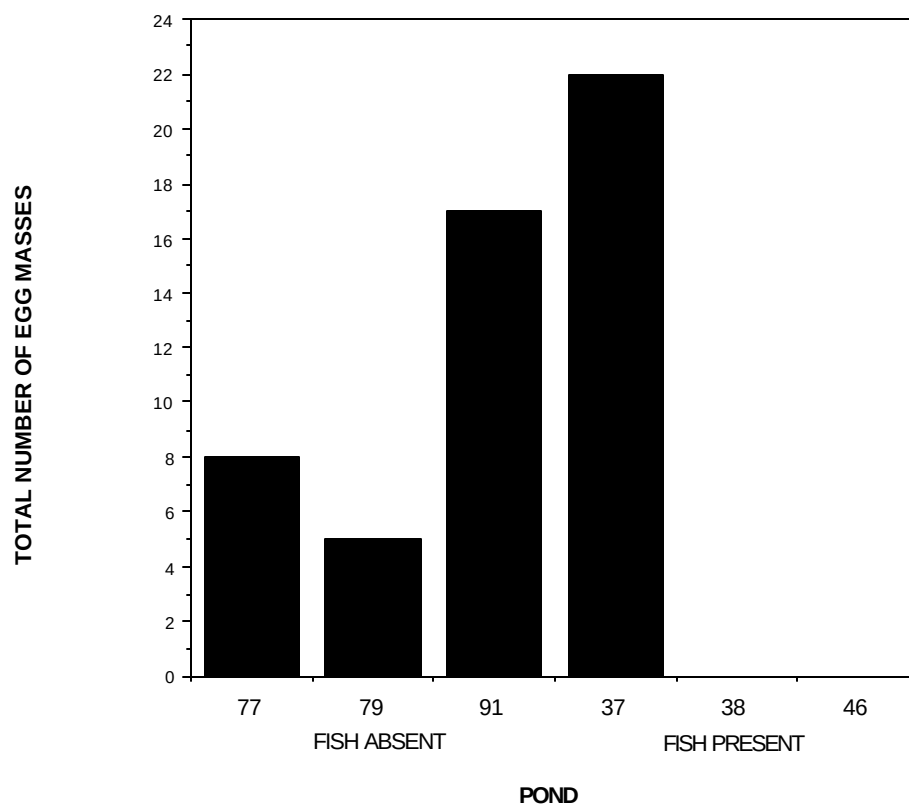


Figure 3.3. Total numbers of California red-legged frog egg masses observed during visual encounter surveys in Study 2. Each pond was surveyed in its entirety twice during the peak breeding season. The number of egg masses in ponds with fish was not significantly different from ponds without fish (Mann-Whitney U test, $P = 0.51$).

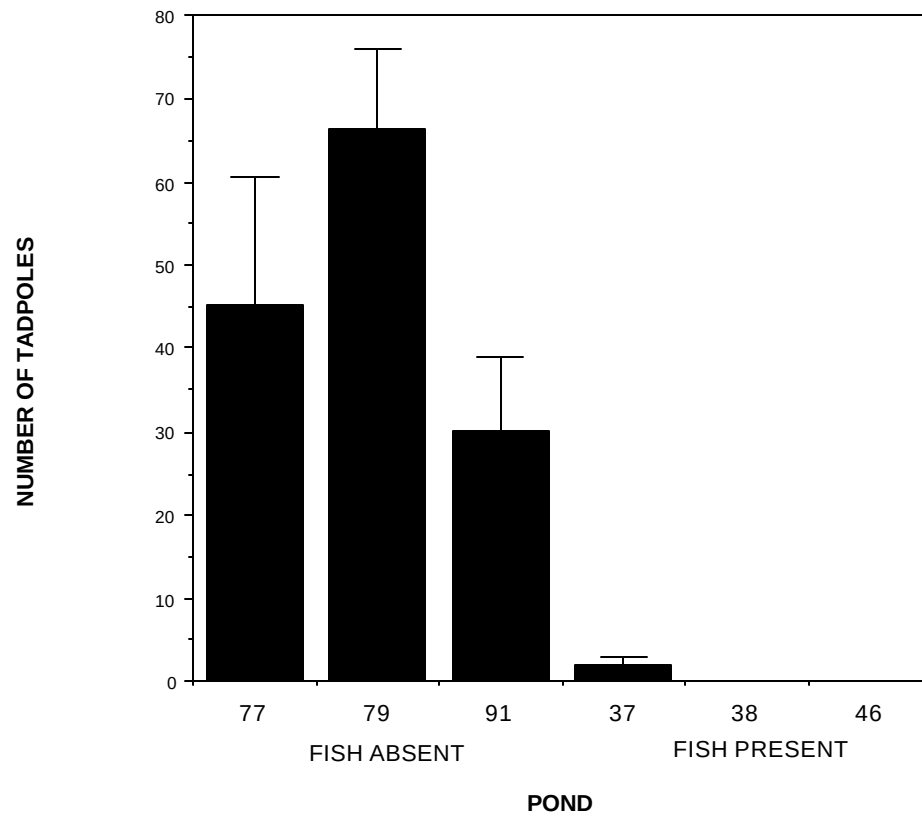


Figure 3.4. Numbers of California red-legged frog tadpoles trapped in ponds (mean ± 1 SE) in Study 2. Each pond was sampled 3 times when tadpoles were at late larval stages. Tadpole abundance in ponds with and without fish was significantly different (Mann-Whitney U test, $P = 0.046$).

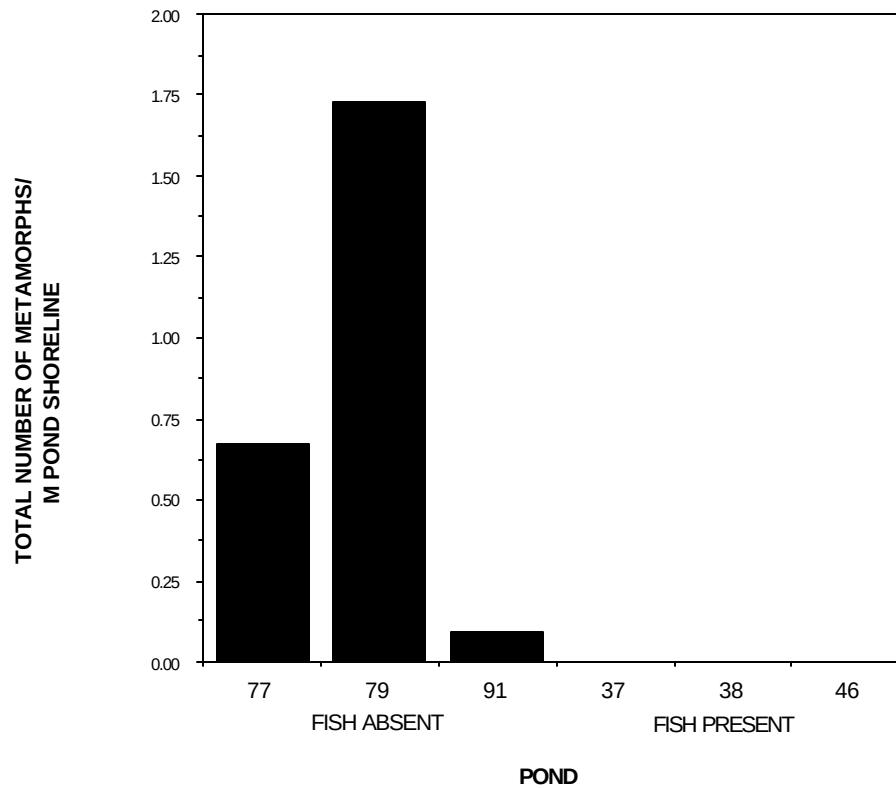


Figure 3.5. Densities of California red-legged frog metamorphs observed during visual encounter surveys in Study 2. Each pond was surveyed in its entirety 3 times during the peak of metamorph activity, except Pond 91 that still had some untransformed tadpoles at the end of the study. Densities are the cumulative number of metamorphs seen at each site across all surveys divided by pond shoreline (m). Metamorph density at ponds with and without fish was significantly different (Mann-Whitney U test, $P = 0.046$).

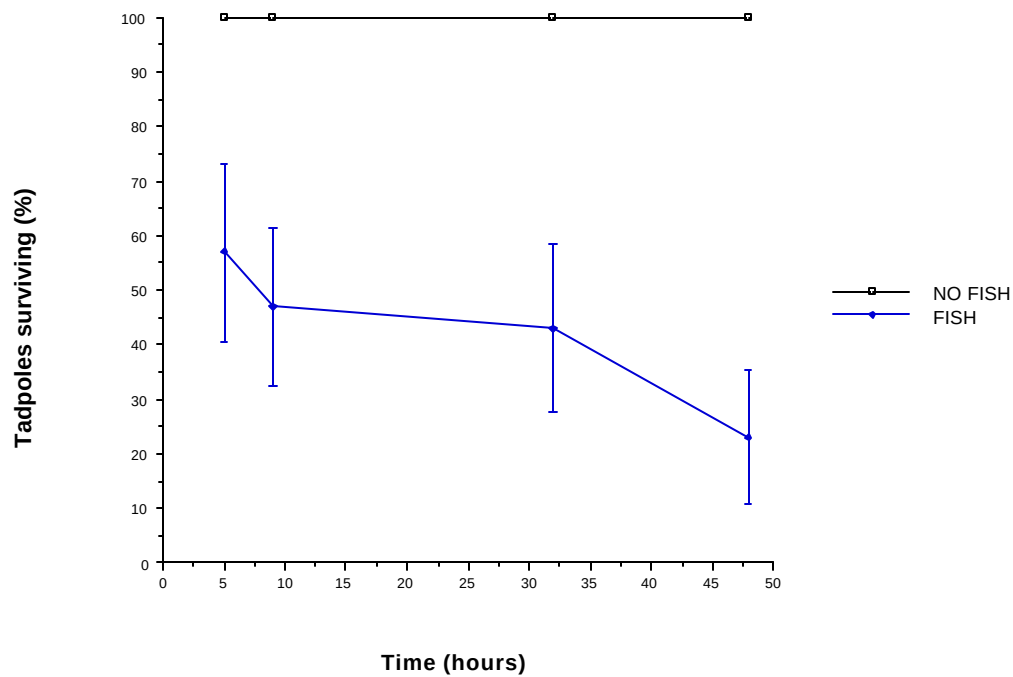


Figure 3.6. Mean percent survival (± 1 SE) of small California red-legged frog tadpoles in microcosm experiments with and without free-ranging western mosquitofish in Study 5. Time is hours following the introduction of mosquitofish. The initial number of tadpoles was 6 per microcosm.

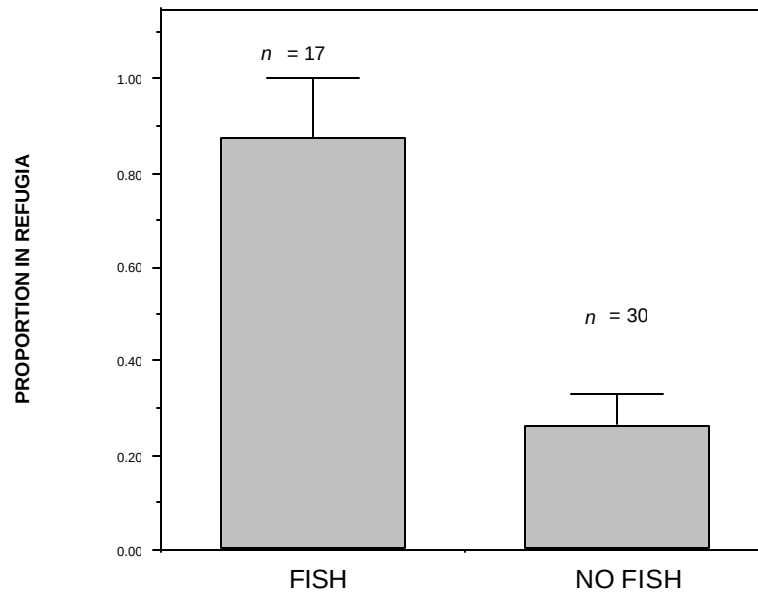


Figure 3.7. Mean proportions (± 1 SE) of small California red-legged frog tadpoles in refugia in microcosms with and without free-ranging mosquitofish in Study 5. Total numbers of tadpoles surviving of the original 30 in microcosms with ($N = 5$) and without ($N = 5$) fish are shown above bars.

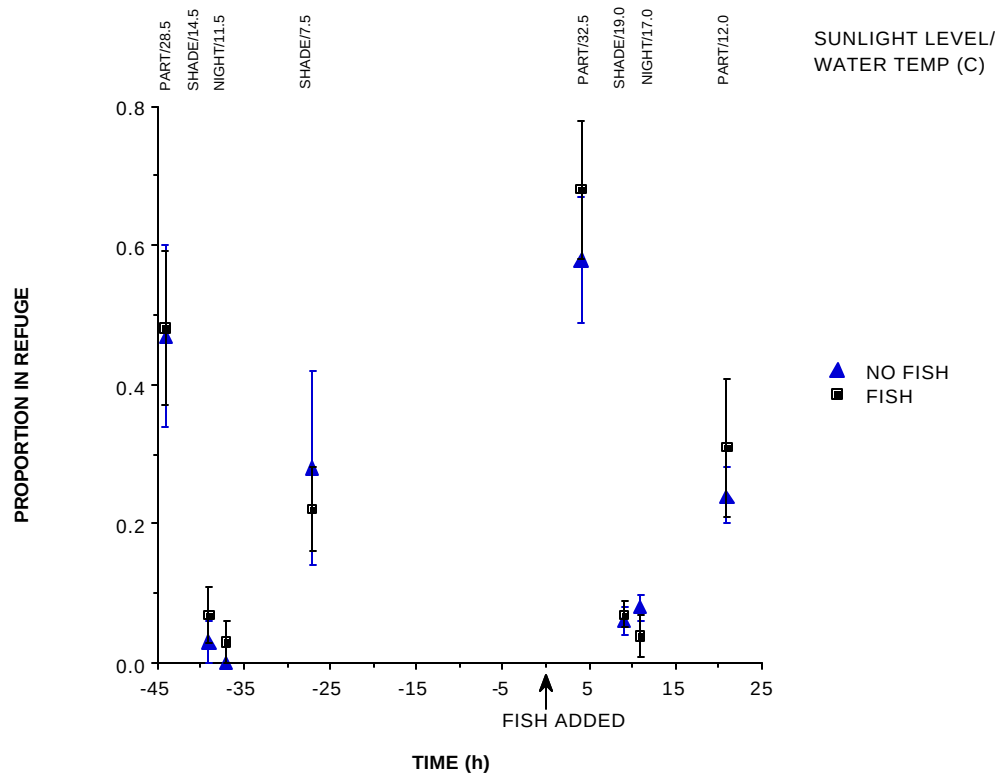


Figure 3.8. Mean proportions (± 1 SE) of California red-legged frog tadpoles in refugia in microcosms with ($N = 5$) and without ($N = 5$) nonlethal (caged) mosquitofish in Study 6. Mosquitofish were added to enclosures at time 0. Each microcosm had 8 small tadpoles.

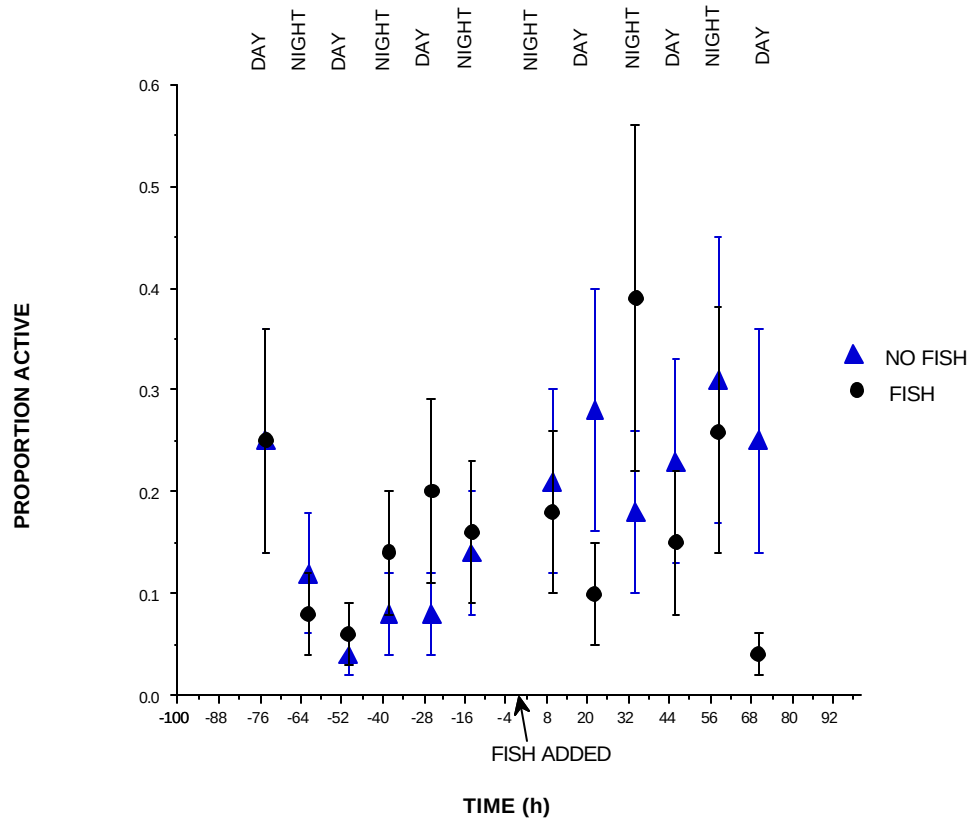


Figure 3.9. Mean proportions (± 1 SE) of California red-legged frog tadpoles active in artificial ponds with ($N = 5$) and without ($N = 5$) nonlethal (caged) bluegill in Study 6. Bluegill were added to enclosures at time 0. Each artificial pond had 10 small tadpoles.

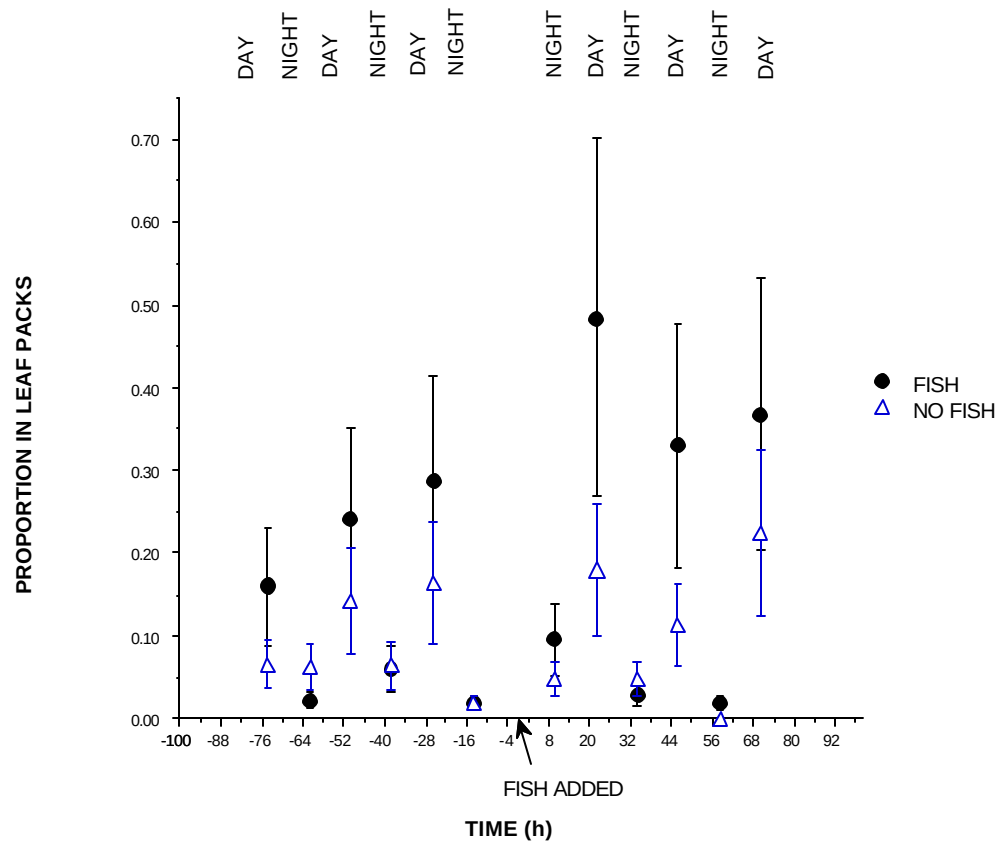


Figure 3.10. Mean proportions (± 1 SE) of California red-legged frog tadpoles in leaf packs in artificial ponds with ($N = 5$) and without ($N = 5$) nonlethal (caged) bluegill in Study 6. Bluegill were added to enclosures at time 0. Each artificial pond had 10 small tadpoles.

Table 3.1. Study design for Chapter 3: Interactions of introduced fish and crayfish with California red-legged frogs (RLF).

Name	Type of Study	Question	Scale
Study 1: Distribution Patterns	Correlational	Is the presence of fish associated with the presence of RLF?	Landscape
Study 2: RLF Reproduction in Ponds	Field Comparisons	Is the presence of fish related to a decreased abundance of RLF eggs, tadpoles, and metamorphs?	Pond
Study 3: Fish predation on RLF eggs	Controlled Experiments	Will mosquitofish, bluegill, & largemouth bass eat RLF eggs?	Mesocosm
Study 4: Predation on RLF tadpoles & antipredator behavior of tadpoles	Controlled Experiments	Will crayfish, bluegill, largemouth bass & brown bullhead eat small and/or large RLF tadpoles? Do RLF larvae use refugia to escape from predators?	Mesocosm
Study 5: Mosquitofish predation on small RLF tadpoles & antipredator behavior of tadpoles	Controlled Experiments	Will mosquitofish consume small RLF tadpoles? Do RLF larvae use refugia to escape from predators?	Microcosm
Study 6: Non-lethal predator effects on small RLF tadpole behavior	Controlled Experiments	Do small RLF tadpoles alter their behavior with caged mosquitofish and bluegill, suggesting a response to chemical, visual, or tactile cues from predators?	Microcosm (Mosquitofish) Mesocosm (Bluegill)

Table 3.2. Predation trials on small and large California red-legged frog tadpoles in Study 4. The numbers of crayfish or fish in each predator pond (5 ponds per trial) and the numbers of tadpoles per pond (10 ponds per trial) are listed under *n*. Size is mean total length (range) of experimental animals in mm. Temperature is minimum and maximum water temperatures (°C) in artificial ponds between the addition of tadpoles and the termination of the trial.

Trial	<i>n</i>	Size	Added	Terminated	Temperature
Crayfish/ Small tadpoles	1 20	104 (100-110) 17 (14-23)	21 Mar 1998 22 Mar 1998 1200 h	23 Mar 1998 1215 h	16.0-21.0
Bluegill/ Small tadpoles	1 20	132 (110-170) 17 (14-23)	7 Mar 1998 14 Mar 1998 1600 h	15 Mar 1998 1530 h	16.0-19.5
LM Bass/ Small tadpoles	1 20	156 (140-200) 17 (14-23)	16 Mar 1998 19 Mar 1998 1200 h	20 Mar 1998 1100 h	12.0-19.0
LM Bass/ Large tadpoles	1 5	231 (210-260) 84 (44-112)	5 Aug 1998 9 Aug 1998 1230 h	10 Aug 1998 1330 h	20.0-28.0
Bullhead/ Large tadpoles	1 5	250 (240-270) 83 (44-114)	14 Aug 1998 16 Aug 1998 1130 h	17 Aug 1998 1130 h	21.0-25.0

Table 3.3. Occurrence of California red-legged frogs and introduced fish species in coastal central California in Study 1. Numbers are total sites per category (ponds, stream reaches). A significant association between frogs and fish was tested using a Chi-square contingency table analysis (df=1, $\alpha=0.5$).

	Fish present	Fish absent	χ^2	<i>P</i>
Red-legged frogs present	17 (2, 15)	58 (27, 31)	22.89	<0.0001
Red-legged frogs absent	16 (7, 9)	4 (0, 4)		

Table 3.4. Numbers of California red-legged frog eggs in artificial ponds with ($N = 5$) and without ($N = 5$) fish in Study 3. Survivorship of eggs in ponds with and without fish was not significantly different for each trial ($P > 0.05$). The initial number of eggs was 10 per pond.

Trial	Fish	Mean Egg Survivorship	Percent of Original	Range Per Pond
Mosquito- fish	Present	9.8	98	9-10
	Absent	10.0	100	10
Bluegill	Present	9.6	96	8-10
	Absent	10.0	100	10
Largemouth Bass	Present	10.0	100	10
	Absent	10.0	100	10

Table 3.5. Numbers of California red-legged frog tadpoles surviving in artificial ponds with ($N = 5$) and without ($N = 5$) crayfish or fish in Study 4. Differences in tadpole survival between ponds with and without predators were tested using Mann-Whitney U tests for each trial. Initial numbers of tadpoles were 20 small or 5 large per pond.

Trial	Fish	Mean Tadpole Survivorship	Percent of Original	Range Per Pond	<i>P</i>
Crayfish/ Small tads	Present	19.4	97	19-20	0.500
	Absent	19.0	95	18-20	
Bluegill/ Small tads	Present	4.6	23	0-10	0.008
	Absent	19.2	96	18-20	
LM Bass/ Small tads	Present	0	0	0	0.004
	Absent	19.8	99	19-20	
LM Bass/ Large tads	Present	2.8	56	1-5	0.034
	Absent	4.8	96	4-5	
Bullhead/ Large tads	Present	3.8	76	3-5	0.004
	Absent	5.0	100	5	

Table 3.6. Behavior of small California red-legged frog tadpoles in artificial ponds with ($N = 5$) and without ($N = 5$) free-ranging crayfish in Study 4. Activity is mean percent (± 1 SE) active, and microhabitat use is mean percent (± 1 SE) of surviving tadpoles in each microhabitat type. The activity of tadpoles was not significantly different between ponds with and without crayfish (Independent t -test, $P = 0.52$). The effect of crayfish on the distribution of tadpoles among microhabitats was nearly significant (MANOVA, $P = 0.052$). Total number surviving of the original 20 tadpoles per pond is n .

	Activity	Microhabitat Use			n
		Floating Plant	Leaf Pack	Open areas	
Absent	7.4 (2.6)	28 (7.1)	4 (2.5)	68 (6.8)	95
Present	12.3 (6.7)	20 (4.6)	7 (2.6)	73 (6.6)	97

Table 3.7. Behavior of small California red-legged frog tadpoles in artificial ponds with ($N = 4$) and without ($N = 5$) free-ranging bluegill in Study 4. Activity is mean percent active (± 1 SE), and microhabitat use is mean percent (± 1 SE) of surviving tadpoles in each microhabitat type. There was a significant effect of bluegill on tadpole activity (Mann-Whitney U test, $P = 0.010$) and microhabitat use (MANOVA, $P = 0.004$). Total number surviving of the original 20 tadpoles per pond is n .

	Activity	Microhabitat Use			n
		Floating Plant	Leaf Pack	Open areas	
Bluegill					
Absent	21 (6.6)	18 (5.9)	4 (2.6)	77 (5.0)	96
Present	0 (0)	0 (0)	78 (14.3)	22 (14.3)	23

Table 3.8. Behavior of large California red-legged frog tadpoles in artificial ponds with ($N = 5$) and without ($N = 5$) free-ranging largemouth bass in Study 4. Activity is mean percent active (± 1 SE), and microhabitat use is mean percent (± 1 SE) of surviving tadpoles in each microhabitat type. The distribution of tadpoles among microhabitats was not significantly different in the presence versus absence of fish (MANOVA, $P = 0.4$). Total number surviving of the original 5 tadpoles per pond is n .

	Activity	Microhabitat Use			n
		Floating Plant	Leaf Pack	Open areas	
LM Bass					
Absent	0 (0)	37 (7.0)	30 (11.0)	33 (9.9)	24
Present	0 (0)	54 (13.9)	31 (8.4)	15 (9.0)	14

Table 3.9. Behavior of large California red-legged frog tadpoles in artificial ponds with ($N = 5$) and without ($N = 5$) free-ranging brown bullhead in Study 4. Activity is mean percent active (± 1 SE), and microhabitat use is mean percent (± 1 SE) of surviving tadpoles in each microhabitat type. The distribution of tadpoles among microhabitats was not significantly different in the presence versus absence of fish (MANOVA, $P = 0.13$). Total number surviving of the original 5 tadpoles per pond is n .

	Activity	Microhabitat Use			n
		Floating Plant	Leaf Pack	Open areas	
Bullhead					
Absent	0 (0)	52 (4.9)	20 (11.0)	28 (10.2)	25
Present	0 (0)	40 (17.0)	55 (16.6)	5 (5.0)	19

CHAPTER 4
A SYNTHESIS OF INDIVIDUAL AND MULTIPLE
PREDATOR EFFECTS ON CALIFORNIA
RED-LEGGED FROG METAPOPOPULATIONS

ABSTRACT

California red-legged frog tadpoles were palatable to introduced largemouth bass, bluegill, brown bullhead, and western mosquitofish, while tadpoles, metamorphs, and juveniles were consumed by introduced bullfrogs. Introduced fish had stronger effects than bullfrogs or crayfish on California red-legged frogs in this study. Largemouth bass were the most efficient predators on California red-legged frog tadpoles in mesocosms, and are probably primarily responsible for decreased recruitment of the frog observed at coastal central California ponds with multiple types of introduced predators. At one pond, the abundances of all life stages of California red-legged frogs declined following the introduction of centrarchid fishes (bass and sunfish species), but appeared to be unaffected by bullfrogs. The presence of bullfrogs alone is probably not a major factor regulating the distribution of adult and juvenile California red-legged frogs in the region studied, but since environmental conditions may influence bullfrog densities, this conclusion may not apply across geographic regions. Nevertheless, predation by introduced bullfrogs may also be a factor in California red-legged frog declines. Evidence from this

study supports the hypothesis that non-native fish may be viewed as “keystone invaders”.

There was a significant positive association between the presence of introduced fishes and bullfrogs in central coastal California. Multiple types of introduced predators appear to have combined negative effects on California red-legged frogs in ponds, but in stream pools interactions between predators may decrease individual predator effects on red-legged frog survivorship. The generalized antipredator responses of California red-legged frog tadpoles to one predator may decrease predation risk to other predators.

The region I studied may differ from other areas in the California red-legged frog’s geographic range in that it had a relatively high proportion of introduced predator-free (source) sites in close proximity to predator (sink) sites. The local coexistence of red-legged frogs with introduced predators is probably maintained by immigration from nearby source sites. Preliminary information on California red-legged frog dispersal suggests that there is high connectivity among frog habitats in the region studied.

INTRODUCTION

Evidence presented in previous chapters indicates that populations of the California red-legged frog are reduced by introduced bullfrogs and fish through predation on tadpoles and metamorphs, which greatly reduces or eliminates

recruitment to frog populations in coastal central California ponds. In this chapter I discuss: 1) the relative importance of bullfrog versus fish and crayfish predation in reducing frog abundances, 2) the combined effects of multiple types of introduced predators, and 3) the role of frog dispersal in maintaining local coexistence between California red-legged frogs and introduced predators. The possible influence of the environmental characteristics of my study area on the results of these studies is also discussed.

The studies described in Chapters 2 and 3 used similar methods for each of the introduced aquatic predators so that the relative importance of these species to California red-legged frog declines could be evaluated. Below I address the hypothesis that bullfrogs were and are the main cause of declines in western North American ranid frogs (Moyle 1973, Bury and Luckenbach 1976, Hammerson 1982). This hypothesis was questioned by Hayes and Jennings (1986), who proposed that introduced fish had a greater potential than bullfrogs to reduce native frog populations. In addition, there has been recent interest in the effects of multiple predators (reviewed below). Although my experimental manipulations did not examine California red-legged frog interactions with multiple predators, my results provide predictions for future studies of multiple predator effects on frog populations. Finally, the results of my studies suggest that California red-legged frog persistence in habitats occupied by introduced predators depends on connectivity between predator-free (source) sites and sites with introduced predators (sink sites).

RELATIVE IMPORTANCE OF BULLFROGS, FISH AND CRAYFISH

California red-legged frog tadpoles were palatable to introduced largemouth bass, bluegill, brown bullhead, and western mosquitofish, while tadpoles, metamorphs, and juveniles were consumed by introduced bullfrogs. Overall, introduced fish had stronger effects than bullfrogs or crayfish on California red-legged frogs in this study. At a landscape scale, the negative correlation between California red-legged frogs and introduced fish was greater than that of bullfrogs, since the frog occurred at 78% of the sites where bullfrogs were present but only 52% of the sites with introduced fishes. California red-legged frog reproduction was reduced to a greater degree in ponds with fish and bullfrogs than in ponds with only bullfrogs. Although the numbers of egg masses did not differ significantly between predator and predator-free ponds, the only ponds where no egg masses were detected had introduced fish. The numbers of tadpoles and densities of metamorphs were reduced in both bullfrog and fish ponds compared to ponds lacking introduced predators, and the reductions tended to be greater at fish than bullfrog sites. Only 1 California red-legged frog metamorph was found at the sites with introduced fish, and it may have been an immigrant from an adjacent site. Bullfrog predation rates on California red-legged frogs in a river system were low since only 1 of 47 adult bullfrogs collected had consumed a red-legged frog, even though red-legged frogs were abundant at the collection site.

Largemouth bass were the most efficient predators of tadpoles in mesocosms (Chapter 3, Study 4). Bass consumed all 20 small tadpoles in each of 5 mesocosms and 44% of large tadpoles within 24 hours. Bullfrogs consumed 25% of large tadpoles (Chapter 2, Experiment II) and brown bullhead 22% of large tadpoles (Chapter 3, Study 4) in 24 hours, with bullfrogs being more effective at consuming entire large tadpoles than brown bullhead. Bluegill consumed 67% of small tadpoles within 24 hours, and crayfish did not consume any. Although trials with small tadpoles and bullfrogs were not performed, it is likely that bluegill prey on small tadpoles at higher rates than bullfrogs because bluegill feed throughout the water column (Moyle 1976) whereas bullfrogs feed almost entirely near or above the water surface (see Bury and Whelan 1984). California red-legged frog tadpoles may be more vulnerable to bullfrogs during late metamorphic stages when tadpoles come to the surface to gulp air. Kiesecker and Blaustein (1998) studied bullfrog predation on the tadpoles and metamorphs of northern red-legged frogs (*R. a. aurora*). In enclosure experiments, they found no effect of adult bullfrogs on the survival of northern red-legged frog tadpoles due to tadpole use of deep water refugia, but bullfrogs significantly decreased the survivorship of northern red-legged frog metamorphs (Kiesecker and Blaustein 1998). However, confining metamorphs to enclosures probably increased their vulnerability to bullfrogs because they are more terrestrial than bullfrogs in nature (Twedt 1993, Pearl et al. 2004).

The greatest reductions in California red-legged frog recruitment ponds with introduced predators appear to occur primarily through fish predation on tadpoles,

since fish did not eat frog eggs in mesocosms and very few or no metamorphs were found at ponds with fish. The 3.5 to 7+ month larval period of the California red-legged frog (Dickerson 1906, Storer 1925, Fellers et al. 2001) results in a long period in which tadpoles can potentially encounter fish. The length of time that tadpoles and metamorphs would encounter bullfrogs is probably 1 to 1.5 months when tadpoles are undergoing transformation and metamorphs are present around pond margins. The tendency of metamorphs to move away from aquatic habitats shortly after transformation (see Characteristics of California Red-legged Frog Dispersal, this chapter; Pearl et al. 2004) and return once they have reached a larger size may offer some protection from bullfrog predation. However, a bullfrog consumed a 75 mm snout-urostyle length California red-legged frog in the field (Chapter 2, Study 4).

Although fish predation on transformed frogs was not studied here, it is likely that largemouth bass and brown bullhead could consume California red-legged frog metamorphs since they ate tadpoles undergoing metamorphosis (which are larger and have greater mass than metamorphs). The other predators studied here probably could not consume metamorphs due to their limited gape size (bluegill, mosquitofish) or inability of capture (crayfish). Bullfrogs consumed California red-legged frog metamorphs and juveniles in field and experimental studies (Chapter 2, Study 4 and Experiment I). Even though the greatest predation rates may be of introduced fish on frog larval stages, predation on postmetamorphic anurans is likely to have proportionally greater population effects (Hellriegel 2000,

Biek et al. 2002). The survivorship of red-legged frog larvae is low even in the absence of introduced predators (Licht 1974). Elasticity analyses suggest that anuran population dynamics are most sensitive to changes in the survivorship rates of juveniles (postmetamorphs to 1 year old) than the larval or adult stages (Biek et al. 2002).

The conclusion that introduced fishes probably contributed more to native frog declines than did bullfrogs, but that bullfrogs may also be a factor in declines, is in accordance with Hayes and Jennings (1986). They observed that early declines in California red-legged frog populations were concurrent with the introduction of 35 exotic fish species to California, and were between 2 and 36 years prior to the earliest known bullfrog introductions. Introduced fishes probably continue to have larger effects than bullfrogs due to specialized feeding modes that make them efficient predators of tadpoles (Hayes and Jennings 1986). Some studies that compared introduced fish and bullfrog effects on native amphibians used larval instead of adult bullfrogs, and therefore primarily examined competition between tadpoles instead of predation (Kiesecker and Blaustein 1998, Lawler et al. 1999, Adams 2000). Other studies reported no effect of introduced fish or bullfrogs on the occurrence or abundance of larval northern red-legged frogs (Richter and Azous 1995, Adams 1999). Northern red-legged frogs and California red-legged frogs differ ecologically, however, and may be different species (Hayes and Miyamoto 1984, Green 1985, Hayes and Kremples 1986).

Effect of Temperature & Climate on Bullfrog Populations

The thermal biology of the bullfrog has been well studied, and all life stages prefer warmer water than other North American anurans (Bury and Whelan 1984). The bullfrog is the last frog species to become active in the spring, emerging after air temperatures warm to 20-24° C and water temperatures exceed 14.0° C (Willis et al. 1956). Bullfrogs select oviposition sites that have relatively warm water (Howard 1978, Cook 1997), and the mean temperature measured at bullfrog egg masses in a California marsh was 18.1° C in spring and 23.2° C in summer (Cook 1997). Bullfrog embryos require warmer water (15-32° C) to develop than other North American frogs (Bury and Whelan 1984). Bullfrog larvae selected relatively warm water (28 - 33° C) in experimental (Lucas and Reynolds 1969, Crawshaw et al. 1992, Nie et al. 1999) and natural situations (Brattstrom 1963, Nie et al. 1999). Juvenile bullfrogs often occupy the warmest microsites available, bask in direct sun or very warm (>30° C), shallow water (Lillywhite 1970), and can withstand temperatures up to 38.2° C (Lillywhite 1970). Adults thermoregulate through microhabitat use and by changing their postures to maintain preferred temperatures (26-33° C; Brattstrom 1963, Lillywhite 1970).

One of the selective advantages of using sites with warm water appears to be the ability of bullfrog tadpoles to complete metamorphosis in one season (George 1940, Viparina and Just 1975, Corse and Metter 1980, Cook 1997, Nie et al. 1999), instead of overwintering one to three times, which occurs in cooler climates (Berven et al. 1979, Collins 1979, Werner and McPeck 1994). Since most amphibian species

suffer the highest mortality rates in their larval stages, shortening the larval period to one or two seasons likely increases population growth rates. In addition, the ability of tadpoles to metamorphose within the same year that eggs are laid can allow bullfrogs to survive seasonal drying of aquatic habitats, which occurs at many sites in California (Cohen and Howard 1958, Cook 1997).

In central California, bullfrog densities tend to be higher in warmer inland areas than near the coast (unpublished data, see Appendix H). I measured the water temperature of coastal and inland sites in central California as part of a preliminary investigation of regional climate effects on bullfrog populations. Water temperatures were measured haphazardly 2 to 16 times along pond margins where bullfrogs were observed, at night in the early fall when air temperature differences between coastal and inland areas are minimal. Coastal areas tended to have lower water temperatures than inland areas (Table 4.1). Differences between inland and coastal sites are probably greater in the summer than those measured in this study, when bullfrog activity is higher.

Thus, the conclusion in Chapter 2 that the presence of bullfrogs is probably not a major factor regulating the distribution of adult and juvenile California red-legged frogs in the region studied may be influenced by regional climatic factors that resulted in low bullfrog densities in my study area. It is possible that bullfrogs may have greater impacts and possibly eliminate California red-legged frogs from sites in warmer regions or other areas where bullfrog densities are higher. Evidence presented here indicates that bullfrogs may reduce native frog population sizes, but

bullfrog densities were probably too low for bullfrogs to eliminate California red-legged frogs from suitable habitats.

Case Study: Before and After Fish Introduction

Further support for the primary importance of introduced fish effects over those of bullfrogs comes from observations in a Vandenberg Air Force Base (VAFB) pond before and after fish introduction. Bullfrogs remained present in this pond over the survey period, from 1995 through 2003. Pond 39, or “Mod III Lake”, was initially stocked with game fish (bluegill, largemouth bass, rainbow trout, channel catfish) for recreational fishing between the 1960s and 1980 (Coulombe and Cooper 1976, Coulombe and Mahrtdt 1976, Cudd 1986). Rainbow trout and channel catfish populations were not self-sustaining, and individuals were stocked annually through the 1970s (Coulombe and Cooper 1976, Coulombe and Mahrtdt 1976). Western mosquitofish and threespine stickleback also occurred in the pond during the 1970s, and may have been introduced by fishermen via their use as bait (Coulombe and Mahrtdt 1976), or pumped into the pond with water from San Antonio Creek which was conducted to maintain water levels (Wilcox 1977).

Apparently, water pumping ceased when the fish stocking program ended in 1980, and fish were eliminated in the pond during the drought of the late 1980s (see Crockford 1986; personal communication, anonymous fishermen). The pond was closed to fishing and swimming during this period due to the detection of petroleum hydrocarbons and heavy metals (Science Applications International Corporation

1990). Pond levels rose in the early 1990s after the end of the drought, and unauthorized fish introductions were conducted by fishermen (personal communication, anonymous fishermen). Fishermen reported that the introduced fish “died off due to toxic conditions that were still present in the lake” through the 1990s (see TetraTech 1996). Fish were not present when I began studying frog populations in this pond in 1995 (unpublished data). However, between late 1997 and early 2002, the unauthorized fish introductions were successful. I first observed fingerling and juvenile bass and sunfish in the pond in August 2002, and centrarchids remained present through September 2003.

California red-legged frogs were not detected in the pond during the 1970s when stocked fish were present, even though they were known to occur in nearby ponds and drainages (Coulombe and Cooper 1976, Coulombe and Mahrtdt 1976). Between 1995 and mid-September 1997, when fish were absent in this pond, California red-legged frogs were abundant (Appendix E). Partial surveys of the pond revealed 15 adult and juvenile California red-legged frogs, and when the entire pond was surveyed on 27 September 1997 approximately 75 California red-legged frogs were observed. During the 27 September 1997 survey, adult California red-legged frogs were so abundant in the emergent vegetation on the eastern shore (the area excluded during the partial pond surveys) that the exact number of individuals present was difficult to determine due to the extremely high density. From 1995 through 1997, California red-legged frogs reproduced successfully in this pond, and tadpoles and metamorphs were detected in moderate numbers (Appendix E).

Bullfrogs were present, but uncommon, throughout this period. Only 1 adult bullfrog and no bullfrog metamorphs were seen during each survey prior to fish reintroduction.

California red-legged frogs declined drastically following the re-establishment of introduced centrarchids in 2002. During a 22 May 2002 survey of the entire pond, only 6 adult and 9 juvenile California red-legged frogs were found. On 30 August 2002, only 2 adult California red-legged frogs were found, and on 16 September 2003 no California red-legged frogs were detected in the pond. Trapping in the late summers of 2002 and 2003 failed to produce any California red-legged frog tadpoles and metamorphs, and no metamorphs were seen during night surveys. Pacific treefrogs (*Pseudacris regilla*) and their larvae were not detected during 2003 trapping and surveys although they had been abundant prior to fish reintroduction.

Initially, bullfrog abundances increased after the reintroduction of fish. Thirty-seven bullfrog metamorphs and 1 tadpole were observed on 30 August 2002, and this was the first time bullfrogs were observed to reproduce successfully in the pond (personal observation). Bullfrog numbers declined in 2003, however, and none were seen during visual surveys and only one was heard calling (Appendix E).

In summary, all life stages of California red-legged frogs were abundant prior to the establishment of centrarchid fish, then drastically declined following centrarchid establishment. Bullfrogs were present in low numbers throughout this period, and probably had little to no effect on California red-legged frogs. The establishment of fish was followed by an increase in bullfrog reproduction,

suggesting that fish may have positively affected the survivorship of bullfrog tadpoles. The influence of potentially toxic materials in the pond remains unknown, but should not have affected California red-legged frogs, bullfrogs, and fish in dissimilar ways. Observations from this pond and the results of studies detailed in previous chapters of this dissertation support the conclusion of Adams et al. (2003) that non-native fish can be viewed as a “keystone invader” in many aquatic habitats of the western U.S. The presence of introduced centrarchids appears to be the primary force altering pond trophic dynamics (Schindler et al. 2001) and facilitating populations of other introduced aquatic predators such as bullfrogs (Adams et al. 2003).

EFFECTS OF MULTIPLE INTRODUCED PREDATORS

The strongest effects of biological introductions on native communities are usually not from single species introductions, but from the introduction of an entire community of species whose coevolutionary adaptations facilitate their survival and growth (Simberloff 1991, Simberloff and Von Holle 1999). Fish introductions are often accompanied by the replacement of most native aquatic fauna by a community of other introduced species (Magnuson 1976, Hecnar and M'Closkey 1997). In California, introduced bullfrogs tend to co-occur with introduced fish species and crayfish (Moyle 1973, Hayes and Jennings 1986). During game fish stocking, crayfish and bullfrogs may be concurrently introduced because they often inhabit

fish hatcheries (Corse and Metter 1980, Hammerson 1982). Bullfrogs, red swamp crayfish, and the centrarchid fishes in this study are native to the eastern United States and have similar environmental requirements (see Moyle 1976), which may facilitate their coexistence in their introduced range.

Bullfrogs (Frost 1935, Korschgen and Baskett 1963, Corse and Metter 1980, Carpenter et al. 2002), large centrarchids and ictalurids (Moyle 1976a, Garvey et al. 1994, Hickley et al. 1994, Garcia-Berthou 2002) often prey on small fish and crayfish, whereas red swamp crayfish consume small fish or compete with them (see Gutierrez-Yurrita et al. 1998). Nevertheless, because of their long coevolutionary history these species possess antipredator adaptations sufficient to maintain their coexistence (Hambright et al. 1986, Hoyle and Keast 1987, Savino and Stein 1989, Garvey et al. 1994, Werner and McPeck 1994). For example, most fish do not prey on bullfrog tadpoles because they are unpalatable (Walters 1975, Kruse and Francis 1977, Cecil and Just 1979, Werner and McPeck 1994). In fact, the presence of bluegill appears to facilitate bullfrog populations because bluegill prey on invertebrate predators and anuran competitors of bullfrog tadpoles (Werner and McPeck 1994, Smith et al. 1999, Eklov and Werner 2000, Adams et al. 2003). Adult crayfish have a size refuge from most fish predators (Nystrom et al. 2001), and crayfish display effective antipredator responses to fish (Stein and Magnuson 1976). Red swamp crayfish and small fish populations are rarely eliminated by bullfrogs because bullfrogs only feed in shallow or surface water, and these prey

have a refuge in deeper water (Viosca 1931). In some cases, red swamp crayfish have been introduced as a food source for bullfrogs (Huner 1977).

I found that there was a highly significant association between the presence of introduced fishes and bullfrogs in central coastal California (Fisher exact test, $P = 0.000$; Table 4.2). Introduced bullfrogs were more commonly observed at sites with than without introduced fish. Of the sites in Chapter 3 (Study 1) that were surveyed extensively enough to detect bullfrogs, bullfrogs were found at 89% of the fish sites but only 18% of the fishless sites. In addition, crayfish were found at 55% of the fish sites and 6% of the sites without fish (Appendix H).

Antipredator Responses and Multiple Predators

Recent studies have indicated that multiple predators can have non-additive effects on their prey (Peckarsky and McIntosh 1998; but see Nystrom and Abjornsson 2000). Predators with different foraging strategies may produce conflicting alternatives to prey (Sih et al. 1998). Prey mortality may increase when several types of predators are present if prey defenses against one predator increase the risk of predation by another predator (Rahel and Stein 1988, Soluk 1993, Wooster and Sih 1995, Kurzava and Morin 1998). Avoidance responses by prey to one predator may be modified when a second predator is present, and prey may tailor their antipredator responses to their relative risk from different predators (McIntosh and Peckarsky 1999, Nystrom et al. 2001). In other cases, prey may exhibit generalized antipredator responses, such as reduced activity, which reduces

their risk from many types of predators (Krupa and Sih 1998, Eklov 2000, Eklov and Werner 2000). Therefore, introductions of multiple predators may have interactive effects on prey because prey may not be able to avoid two or more types of predators. Prey responses to multiple predators also may result in declines in prey growth and development rates because prey may become restricted to suboptimal habitats or exhibit reduced activity and foraging.

Predator-Predator Interactions

Predators also can modify the behavior of other types of predators, which can alter predator impacts on shared prey (Soluk and Collins 1988, Fauth 1990, Huang and Sih 1991, Wissinger and McGrady 1993). Eklov and Werner (2000) found that predation rates by the odonate larva *Anax junius* on bullfrog and green frog (*Rana clamitans*) tadpoles decreased in the presence of caged bluegill because *Anax* reduced activity when bluegill were present. Physical interference between predators also can decrease predation rates on shared prey (Soluk 1993). Therefore, studies of pairwise species interactions may not provide accurate predictions about the complex direct and indirect effects of multiple predators on prey populations (Werner and Anholt 1996, Peckarsky and McIntosh 1998, Sih et al. 1998).

Multiple Introduced Predator Effects on California Red-legged frogs

A limitation of my study is that while California red-legged frogs often co-occur with more than one type of introduced aquatic predator, multiple predator

effects on frogs were not specifically addressed. Because ponds with introduced fishes tended to have bullfrogs and crayfish (Appendix H), introduced fish effects alone could not be examined at the pond scale. The results of my studies, however, provide predictions about multi-predator interactions and their effects on California red-legged frog populations. Bullfrogs collected in the wild and those in mesocosms showed no preference for California red-legged frogs over crayfish and fish. Therefore, bullfrogs could have positive indirect effects on red-legged frogs in isolated stream pools, where bullfrog predation on crayfish and fish may reduce crayfish and fish abundances and consequently reduce their predation rates on red-legged frog tadpoles. In ponds, however, bullfrogs are probably ineffective at reducing fish and crayfish populations because fish and crayfish have deep water refugia from bullfrog predation. Conversely, the presence of crayfish and small fish may increase the size of bullfrog populations by providing an abundant food source (Huner 1977, Corse and Metter 1980; see Chapter 2). Introduced crayfish may reduce the availability of potential refugia for tadpoles by decreasing cover of aquatic macrophytes (Nystrom et al. 2001), or they may physically exclude tadpoles from refugia, either of which may increase predation rates by fish (Bryan et al. 2002).

Interference between large fish and adult bullfrogs is not expected because they do not prey on each other because of their similarity in size and differences in microhabitat use. The presence of fish and bullfrogs may increase crayfish refuge use, and decrease their activity and feeding rates (Stein and Magnuson 1976, Garvey

et al. 1994), which would in turn decrease crayfish effects on California red-legged frogs. Multiple species of introduced fish may interact in ways that alter the effects of single fish species on California red-legged frogs. For example, bluegill alter habitat use when largemouth bass are present (Mittlebach 1981, Werner et al. 1983), which consequently may change bluegill feeding rates on California red-legged frog tadpoles. In systems with two or more introduced fish species it is likely that larger piscivorous fish have greater effects on California red-legged frog populations due to having higher feeding rates than smaller fish species.

Small California red-legged frog tadpoles decreased activity and increased refuge use in the presence of free-ranging bluegill (Chapter 3, Study 4) and increased refuge use when free-ranging mosquitofish were present (Chapter 3, Study 5). If decreased activity and increased refuge use are generalized responses displayed by California red-legged frog tadpoles to predators (or to physical disturbance caused by the predators that may be perceived as potential predator risk), these responses are likely to decrease encounter rates with several predator types.

Kiesecker and Blaustein (1998) detected negative indirect effects of introduced bullfrog larvae and introduced smallmouth bass (*Micropterus dolomieu*) on northern red-legged frogs in experimental enclosures. Smallmouth bass alone and bullfrog tadpoles alone did not affect red-legged tadpole survival, but when bass and bullfrog tadpoles were together bass predation decreased the survivorship of northern red-legged frog tadpoles. Apparently, competition between bullfrog larvae

and red-legged frog larvae caused a shift in microhabitat use by red-legged frog tadpoles, resulting in increased spatial overlap of red-legged frogs and smallmouth bass (Kiesecker and Blaustein 1998). In contrast, Lawler et al. (1999) found that bullfrog tadpoles decreased the survivorship of California red-legged frog tadpoles in experimental ponds, but that mosquitofish alone or with larval bullfrogs had no negative effect on the survival of red-legged frog tadpoles. In fact, mosquitofish may have indirectly increased the survivorship of California red-legged frog tadpoles because the abundances of predatory invertebrates were reduced by fish (Lawler et al. 1999).

In conclusion, the combined effects of multiple introduced predators on California red-legged frog life stages are complex and deserve further study. Field studies suggest that the outcome of tadpole interactions with multiple predators may depend on habitat type. In ponds, multiple predators seem more likely to have combined negative effects on recruitment to frog populations. In stream pools, predator-predator interference and predation on each other may have positive effects on recruitment to frog populations. Interactions with bullfrog tadpoles or exclusion from refugia by crayfish may increase red-legged frog tadpole exposure to other predators. Tadpole antipredator responses probably decrease encounter rates with several types of predators and may decrease growth and development rates in an additive manner.

CONNECTIVITY AND DISPERSAL

The region I studied may differ from other areas presently occupied by California red-legged frogs because there was a high proportion of sites lacking introduced predators in close proximity to sites with introduced predators. Evidence presented here indicates that most sites where the California red-legged frog co-occurs with introduced fish and/or bullfrogs represent sink habitats, where frog population growth rate is negative or zero in the absence of immigration (Danielson 1992, Hanski and Simberloff 1997). Immigrants come from source habitats, which are sites where reproduction exceeds mortality and the per capita growth rate is greater than one (Danielson 1992). From the perspective of an organism, the third type of habitat in a landscape is unusable habitat, through which a dispersing animal must travel when searching for usable (source or sink) habitats (Danielson 1992). Unusable habitat varies in the degree to which animals can move through it. California red-legged frogs may be able to coexist with introduced predators when there is high connectivity between source and sink sites.

Connectivity among usable habitat patches depends on the density and spatial arrangement of habitats across a landscape, as well as the movement patterns and densities of organisms (Hanski and Gilpin 1991, Sjoren 1991, Taylor et al. 1993, Keitt et al. 1997). Dispersal probabilities tend to decline as the distances between usable sites increase (Trenham et al. 2001). When there is high connectivity between subpopulations, some species may benefit from the presence

of sink habitats if more individuals are produced in nearby source habitats than those sites can support (Pulliam and Danielson 1991). If connectivity is low or the abundance of sink habitats is too high, the landscape will not be able to support a viable population (Danielson 1992).

Pond-breeding amphibians that characteristically exhibit wide variations in population size and recruitment, and undergo local extinctions, depend on recolonization by immigrants from other local populations (Pechmann et al. 1991, Semlitsch 2002). The probability of recolonization following local extinction is determined by the degree of isolation among local populations, and is strongly affected by the presence of introduced predators at some of the potential habitats (Sjogren 1991). Persistence of some amphibian species is dependent on periodic “boom” years, which may vary in timing between local populations (Gill 1978, Berven and Grudzien 1990). Multiple years of recruitment failure due to the early drying of predator-free ponds (which are typically less permanent than sites that have bullfrogs and fish), combined with reduced recruitment at permanent sites because of the presence of introduced predators, can lead to the extinction of an amphibian species in a given area (Dodd 1993, Semlitsch et al. 1996).

Characteristics of California Red-legged Frog Dispersal

In many amphibian species, adults often return to natal ponds to breed (Oldham 1966, Breden 1987, Berven and Grudzien 1990; but see Trenham et al. 2001) and recently metamorphosed frogs are the main dispersal stage (Gill 1978,

Breden 1987, Sinsch 1992, Sinsch and Seidel 1995). Because recently metamorphosed California red-legged frogs are too small to carry radio transmitters, I used pitfall trapping to gather data on juvenile dispersal. I installed pitfall trap/drift fence arrays (Figure 4.1) in upland habitats around two ponds (77 and 79) at VAFB to examine California red-legged frog dispersal away from breeding habitats. Drift fences were installed parallel to pond perimeters 20 m from the water's edge. Ponds could not be completely encircled by drift fences due to incidental capture and movement restriction of other animals, therefore pitfall trapping sampled less than 50% of the area through which frogs could have traveled while emigrating from the ponds. Frogs would run into the drift fence, then travel along the fence until falling into one of the pitfall traps at the ends of the fence (personal observation; see Figure 4.1). In accordance with federal permit restrictions, pitfall traps were designed so that raccoons could not capture trapped frogs (diameter 15.24 cm, depth 61 cm). As a consequence of this modification, the traps may have been more effective at capturing metamorphs than adult frogs.

Trapping was conducted during winter 1997/1998 and summer/fall 1998. For each trapping session, lids were removed from the traps at dusk and the traps were checked between 0800 and 1100 hours the following morning. Lids were replaced after each trap was checked. Rainfall amounts during the period the traps were open were recorded on site. Sampling was conducted 2 - 3 times a week. Sampling nights were selected haphazardly, but sampling was attempted on each night that rain was predicted.

A large proportion of California red-legged frogs that dispersed away from ponds did so during early-season rain events (Figure 4.2), consistent with the conclusions of other researchers (Stebbins 1985; Bulger et al. 2003). A surprising finding from this study was that metamorphs began emigrating from ponds shortly after metamorphosis, as much as 3 months prior to the onset of winter rains (Figure 4.2 B). Adult frogs, in contrast, were captured only during rain. Metamorph dispersal became less common as the winter progressed, even when there was substantial rainfall (Figure 4.2 A). Bulger et al. (2003) also found little use of upland habitats by California red-legged frogs in mid- to late winter despite frequent and copious rainfall. Metamorphs dispersing from Pond 79 in summer/fall 1998 tended to be larger than those from winter 1997/1998 and from Pond 77 (Table 4.3). Of the juveniles and adults captured, 2 males were captured at Pond 77, and 2 males and 5 females from Pond 79.

It is possible that adult California red-legged frogs contribute to dispersal, but this question requires further study. Adult California red-legged frogs can migrate between summer residence and winter breeding sites up to 2800 m apart (Bulger et al. 2003). While most frogs returned to their original sites of summer residence following breeding, some moved to adjacent ponds and streams that were not their original sites of capture (Bulger et al. 2003). At VAFB ponds, radio-tagged adult frogs ($N = 26$) remained within 25 m of breeding ponds while in upland habitats, and none migrated away from the vicinity of the study ponds over a period of two breeding seasons (unpublished data). Some frogs in my study area moved

< 25 m overland to different ponds during the breeding season, and returned to their original ponds after breeding. The greatest frog movements (up to 130 m) that I recorded were within individual ponds (unpublished data). When a few of the ponds dried in late summer, adult frogs moved about 25 m overland to ponds that still contained water. Similarly, Bulger et al. (2003) detected late-summer movements away from drying ponds. It is possible that adult California red-legged frogs prefer to return to the same ponds to breed each year, but when ponds dry they are forced to move to different sites and consequently may colonize new habitats.

Corridors of riparian or other favorable vegetation between aquatic sites have been proposed to increase dispersal probabilities between sites (Saunders and Hobbs 1991, Hobbs 1992, Puth and Wilson 2001). My pitfall trapping study was conducted in a system of dune ponds where standing water was present in the bottom of swales that were separated by dune ridges. Swales tend to have more mesic conditions and higher densities of vegetation than the surrounding dunes. One of the 9 drift fences around Pond 77 was constructed across the bottom of a swale, and 2 of the 7 at Pond 79 were constructed across a swale bottom. If frog movement was unrelated to vegetation or topography, the proportion of captures for each trap array should be about the same. At Pond 77, there were more captures in swales (26 of 100) than expected (11) if frog movement away from ponds was unrelated to the presence of swales versus dune habitats. At Pond 79, there was no difference in swale trap catches (14 of 51) from expectations based on random frog movement (14 captures expected). In the Santa Cruz Mountains, migrating adult

California red-legged frogs showed no preference for riparian corridors, and moved overland in approximately straight lines apparently without selection for or avoidance of vegetation type or particular topographic conditions (Bulger et al. 2003). In landscapes modified by human activity, California red-legged frogs may or may not become more dependent on topographic or vegetative corridors for dispersal (see Bulger et al. 2003). Other amphibian species do not move through power line right-of ways (deMaynadier and Hunter 1999), open fields (Semlitsch 2002), and roads (Vos and Chardon 1998).

Further evidence concerning the high dispersal rates of California red-legged frog metamorphs and the high connectivity of VAFB sites also can be inferred from presence/absence surveys that I conducted during drought and El Niño cycles. Initial surveys (1994 - 1997) were conducted following the end of a prolonged drought, and California red-legged frogs occurred primarily in permanent aquatic habitats during this period. Following wet El Niño conditions in winter 1997/1998, many new freshwater habitats appeared, and almost every new site was naturally colonized by the frog within 1 or 2 years (see Appendix E).

In conclusion, the connectivity of California red-legged frog habitats at VAFB appears to be sufficient to maintain their coexistence with introduced predators. The reproductive rates and population sizes of the frog at sites lacking introduced predators have varied substantially over dry and wet cycles (see Appendix E). During wet years, there may be high recruitment at many sites that produce a substantial number of immigrants to sites with introduced predators.

During extended droughts, all of the California red-legged frog populations at VAFB decline and persistence probably depends on only a few permanent sites lacking introduced predators (unpublished data). Because VAFB remains in a relatively “natural” state, where there are few barriers to dispersal for California red-legged frogs and a high density of suitable freshwater habitats, the VAFB landscape retains a high degree of connectivity between frog subpopulations that was formerly present throughout most of the frog’s historic geographic range.

DIRECTIONS FOR FUTURE RESEARCH

Many questions remain unanswered concerning interactions between California red-legged frogs and introduced predators. Below is a summary of a few potential directions for future research that would greatly augment information gained from the present study.

- Are bullfrog tadpoles unpalatable to introduced or native fish species in their introduced range? Despite the long-held notion that they are unpalatable to fish (see Kruse and Francis 1977, Werner and McPeck 1994), a few studies have suggested that they are consumed by fish under some conditions. Pearl et al. (2003) showed that bullfrog larvae were consumed by fishes native to the Pacific Northwest, where bullfrogs had been introduced, but were not consumed by fish species native to the bullfrog’s native range. In the bullfrog’s native range in Alabama, Nie et al. (1999) observed that bullfrog tadpoles were less abundant in

ponds with than without fish, and that their abundance sharply decreased following the introduction of channel catfish (*Ictalurus punctatus*) to one pond. Largemouth bass and green sunfish consumed bullfrog tadpoles in an experimental setting without alternative prey (Kruse and Francis 1977).

- Can pond drying be used as an effective management technique to eliminate or reduce introduced aquatic predators, thereby making these ponds more suitable for native amphibian species (see Semlitsch 2000)?
- Do California red-legged frog larvae display antipredator responses to native fish species? If so, it is possible that antipredator responses to introduced fish observed in Chapter 3 represented generalized responses to fish predators. It is possible that, given enough time, selection could strengthen these antipredator behaviors allowing California red-legged frogs to coexist with some introduced fish species.
- What are dispersal rates and distances for California red-legged frog metamorphs? Semlitsch (2002) stressed the importance of acquiring data on dispersal behavior, habitat use, local population dynamics, and connectivity between populations when developing recovery plans for threatened and endangered amphibian species. Intensive mark-recapture studies (e.g. Trenham et al. 2001), and radio tracking with very small transmitters could be employed to gain a better understanding of the habits of this elusive life stage.

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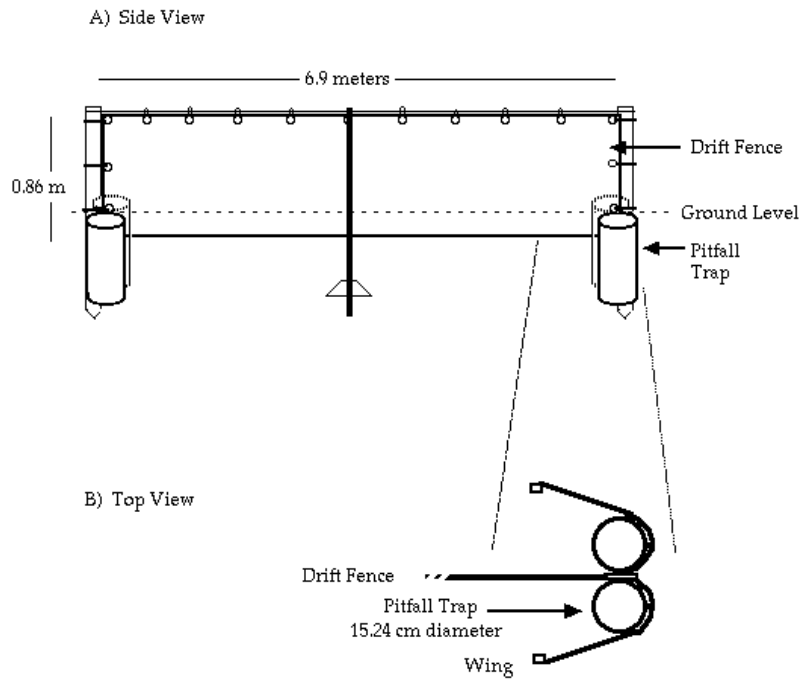
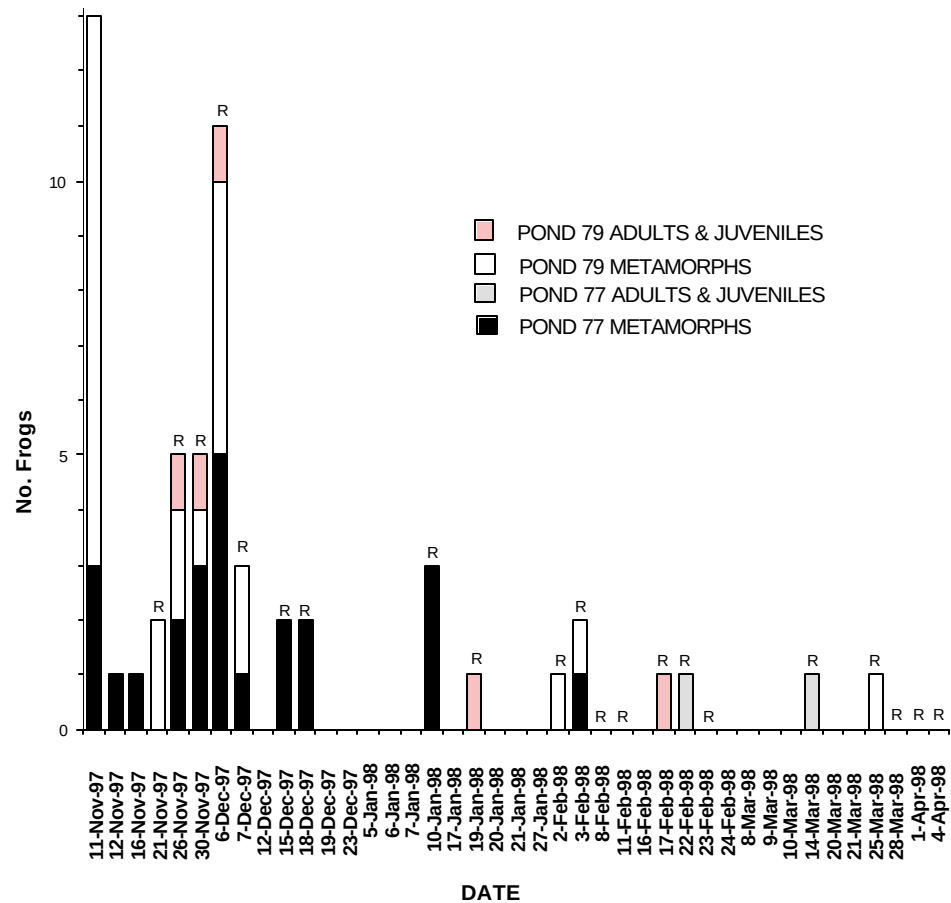


Figure 4.1. Pitfall trap design used to sample California red-legged frog dispersal away from ponds showing A) side view of one array, consisting of 4 traps (wings not shown), and B) top view of 2 pitfall traps, with wings that direct frogs into the traps.

A) Winter 1997/1998:



B) Summer/Fall 1998:

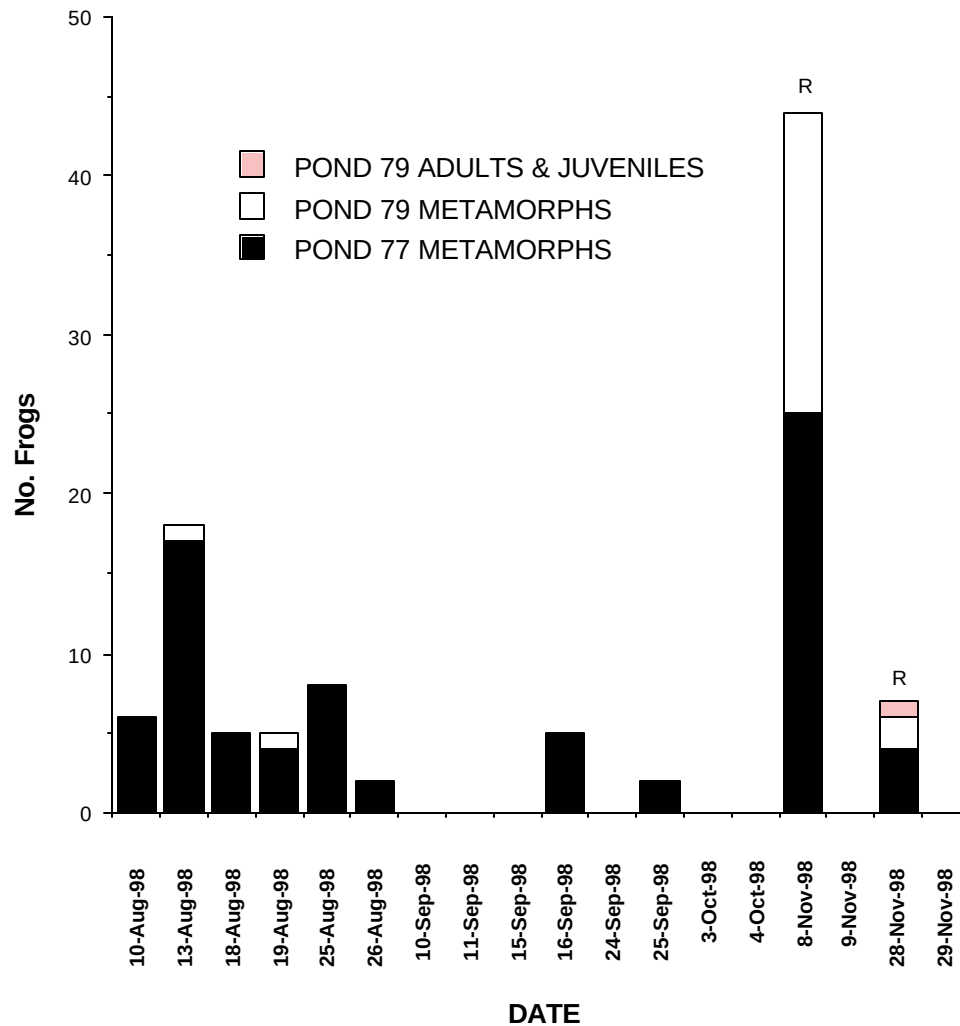


Figure 4.2. Total pitfall trap captures of California red-legged frogs at Vandenberg Air Force Base, California in A) winter 1997/1998 and B) summer/fall 1998. Drift fence/pitfall trap arrays were installed in upland habitats near Ponds 77 (9 arrays) and 79 (7 arrays). Shown are the dates that traps were set (left uncovered) overnight. Rainfall > 1 mm over the time traps were set is indicated by "R". Metamorphs were ≤ 65 mm and adults/juveniles > 65 mm snout-urostyle length.

Table 4.1. Water temperatures measured at ponds with bullfrogs in coastal (Vandenberg AFB) and inland sites. Mean water temperatures (range) are in °C. Measurements were taken within 2 hours after dusk 22 September - 13 October 1999 at pond margins.

Coastal		Inland	
Site	Temperature	Site	Temperature
4804	17.1 (16.5 - 17.5)	Rose Valley	19.9 (18.0 - 21.0)
45 Upper	17.5 (16.0 - 18.0)	Paso Hot Springs	20.5 (17.0 - 23.5)
45 Middle	19.5 (19.5)	Franklin Lakes Lg.	19.1 (16.5 - 21.5)
45 Lower	19.3 (19.0 - 19.5)	Franklin Lakes Sm.	20.8 (20.0 - 21.5)
46	17.0 (17.0)		

NOTE: Pond locations are as follows.

4804	34° 40' 51.20"N	120° 33' 46.46"W
45 Upper	34° 43' 38.13"N	120° 30' 34.95"W
45 Middle	34° 43' 26.58"N	120° 30' 30.90"W
46	34° 46' 2.46"N	120° 31' 16.04"W
Rose Valley	34° 32' 27.74"N	119° 11' 11.54"W
Paso Hot Springs	35° 39' 48.10"N	120° 40' 36.03"W
Franklin Lakes Lg.	35° 35' 16.24"N	120° 38' 25.81"W
Franklin Lakes Sm.	35° 35' 16.36"N	120° 38' 16.44"W

Table 4.2. Occurrence of the bullfrog and introduced fish at sites in Chapter 3, Study 1. Numbers are total sites per category. A significant association between bullfrogs and fish was tested using a Fisher exact test (df=1, $\alpha=0.05$).

	Fish present	Fish absent	<i>P</i>
Bullfrogs present	25	11	0.0000
Bullfrogs absent	3	49	

Table 4.3. Size (snout-urostyle length in mm) of California red-legged frog metamorphs dispersing from ponds that were caught in pitfall traps at Vandenberg Air Force Base.

Pond	Winter 1997/1998		Summer/Fall 1998	
	Range (Median)	<i>n</i>	Range (Median)	<i>n</i>
77	35 - 64 (39)	21	30 - 54 (38)	77
79	36 - 51 (41)	21	40 - 65 (50)	23

Appendix A
Literature Reviewed for Types of Introduced Species Effects
in Chapter 1

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- Kornberg, H., and M. H. Williamson. 1987. Quantitative aspects of the ecology of biological invasions. Proceedings of a Royal Society Discussion Meeting held on 26 and 27 February 1986. The Royal Society, London. vi + 240 pp.
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Appendix B
Sites Surveyed in Chapter 2, Study 1
And Maximum Number of California Red-legged
Frogs & Bullfrogs Seen During Any One Survey

CO ¹	AREA	SITE	LOCALITY	RLF	BF	DATE
MON		ELKHORN SLOUGH	WATERING TROUGH	4	0	13MAY1994
SB		GAVIOTA CR	MOUTH TO JUST ABOVE CG RD XING	7	0	24MAR1997
SB		REFUGIO CR	1ST XING N OF HWY 101	98 ²	0	14APR1994
SB		TECOLOTE CR	MOUTH TO 1ST RD N OF HWY 101	2	0	16JAN1997
SB	LPNF	ALDER CR	DOWNSTREAM FROM CAR PARK	2	0	28JUL1996
SB	LPNF	ALDER CR	CAR PARK TO WATERFALL	3	0	11JUL1996
SB	LPNF	FOX CR	SANTA YNEZ TO WATERFALL	1	0	1APR1996
SB	LPNF	JAMESON LAKE	N SHORE	4	20	28MAY1996
SB	LPNF	MANZANA CR	NEAR NIRA CG	2	0	16APR1996
SB	LPNF	MONO CR	BTW 1ST & 3RD XING OGILVY RD	19	0	16AUG1996
SB	LPNF	MONO CR	BTW 4TH & 6TH XING OGILVY RD	17	0	16AUG1996
SB	LPNF	SANTA YNEZ R	DOWNSTREAM FROM JUNCAL CG	6	0	24JUL1996
SB	LPNF	SANTA YNEZ R	UPSTREAM FROM JUNCAL CG	14	0	19JUL1996
SB	VAFB	17		6	0	11FEB1995
SB	VAFB	26		4	0	11FEB1995
SB	VAFB	27		8	0	10JUL2001
SB	VAFB	29		12	0	19JUL1997
SB	VAFB	30		0	3	22JUN1995
SB	VAFB	30		9	0	22AUG2001
SB	VAFB	35		2	0	15FEB2001
SB	VAFB	36		3	0	19FEB1995
SB	VAFB	36		1	11	26JUL1995
SB	VAFB	39		1	2	23OCT1996
SB	VAFB	39		75	1	27SEP1997
SB	VAFB	47		20	0	27NOV1996
SB	VAFB	48 (01)	WATERFOWL PONDS	10	0	24JAN1997
SB	VAFB	48 (02)	WATERFOWL PONDS	2	0	15FEB1998
SB	VAFB	48 (02)	WATERFOWL PONDS	0	1	15JUL1998
SB	VAFB	48 (04)	WATERFOWL PONDS	94	3	17SEP2000
SB	VAFB	48 (04)	WATERFOWL PONDS	51	8	21AUG1999
SB	VAFB	48 (05)	WATERFOWL PONDS	0	12	26MAY1995
SB	VAFB	48 (05)	WATERFOWL PONDS	40	0	20AUG1999
SB	VAFB	50A		21	0	16JUN2001
SB	VAFB	50B		4	0	16JUN2001
SB	VAFB	58		3	?	18APR1999
SB	VAFB	61		2	1	10AUG1995
SB	VAFB	61		0	4	21FEB1997
SB	VAFB	68		0	4	27JUN1995
SB	VAFB	71		5	0	3JUL2001
SB	VAFB	72		12	0	27JUN2001
SB	VAFB	73		16	0	31MAY1996
SB	VAFB	75		1	0	2AUG1995
SB	VAFB	76		4	0	2AUG1995

¹County

²Tadpoles

Appendix B (Continued)

CO ¹	AREA	SITE	LOCALITY	RLF	BF	DATE
SB	VAFB	77		8	0	16AUG1997
SB	VAFB	78		65	0	1AUG2001
SB	VAFB	79		31	0	10OCT2001
SB	VAFB	80		41	1	4AUG2002
SB	VAFB	81	LOWER OCEAN AVE DITCH	1	0	23OCT2002
SB	VAFB	83		1	1	10AUG1995
SB	VAFB	87		65	0	21AUG2002
SB	VAFB	91		21	0	23SEP2002
SB	VAFB	92		11	0	5AUG1998
SB	VAFB	110C		34	0	13JUN2002
SB	VAFB	120B		21	0	11OCT2002
SB	VAFB	123		61	0	15AUG2002
SB	VAFB	126		0	4	1MAY2001
SB	VAFB	128		70	0	26AUG2002
SB	VAFB	130		17	0	30MAY2002
SB	VAFB	140		55	8	23AUG2002
SB	VAFB	150	SLC-6 WASTEWATER POND (N)	43	0	21APR2000
SB	VAFB	150	SLC-6 WASTEWATER POND (MIDDLE)	17	0	24APR1999
SB	VAFB	150	SLC-6 WASTEWATER POND (S)	4	0	25APR1999
SB	VAFB	151	BEAR VALLEY POND	13	0	9MAY2002
SB	VAFB	155	TITAN GATE DRAINAGE	16	0	28MAY2002
SB	VAFB	157		1	0	28FEB2001
SB	VAFB	179		13	0	30AUG2001
SB	VAFB	181		5	0	21JUN2002
SB	VAFB	255		22	0	22NOV2002
SB	VAFB	256		2	0	3JUL2001
SB	VAFB	280		18	0	26MAR02
SB	VAFB	330		3	0	23MAY2002
SB	VAFB	HONDA CR	MOUTH TO WATERFALL	14	0	11OCT2001
SB	VAFB	HONDA CR	1ST XING TO 3RD XING OF OLD RD	1	0	24AUG1995
SB	VAFB	HONDA CR	WOODEN BRIDGE TO POWERLINE	1	0	28JUL1995
SB	VAFB	IRP SITE 31	N END PEGA RD, NOW FILLED IN	20	0	12JUL1997
SB	VAFB	OCEAN AVE DITCH		2	0	4AUG1997
SB	VAFB	JALAMA CR	MOUTH TO 150 M UPSTREAM UPRR	18	0	5JUL1995
SB	VAFB	MONROE ST (171)	DITCH AT JCT MONROE ST X SWEENY	7	0	21APR2000
SB	VAFB	SAN ANTONIO CR	SIDE CHANNELS AT EL RANCHO RD	4	1	5MAR1999
SB	VAFB	SHUMAN CR	MOUTH	5	0	18JUL1995
SB	VAFB	SHUMAN CR	AT JCT CASMALIA CR	1	0	2SEP1995
SB	VAFB	UNNAMED	NEAR LION'S HEAD	1	0	2SEP1995
SC		BIG CR	SWANTON RD TO SCOTT CR	2	0	12MAR1997
SC		SCOTT CR AREA	POND 1	MD	0	10MAR1997
SC		SCOTT CR AREA	POND 2	MD	0	10MAR1997
SC		SCOTT CR AREA	POND 3	3	0	25JUL1998
SLO		ARROYO LAGUNA	MOUTH UPSTREAM ~1 MI	13	0	22SEP1994
SLO		LITTLE PICO CR	MOUTH UPSTREAM ~1 MI	5	0	23APR1996
SLO		PICO CR	MOUTH UPSTREAM ~1 MI	7	0	24SEP1994
SLO		SAN SIMEON CR	MOUTH UPSTREAM ~1 MI	36	0	23SEP1994

¹County

MD = Missing data, but confirmed present

Appendix B (Continued)

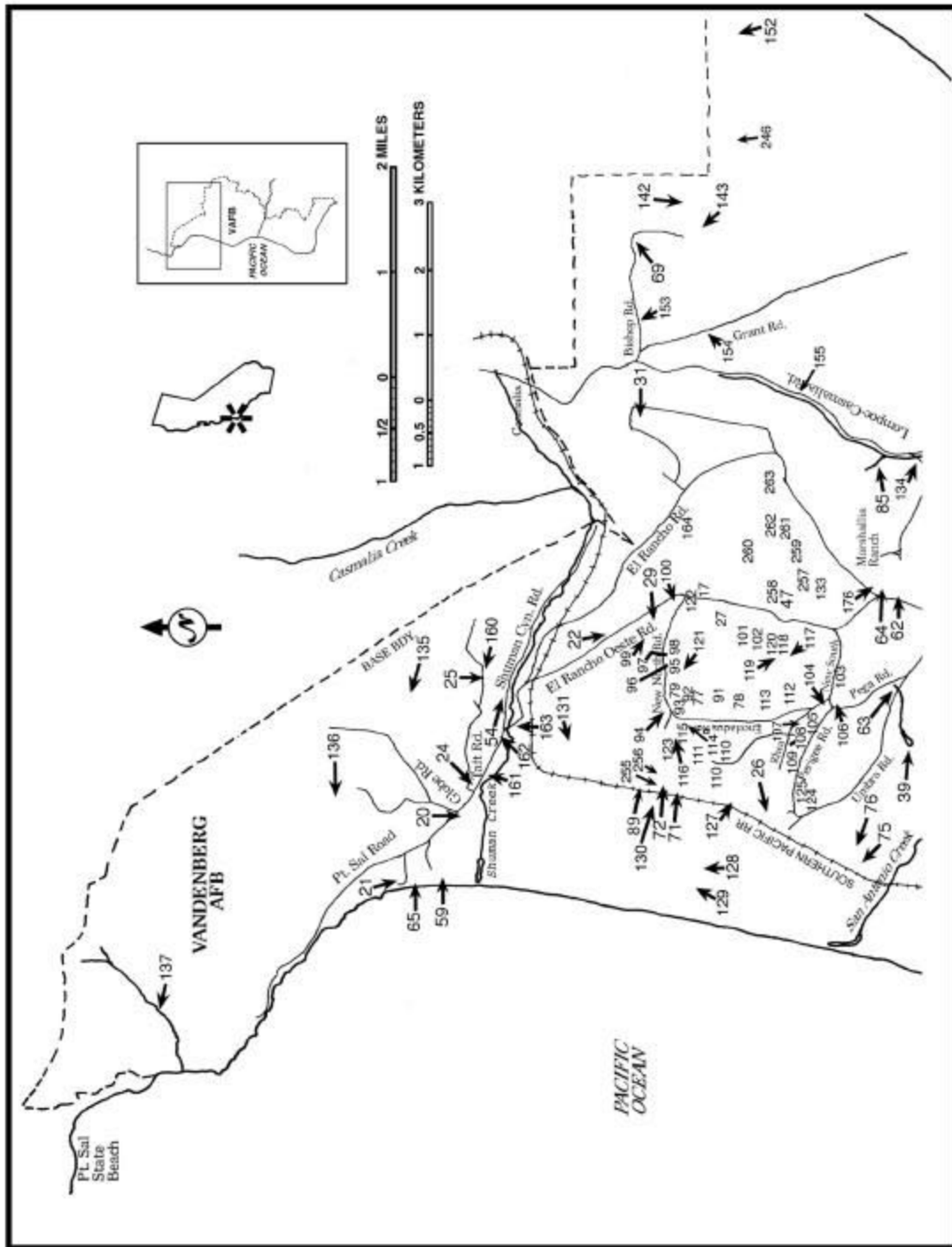
CO ¹	AREA	SITE	LOCALITY	RLF	BF	DATE
SLO	GUAD	A8 (N)		1	0	14MAR1999
SLO	GUAD	A8 (S)		10	0	14MAR1999
SLO	GUAD	L11		10	0	5MAY1999
SLO	GUAD	M12		9	0	18APR1999
SLO	GUAD	POND A	JUST N SANTA MARIA RIVER MOUTH	28	0	19JUN1996
SLO	GUAD	POND B		2	0	14MAR1999
SLO	GUAD	POND X	B2/3	8	0	14MAR1999
SLO	GUAD	TB8	RETENTION PONDS	7	0	15APR1999
VEN	LPNF	AGUA BLANCA CR	NEAR DEVIL'S GATEWAY	0	1	25MAY1996
VEN	LPNF	AGUA BLANCA CR	NEAR RANCH	0	2	3AUG1994
VEN	LPNF	N FORK MATILIJA	WHEELER GORGE	0	0	MAR 1999
VEN	LPNF	TULE CR	JCT. SESPE CR TO ~0.5 MI UPSTREAM	0	0	1997, 1999

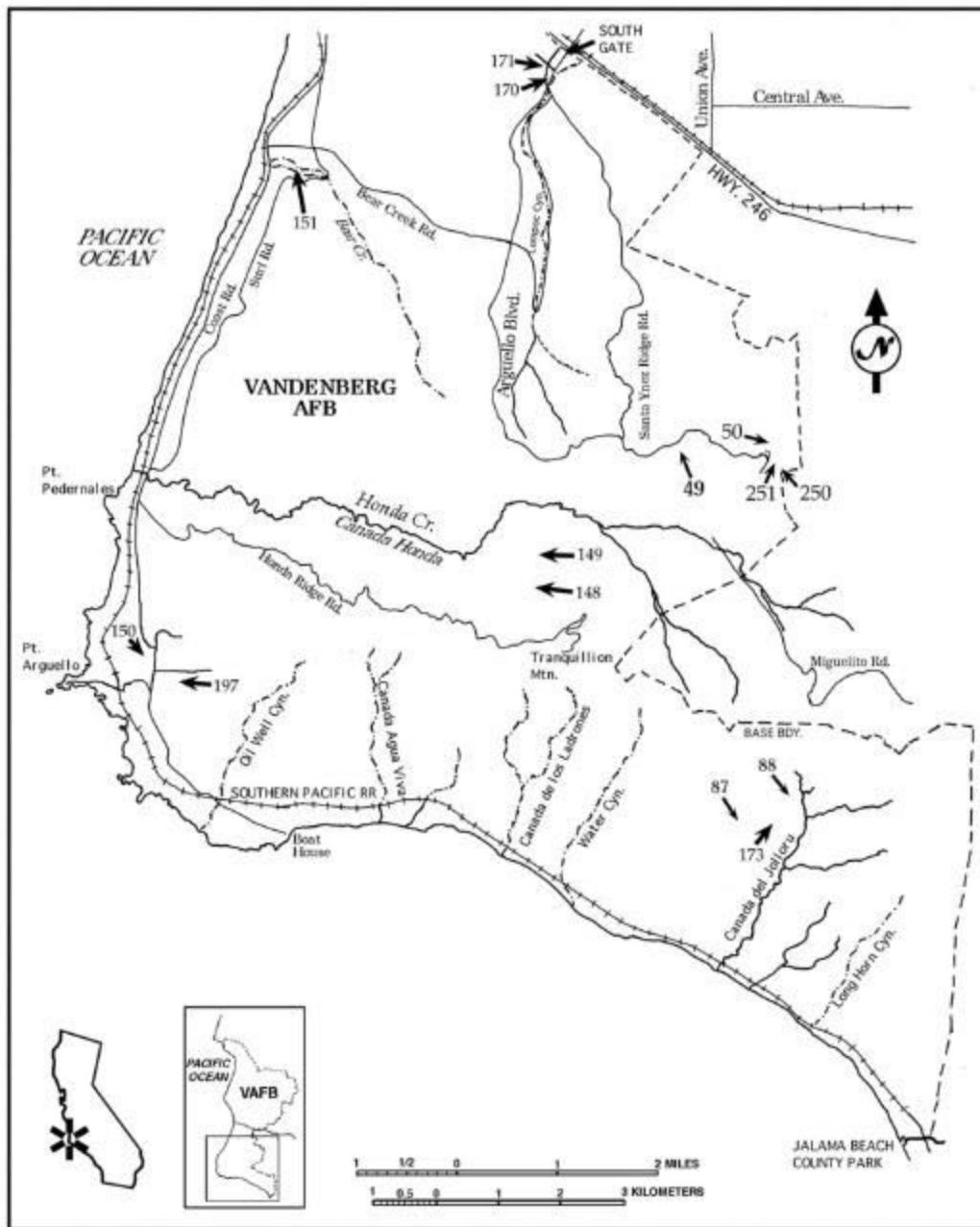
¹County

Notes: LPNF = Los Padres National Forest; VAFB = Vandenberg Air Force Base (Maps of sites are given in App. C); GUAD = Unocal's Guadalupe Former Oil Field

Appendix C
Wetlands and Drainages at
Vandenberg Air Force Base, California

Numbers indicate wetland sites, and include vernal pools, vernal wetlands, and semi-permanent ponds, permanent ponds, and permanent wetlands. The numbering system is consistent throughout all studies described in this document. Data from Sites 93 through 256 (excluding Sites 150 and 171) were collected subsequent to studies covered by this dissertation, but data are included in Appendix E.





Appendix D
Physical Characteristics of Ponds
In Chapter 2, Studies 2 & 3

Pond	Surface area (m ²)	Peri- meter (m)	Maxi- mum depth (m)	Shore & emergent vegetation
30	14,469	496	1.1	Dense bulrushes (<i>Scirpus</i> sp.) around entire perimeter.
36	25,044	753	2.1	Most of shore bare with a small amount of willow (<i>Salix</i> sp.); no emergent vegetation.
39	37,193	977	7.1	Dense bulrushes and some cattails (<i>Typha</i> sp.) around perimeter, with several patches of willow.
77	10,087	463	1.8	Cattails and some patches of bulrushes and willow around entire perimeter. Mats of marsh pennywort (<i>Hydrocotyle</i> sp.).
79	8,708	459	1.35	Cattails around most of perimeter, with some open shore and a small clump of willows. Mats of marsh pennywort.
91	7,483	382	1.6	Cattails around entire perimeter with some patches of bulrushes and willow. Mats of marsh pennywort.

Appendix E
Survey Data for California Red-legged Frogs
and Bullfrogs at Vandenberg Air Force Base,
Santa Barbara County, California
1995 - 2002

Maps showing the location of the sites are given in Appendix C.

KEY FOR APPENDIX E SPREADSHEET

SITE: Arbitrary ID number given to individual sites which could potentially be habitat for sensitive amphibian species. The sites were numbered in the order in which they were identified.

SUB: Subsection of the site ID. Letters A, B, C, etc. correspond to subsections of wetland habitat as they were GPSed in the field. Compass directions (in parentheses) are given to aid in field identification of the subsections.

MAP: Map number that the site is shown on in Appendix C.

DESCRIPTION: Follows the general definitions below.

EPHEMERAL: Has water for several weeks to a few months, usually in the spring, but is not a vernal site due to the lack of vernal pool vegetation.

SEMI-PERMANENT: Has standing water in the spring through late summer. May dry in the fall of some years.

PERMANENT/SEMI-PERMANENT: Sites where standing water may be maintained all year depending on the amount of rainfall received that year or the condition of the groundwater table.

PERMANENT: Has standing water all year, with the possible exception of during extreme drought conditions.

POOL/POND: Standing water with little or no flow that has some area with open water lacking vegetative cover.

WETLAND: Standing water with little or no flow that has the entire surface area covered by vegetation.

MARSH: A type of wetland vegetated mainly or exclusively by emergent vegetation such as cattails (*Typha*), sedge (*Carex*), rushes (*Juncus*), tules (*Scirpus*), or grasses. Lacks cover by willows (*Salix*).

WILLOW WETLAND: A type of wetland vegetated mainly by willows, and may also have emergent, non-woody vegetation.

WILLOW WOODLAND: A type of wetland that is densely vegetated by willows and lacks emergent, non-woody vegetation.

DUNE SWALE: Low area among old, stabilized dunes on San Antonio Terrace. Standing water is a result of surfacing groundwater.

CATTLE POND: Usually a modified wetland or drainage that was created for or is still being used for cattle.

PIT POND: Created habitat associated with buildings. Their purpose is unknown, but they may collect and retain precipitation runoff from facilities. Usually square, with steeply sloping sides, and may be lined with concrete.

DATE: Date of the field survey.

SURVEY: Follows the descriptions below.

NIGHT: Visual encounter survey of all accessible areas using Koehler Wheat Cap Lamps to detect frog eyeshine. Usually performed by wading or float tube, and rarely performed from the shore. Always performed after “full” darkness.

DAY: Visual encounter survey performed during daylight hours. Usually performed concurrent to a habitat assessment, or a visual search for tadpoles or recently metamorphosed frogs (“metamorphs”).

TRAPPING: Steel minnow traps with small funnel-shaped openings at either end and hoop net traps with one large funnel-shaped opening were used. California red-legged frog tadpoles, metamorphs, and occasionally juveniles could be captured in the minnow traps. Minnow traps were also used to sample for spadefoot and California tiger salamander larvae, and occasionally two-striped garter snakes were caught in the minnow traps. California red-legged frogs, their large tadpoles, and southwestern pond turtles could be captured in the hoop net traps. All traps were set so that trapped animals had access to air, and/or were checked frequently enough to prevent mortality, as required by the collecting permits. Usually the traps were not baited, but when sampling for southwestern pond turtles and introduced species of fish, bait may have been used in the hoop net traps. Since the type of traps, number of traps, and length of time the traps were set varied, direct comparisons of trap data cannot be made from these data summaries.

CALLING: Listened quietly for calling frogs for a minimum of 5 minutes from the edge of the wetland habitat.

EGG MASS: Daytime search for egg masses, with extreme care taken not to tread upon any egg masses.

DIP NETTING: Sweeps with a long-handled aquatic net to sample for tadpoles.

SEINE: Two people dragged an 8 - 10’ wide seine net through the water.

NOTES: Incidental sighting while visiting the site for some other purpose.

ADLTS*: Adult California red-legged frogs > 70 mm snout-urostyle length.
Adult bullfrogs > 120 mm snout-urostyle length.

JUV*: Juvenile California red-legged frogs 55 - 70 mm snout-urostyle length.
Juvenile bullfrogs 70 - 120 mm snout-urostyle length.

*Note: In some periods during the study, all frogs larger than metamorphs were grouped into the adult category, and they were not separated into adult and juvenile size categories.

META: Metamorphs were frogs that had transformed that same season, and California red-legged frog metamorphs were generally < 55 mm snout-urostyle length (but in some cases frogs up to 65 mm SUL were considered metamorphs, depending on time of year, and the age of frogs ~65 mm SUL is poorly understood) and bullfrogs < 70 mm snout-urostyle length.

LARV: Larvae were any tadpoles that had tails, even if limbs had emerged.

EGG MS: Egg masses were clutches of 100s of eggs, and one clutch is laid by one female.

CALL: Individual males giving breeding calls.

Numbers of individuals given are the *minimum number that was positively identified*. Frogs which were seen only by eyeshine, those which were heard jumping in from the shore, and those which could not be approached close enough to positively identify them to species are not enumerated, but are indicated by “+”. In some cases, there may have been more frogs that were not positively identified than which *were* positively identified. Therefore, the numbers given indicate the most conservative count of how many were detected. A (+) which is not preceded by a number indicates that frogs were detected but either the number was not recorded or they were not positively identified. 0 means they were not detected, but does not mean that they were not present, or that the survey type or timing was appropriate for their detection. There are a few (?) for incomplete survey notes that came from an assistant. “~” indicates approximately.

SITE	SUB	MAP	DESCRIPTION	DATE	SURVEY	#ADULTS	CALIFORNIA RED-LEGGED FROGS #JUV #META #LARV #EGG MS	#CALL	#ADULTS	#JUV #META #LARV #EGG MS	BULLFROGS #JUV #META #LARV	#EGG MS	#CALL
17		C - 2	Ephemeral pond, not well vegetated										
				11-Feb-95	NIGHT	6+	1	0	0	0	0	0	0
				27-May-95	TRAPPING	0	0	0	0	0	0	0	0
				14-Jul-95	DAY	0	0	0	0	0	0	0	0
				14-Jul-95	NIGHT	0	3	0	0	0	0	0	0
				3-Jun-96	NIGHT	0	0	0	0	0	0	0	0
				10-Feb-98	EGG MASS	0	0	0	0	0	0	0	0
				19-Mar-01	CALLING	0	0	0	0	0	0	0	0
				10-Jul-01	NIGHT	0	0	0	1	0	0	0	0
26		C - 2	Created permanent dune swale pond, "Wildflower Wetland"										
				11-Feb-95	NIGHT	4+	0	0	0	0	0	0	0
				15-Feb-95	CALLING	0	0	0	0	0	0	0	0
				23-Feb-95	EGG MASS	0	0	0	0	0	0	0	0
				27-May-95	TRAPPING	0	0	0	0	0	0	0	0
				1-Mar-98	NOTES	0	0	0	0	0	0	0	0
				11-Apr-02	NIGHT	16+	5	0	0	0	0	0	0
27		C - 2	Created permanent dune swale pond, "Live Oak Wetland"										
				11-Feb-95	NIGHT	5	0	0	0	0	0	0	0
				18-Feb-95	EGG MASS	0	0	0	0	0	0	0	0
				22-Jun-95	DAY	0	0	0	6+	0	0	0	0
				22-Jun-95	TRAPPING	0	0	0	4	0	0	0	0
				6-Jul-95	NIGHT	(+)	0	0	0	0	0	0	0
				7-Jul-95	TRAPPING	0	0	10	48	0	0	0	0
				8-Jul-95	TRAPPING	0	0	0	7	0	0	0	0
				15-Jul-95	DAY	0	0	0	0	0	0	0	0
				19-Oct-96	DAY	0	0	3	0	0	0	0	0
				10-Jul-01	NIGHT	8+	1	0	0	0	0	0	0
				4-Oct-02	NIGHT	37+	9	0	0	0	0	0	0
29A		C - 2	Semi-permanent cattle pond										
A				27-May-95	TRAPPING	0	0	0	0	0	0	0	0
A				14-Jul-95	DAY	0	0	0	0	0	0	0	0
A				3-Jun-96	NIGHT	7+	0	0	0	0	0	0	0
A				10-Jul-97	DAY	(+)	0	1	0	0	0	0	0
A				11-Jul-97	DAY	1+	4+	1	0	0	0	0	0
A				11-Jul-97	TRAPPING	0	0	1	71	0	0	0	0

SITE	SUB	MAP	DESCRIPTION	DATE	SURVEY	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL
35		C - 3	Large vernal pool	23-Feb-95	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0
				3-Mar-95	DIP NETTING	0	0	0	0	0	0	0	0	0	0	0	0
				5-May-95	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				6-May-95	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				15-Feb-01	NIGHT	2+	0	0	0	0	0	0	0	0	0	0	0
36		C - 3	Several large, old wastewater ponds														
				15-Feb-95	CALLING	0	0	0	0	0	0	0	0	0	0	0	0
				18-Feb-95	CALLING	0	0	0	0	0	0	0	0	0	0	0	0
				19-Feb-95	NIGHT	3	0	0	0	0	3+	0	0	0	0	0	0
				2-Jun-95	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				22-Jun-95	NIGHT	1	0	0	0	0	0	0	0	0	0	0	5
				16-Jul-95	DAY	0	0	0	0	0	0	5	0	0	0	0	2
				26-Jul-95	NIGHT	1	0	0	0	0	0	11	0	0	0	0	0
				18-Oct-96	NIGHT	0	0	0	0	0	0	0	2	0	0	0	0
				13-Feb-97	EGG MASS	0	0	0	0	0	5	0	0	0	0	0	0
				26-Feb-97	EGG MASS	0	0	0	0	0	0	2+	(+)	0	0	0	0
				5-Jul-97	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				5-Jul-97	NIGHT	2	0	0	0	0	0	8	0	0	0	0	0
				20-Jul-97	TRAPPING	0	0	0	0	0	0	0	0	0	0	1	0
				4-Aug-97	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				1-Sep-97	NIGHT	(+)	0	0	0	0	0	(+)	0	0	0	0	0
				10-Sep-97	NIGHT	1	0	0	0	0	0	8+	0	8+	0	0	0
				21-Sep-97	NIGHT	2+	0	0	0	0	0	2+	6+	0	0	0	0
				31-Mar-01	NOTES	0	0	0	0	0	0	0	1	0	0	0	0
				21-Jul-01	NIGHT	1+	0	0	0	0	0	18+	3	23	1	0	2
				7-Oct-02	NIGHT	0	0	17+	0	0	0	10+	0	0	0	0	0
37		C - 3	Semi-permanent beaver pond, "Triangle Pond"														
			Sculpin, mosquitofish, crayfish	3-Mar-95	CALLING	0	0	0	0	0	2	0?	?	?	?	?	?
				15-Apr-95	TRAPPING	0	0	0	0	0	0	?	?	?	?	?	?
				20-Jan-97	TRAPPING	0	0	0	0	0	0	0?	?	?	?	?	?
				21-Jan-97	TRAPPING	0	0	0	0	0	0	0?	?	?	?	?	?
				23-Jan-97	TRAPPING	0	0	0	0	0	0	1	0	0	0	0	0
				26-Jan-97	NOTES	0	1	0	0	0	0	0	0	0	0	0	0
				2-Feb-97	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				2-Feb-97	EGG MASS	0	0	0	0	0	17	0	0	0	0	0	0
				11-Feb-97	EGG MASS	0	0	0	0	0	2	0	0	0	0	0	0
				16-Feb-97	CALLING	0	0	0	0	0	0	0	0	0	0	0	0
				17-Feb-97	EGG MASS	0	0	0	0	0	0	0	0	0	0	0	0
				4-Mar-97	EGG MASS	0	0	0	0	0	3	0	0	0	0	0	0

SITE	SUB	MAP	DESCRIPTION	DATE	SURVEY	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL
39				10-Sep-02	TRAPPING	0	0	0	0	0	0	0	1	0	0	0	0
				27-Sep-02	NETTING	0	0	0	0	0	0	0	0	0	0	0	0
41		C - 3	Large lake in steep canyon														
				3-Mar-95	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0
				7-Jul-95	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0
				23-Aug-95	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				24-Aug-95	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				19-Mar-01	CALLING	0	0	0	0	0	0	0	0	0	0	0	0
				4-Apr-01	NIGHT	1	1+	0	0	0	0	0	0	0	0	0	0
45 A(S)		C - 3	Permanent created large pond: "lower Pine Cyn. Lake"														
			Introduced fish, crayfish	15-Feb-95	CALLING	0	0	0	0	0	0	8	0	0	0	0	0
				18-Feb-95	NIGHT	0	0	0	0	0	0	9+	0	0	0	0	0
				19-Feb-95	NIGHT	0	0	0	0	0	0	4	1	0	0	0	0
				8-Jul-95	NIGHT	0	0	0	0	0	0	2	0	0	0	0	MANY
				3-Jun-96	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	LOTS
				4-Jun-96	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				5-Jun-96	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				5-Jun-96	NIGHT	0	0	0	0	0	0	3	0	0	0	0	LOTS
				10-Feb-98	CALLING	0	0	0	0	0	0	3	0	0	0	0	0
				11-Jul-98	DIP NETTING	0	0	0	0	0	0	0	0	0	0	0	0
				22-Sep-99	NIGHT	0	0	0	0	0	0	4	2	0	0	0	0
				23-Sep-99	DAY	0	0	0	0	0	0	0	1	0	0	1	0
				15-Mar-01	CALLING	0	0	0	0	0	0	0	0	0	0	0	0
				8-Jun-01	NIGHT	0	0	0	0	0	0	1	0	0	0	0	~34
				23-Apr-02	NIGHT	0	0	0	0	0	0	1	0	0	0	0	1
45 B(M)		C - 3	Permanent created large pond: "middle Pine Cyn. Lake"														
			Introduced fish, crayfish	18-Aug-95	NIGHT	0	0	0	0	0	0	10	0	0	0	1	0
				4-Jun-96	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				5-Jun-96	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				5-Jun-96	NOTES	0	0	0	0	0	0	0	0	0	LOTS	0	0
				11-Jul-98	DIP NETTING	0	0	0	0	0	0	0	0	0	LOTS	0	0
				22-Sep-99	NIGHT	0	0	0	0	0	0	1	1	0	0	0	0
				23-Sep-99	DAY	0	0	0	0	0	0	0	3+	1	0	0	0
				15-Mar-01	CALLING	0	0	0	0	0	0	0	0	0	0	0	0
				19-Jun-01	NIGHT	0	0	0	0	0	0	0	0	0	0	0	09 TO 10
				25-Apr-02	NIGHT	0	0	0	0	0	0	1	0	0	0	0	0

SITE	SUB	MAP	DESCRIPTION	DATE	SURVEY	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL
46				29-Jul-98	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				31-Jul-98	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				1-Aug-98	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				2-Aug-98	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				3-Aug-98	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				5-Aug-98	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
			(Partial survey)	10-Oct-99	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0
			(Partial survey)	19-Oct-99	NIGHT	0	0	0	0	0	0	1	0	0	0	0	0
			(Entire pond)	13-Oct-02	NIGHT	9+	0	0	0	0	0	0	0	0	0	0	0
47		C - 2	Medium dune swale pond														
				15-Feb-95	NIGHT	1+	0	0	0	0	0	0	0	0	0	0	0
				18-Feb-95	EGG MASS	0	0	0	0	0	0	0	0	0	0	0	0
				18-Feb-95	NIGHT	2	0	0	0	0	0	0	0	0	0	0	0
				6-Jul-95	NIGHT	2+	0	0	0	0	0	0	0	0	0	0	0
				13-Jul-95	DAY	(+)	0	0	0	0	0	0	0	0	0	0	0
				3-Jun-96	NIGHT	0	7+	0	0	0	0	0	0	0	0	0	0
				27-Nov-96	NIGHT	~20	0	0	0	0	0	0	0	0	0	0	0
				25-Jul-97	DAY	0	0	0	0	0	0	0	0	0	0	0	0
				25-Jul-97	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				26-Jul-97	TRAPPING	0	0	0	0	8	0	0	0	0	0	0	0
				26-Jul-98	TRAPPING	0	0	0	0	60+	0	0	0	0	0	0	0
				15-Aug-98	TRAPPING	0	1	8	13	0	0	0	0	0	0	0	0
				15-Aug-98	NOTES	6+	0	0	0	0	0	0	0	0	0	0	0
				16-Aug-98	TRAPPING	0	0	8	6	0	0	0	0	0	0	0	0
				19-Aug-98	TRAPPING	0	0	8	13	0	0	0	0	0	0	0	0
				19-Aug-98	TRAPPING	0	0	3	5	0	0	0	0	0	0	0	0
				20-Aug-98	TRAPPING	0	0	8	2	0	0	0	0	0	0	0	0
				25-Aug-98	TRAPPING	0	0	8	5	0	0	0	0	0	0	0	0
				25-Aug-98	TRAPPING	0	0	6	5	0	0	0	0	0	0	0	0
				26-Aug-98	TRAPPING	0	0	8	2	0	0	0	0	0	0	0	0
				26-Aug-98	TRAPPING	0	0	8	10	0	0	0	0	0	0	0	0
				27-Jun-01	NIGHT	2	10	0	0	0	0	0	0	0	0	0	0
				23-Mar-02	CALLING	0	0	0	0	0	5+	0	0	0	0	0	0
			Created ephemeral pond: "Waterfowl Natural Res. Area"														
48	1(NE)	C - 3															
48	1(NE)			8-Oct-96	DAY	0	0	0	0	0	0	0	0	0	0	0	0
48	1(NE)			8-Oct-96	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0
48	1(NE)			23-Nov-96	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0
48	1(NE)			28-Dec-96	NIGHT	0	0	0	0	0	6+	0	0	0	0	0	0
48	1(NE)			24-Jan-97	NIGHT	10	0	0	0	0	~20	0	0	0	0	0	0
48	1(NE)			16-Feb-97	CALLING	0	0	0	0	0	4 TO 5	0	0	0	0	0	0

SITE	SUB	MAP	DESCRIPTION	DATE	SURVEY	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL
	48 1(NE)			2-Mar-97	NIGHT	8+	0	0	0	0	-8	0	0	0	0	0	0
	48 1(NE)			14-Jan-98	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0
	48 1(NE)			17-Jan-98	NIGHT	6	0	0	0	0	2	0	0	0	0	0	0
	48 1(NE)			26-Jan-98	NIGHT	0	0	0	0	0	-5	0	0	0	0	0	0
	48 1(NE)			11-Feb-98	EGG MASS	0	0	0	0	0	2	0	0	0	0	0	0
	48 1(NE)			15-Feb-98	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0
	48 1(NE)			18-Feb-98	EGG MASS	0	0	0	0	0	1	0	0	0	0	0	0
	48 1(NE)			20-Feb-98	EGG MASS	0	0	0	0	0	2	0	0	0	0	0	0
	48 1(NE)			22-Feb-98	EGG MASS	0	0	0	0	0	3	0	0	0	0	0	0
	48 1(NE)			5-Mar-98	EGG MASS	0	0	0	0	0	0	0	0	0	0	0	0
	48 1(NE)			7-Mar-98	NOTES	0	0	0	0	0	-3	0	0	0	0	0	0
	48 1(NE)			9-Mar-98	EGG MASS	0	0	0	0	0	1	0	0	0	0	0	0
			Created ephemeral pond, "Waterfowl Natural Res. Area"														
	48 2(NW)	C - 3															
	48 2(NW)			8-Oct-96	DAY	0	0	0	0	0	0	0	0	0	0	0	0
	48 2(NW)			24-Jan-97	NOTES	0	0	0	0	0	1	0	0	0	0	0	0
	48 2(NW)			16-Feb-97	CALLING	0	0	0	0	0	0	0	0	0	0	0	0
	48 2(NW)			26-Feb-97	EGG MASS	0	0	0	0	0	0	0	0	0	0	0	0
	48 2(NW)			28-Feb-97	EGG MASS	0	0	0	0	0	0	0	0	0	0	0	0
	48 2(NW)			23-Jan-98	EGG MASS	0	0	0	0	0	2	0	0	0	0	0	0
	48 2(NW)			15-Feb-98	NIGHT	2	0	0	0	0	1	4	0	0	0	0	0
	48 2(NW)			22-Feb-98	EGG MASS	0	0	0	0	0	2	0	0	0	0	0	0
	48 2(NW)			5-Mar-98	EGG MASS	0	0	0	0	0	4	0	0	0	0	0	0
	48 2(NW)			7-Mar-98	NOTES	0	0	0	0	0	1 OR 2	0	0	0	0	0	0
	48 2(NW)			15-Jul-98	TRAPPING	0	0	0	6	1	0	0	0	0	0	0	1
	48 2(NW)			16-Jul-98	TRAPPING	0	0	20	4	0	0	0	0	0	0	0	0
	48 2(NW)			17-Jul-98	TRAPPING	0	0	54	4	0	0	0	0	0	0	0	0
	48 2(NW)			18-Jul-98	TRAPPING	0	0	58	2	0	0	0	0	0	0	0	0
			(dry)	10-Nov-02	NOTES	0	0	0	0	0	0	0	0	0	0	0	0
			Created permanent pond, "Waterfowl Natural Res. Area"														
	48 4(SE)	C - 3															
	48 4(SE)			31-May-96	NIGHT	1	0	0	0	0	0	0	0	0	0	0	0
	48 4(SE)			8-Oct-96	DAY	0	0	0	0	0	0	0	0	0	0	0	0
	48 4(SE)			8-Oct-96	NIGHT	0	0	0	1	0	0	0	0	0	0	0	0
	48 4(SE)			14-Oct-96	NIGHT	2+	0	0	0	0	0	0	0	0	0	0	0
	48 4(SE)			18-Oct-96	NIGHT	4	2	0	0	0	0	0	0	0	0	0	0
	48 4(SE)			23-Oct-96	NIGHT	(+)	1	0	0	0	0	0	0	0	0	0	0
	48 4(SE)			20-Nov-96	NOTES	0	4+	0	0	0	0	0	0	0	0	0	0
	48 4(SE)			23-Nov-96	NIGHT	1	2	0	0	0	0	0	0	0	0	0	0
	48 4(SE)			30-Nov-96	NIGHT	1	0	0	0	0	1	0	0	0	0	0	0
	48 4(SE)			14-Dec-96	NIGHT	1	4	0	0	0	1	0	0	0	0	0	0

SITE	SUB	MAP	DESCRIPTION	DATE	SURVEY	#ADULTS	CALIFORNIA RED-LEGGED FROGS				#CALL		#ADULTS	#JUV	#META	BULLFROGS		#EGG MS	#CALL
							#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL				#LARV			
48 4(SE)				15-Dec-96	NIGHT	2	0	0	0	0	0	1		0	0	0	0	0	0
48 4(SE)				28-Dec-96	NIGHT	1	1	0	0	0	0	1		0	0	0	0	0	0
48 4(SE)				24-Jan-97	NOTES	0	0	0	0	0	0	1		0	0	0	0	0	0
48 4(SE)				16-Feb-97	CALLING	0	0	0	0	0	0	0		0	0	0	0	0	0
48 4(SE)				21-Feb-97	EGG MASS	0	0	0	0	0	1	0		0	0	0	0	0	0
48 4(SE)				22-Feb-97	NIGHT	3	0	0	0	0	0	2 TO 3		0	0	0	0	0	0
48 4(SE)				28-Feb-97	NIGHT	7	0	0	0	0	0	4 TO 5		0	0	0	0	0	0
48 4(SE)				2-Mar-97	EGG MASS	0	0	0	0	0	0	0		0	0	0	0	0	0
48 4(SE)				2-Mar-97	NIGHT	5+	0	0	0	0	0	3		0	0	0	0	0	0
48 4(SE)				5-Apr-97	NIGHT	6+	0	0	0	0	0	1		0	0	0	0	0	0
48 4(SE)				11-Apr-97	NIGHT	11+	0	0	0	0	0	2		0	0	0	0	0	0
48 4(SE)				12-Apr-97	NIGHT	3	0	0	0	0	0	1		0	0	0	0	0	0
48 4(SE)				25-Apr-97	NIGHT	4+	0	0	0	0	0	1		0	0	0	0	0	0
48 4(SE)				11-May-97	NIGHT	6+	0	0	0	0	0	0		0	0	0	0	0	0
48 4(SE)				18-Jul-97	NIGHT	8	0	6	0	0	0	0		0	0	0	0	0	0
48 4(SE)				27-Jul-97	NIGHT	6	0	2	0	0	0	0		0	0	0	0	0	0
48 4(SE)				1-Aug-97	NOTES	0	0	2	0	0	0	0		0	0	0	0	0	0
48 4(SE)				9-Aug-97	NIGHT	6	0	35	0	0	0	0		0	0	0	0	0	0
48 4(SE)				10-Aug-97	TRAPPING	0	0	0	1	0	0	0		0	0	0	0	0	0
48 4(SE)				1-Sep-97	NIGHT	4	0	8	0	0	0	0		0	0	0	0	0	0
48 4(SE)				16-Sep-97	NIGHT	8	0	6	0	0	0	0		0	0	0	0	0	0
48 4(SE)				16-Oct-97	NIGHT	3	0	0	0	0	0	0		0	0	0	0	0	0
48 4(SE)				17-Oct-97	NIGHT	3	0	0	0	0	0	0		0	0	0	0	0	0
48 4(SE)				20-Nov-97	NIGHT	1	0	0	1	0	0	0		0	0	0	0	0	0
48 4(SE)				11-Dec-97	NIGHT	0	0	0	0	0	0	0		0	0	0	0	0	0
48 4(SE)				13-Feb-98	EGG MASS	0	0	0	0	0	0	0		0	0	0	0	0	0
48 4(SE)				15-Feb-98	NIGHT	2	0	0	0	0	1	5		0	0	0	0	0	0
48 4(SE)				18-Feb-98	EGG MASS	0	0	0	0	0	5	0		0	0	0	0	0	0
48 4(SE)				22-Feb-98	EGG MASS	0	0	0	0	0	0	0		0	0	0	0	0	0
48 4(SE)				7-Mar-98	NIGHT	(+)	0	0	0	0	0	7		0	0	0	0	0	0
48 4(SE)				22-Mar-98	EGG MASS	0	0	0	0	0	0	0		0	0	0	0	0	0
48 4(SE)				15-Jul-98	NOTES	0	0	0	0	0	0	0		0	0	0	0	0	2 TO 3
48 4(SE)				17-Jul-98	NOTES	0	0	0	0	0	0	0		0	0	0	0	0	~3
48 4(SE)				18-Jul-98	NOTES	0	0	0	0	0	0	0		0	0	0	0	0	1
48 4(SE)				20-Jul-98	TRAPPING	0	0	3	7	0	0	0		0	2	0	0	0	0
48 4(SE)				22-Jul-98	TRAPPING	0	0	5	3	0	0	0		0	0	0	0	0	0
48 4(SE)				6-Aug-98	TRAPPING	0	0	3	12	0	0	0		0	0	0	0	0	0
48 4(SE)				6-Aug-98	NOTES	1	0	0	0	0	0	0		0	0	0	0	0	0
48 4(SE)				12-Aug-98	NIGHT	7	0	6	0	0	0	0		2+	0	0	0	0	0 3 TO 4
48 4(SE)				13-Aug-98	TRAPPING	0	0	0	0	0	0	0		0	0	0	0	0	0
48 4(SE)				25-Aug-98	NIGHT	18+	0	9	0	0	0	0		(+)	1	0	0	0 SEVERAL	
48 4(SE)				14-Sep-98	NIGHT	0	0	0	0	0	0	0		1+	0	0	0	0	0
48 4(SE)				20-Aug-99	NOTES	0	0	0	0	0	0	0		0	0	0	0	0	0 FEW
48 4(SE)				21-Aug-99	NIGHT	51+	0	1	0	0	0	0		8	0	0	0	0	0
48 4(SE)				5-Sep-99	NIGHT	13	0	0	0	0	0	0		0	0	0	0	0	0
48 4(SE)				10-Sep-99	NIGHT	43	0	2	0	0	0	0 COUPLE		7+	0	0	0	0	0

SITE	SUB	MAP	DESCRIPTION	DATE	SURVEY	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL
	48 4(SE)			16-Sep-99	DAY	2+	0	0	0	0	0	0	0	(+)	0	0	0
	48 4(SE)			23-Sep-99	DAY	0	0	19	5	0	0	0	0	0	0	0	0
	48 4(SE)			25-Sep-99	DAY	0	(+)	12	1	0	0	0	0	0	0	0	0
	48 4(SE)			25-Sep-99	NIGHT	21	0	1	0	0	0	5	0	0	0	0	0
	48 4(SE)			25-Sep-99	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
	48 4(SE)			26-Sep-99	TRAPPING	0	0	1	0	0	0	0	0	0	0	0	0
	48 4(SE)			10-Oct-99	DAY	0	0	1	0	0	0	0	0	0	0	0	0
	48 4(SE)			3-May-00	DAY	0	(+)	0	0	0	0	0	0	0	0	0	0
	48 4(SE)			24-May-00	DAY	0	0	0	0	0	0	0	0	0	0	0	1
	48 4(SE)			3-Jun-00	NIGHT	45(+)	0	0	0	0	1	2+	0	0	0	0	0
	48 4(SE)			24-Jun-00	NOTES	1	0	0	0	0	0	0	0	0	0	0	0
	48 4(SE)			1-Jul-00	DAY	(+)	0	0	0	0	0	0	0	0	0	0	0
	48 4(SE)			24-Aug-00	NIGHT	63	0	6	0	0	0	3	0	0	0	0	1
	48 4(SE)			30-Aug-00	NIGHT	67	0	4	0	0	0	1	0	0	0	0	0
	48 4(SE)			7-Sep-00	NIGHT	59	0	7	0	0	0	1	0	0	0	0	0
	48 4(SE)			17-Sep-00	NIGHT	94	0	13	0	0	1	3	0	0	0	0	0
	48 4(SE)			8-Aug-01	NIGHT	50+	18	2	0	0	0	2+	0	0	0	0	0
	49 4(SE)			10-Nov-02	NIGHT	9	1	0	0	0	0	1	0	0	0	0	0
			Created permanent pond: "Waterfowl Natural Res. Area"														
	48 5(SW)	C - 3		26-May-95	DAY	0	0	0	0	0	0	0	0	0	0	0	1
	48 5(SW)			26-May-95	NIGHT	0	0	0	0	0	0	12	0	0	0	0	0
	48 5(SW)			8-Oct-96	DAY	0	0	0	0	0	0	0	0	0	0	0	0
	48 5(SW)			14-Oct-96	NIGHT	2	5	6+	0	0	0	0	0	0	0	0	0
	48 5(SW)			18-Oct-96	NIGHT	0	1	1	0	0	0	0	0	0	0	0	0
	48 5(SW)			19-Oct-96	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
	48 5(SW)			23-Oct-96	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
	48 5(SW)			23-Oct-96	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0
	48 5(SW)			24-Nov-96	NOTES	0	0	0	0	0	1	0	0	0	0	0	0
	48 5(SW)			24-Nov-96	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0
	48 5(SW)			30-Nov-96	NIGHT	3	3	1	0	0	0	0	0	0	0	0	0
	48 5(SW)			14-Dec-96	NIGHT	0	0	0	0	0	1	0	0	0	0	0	0
	48 5(SW)			15-Dec-96	NIGHT	1	0	0	0	0	0	0	0	0	0	0	0
	48 5(SW)			28-Dec-96	NIGHT	2	1	0	0	0	0	0	0	0	0	0	0
	48 5(SW)			24-Jan-97	NOTES	0	0	0	0	0	1	0	0	0	0	0	0
	48 5(SW)			16-Feb-97	CALLING	0	0	0	0	0	0	0	0	0	0	0	0
	48 5(SW)			22-Feb-97	NIGHT	1	0	0	0	0	0	0	0	0	0	0	0
	48 5(SW)			28-Feb-97	EGG MASS	0	0	0	0	2	2	0	0	0	0	0	0
	48 5(SW)			28-Feb-97	NIGHT	6	0	0	0	0	4 TO 5	0	0	0	0	0	0
	48 5(SW)			1-Mar-97	EGG MASS	0	1	0	0	1	0	0	0	0	0	0	0
	48 5(SW)			2-Mar-97	EGG MASS	0	0	0	0	6	0	0	0	0	0	0	0
	48 5(SW)			2-Mar-97	NIGHT	5+	0	0	0	1	1	0	0	0	0	0	0
	48 5(SW)			28-Mar-97	NIGHT	7+	0	0	0	0	0	0	0	0	0	0	0
	48 5(SW)			5-Apr-97	NIGHT	9+	0	0	0	0	1	0	0	0	0	0	0

SITE	SUB	MAP	DESCRIPTION	DATE	SURVEY	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL
	48 5(SW)			24-Aug-00	NIGHT	26	0	2	0	0	0	1	0	0	0	0	0
	48 5(SW)			30-Aug-00	NIGHT	20	1	0	0	0	0	0	0	0	0	0	0
	48 5(SW)			7-Sep-00	NIGHT	25	0	1	0	0	0	0	0	0	0	0	0
	48 5(SW)			17-Sep-00	NIGHT	19	0	1	0	0	0	0	0	0	0	0	0
	48 5(SW)			8-Aug-01	NOTES	5	2	0	0	0	0	0	0	0	0	0	0
	48 5(SW)			8-Aug-01	NIGHT	5+	3	1	0	0	0	0	0	0	0	0	0
	48 5(SW)		(dried to small pools)	10-Nov-02	NIGHT	0	0	2	0	0	0	0	0	0	0	0	0
			Small semi-permanent spring-fed pond (Upper & Lower)														
50	A(E)	C - 4		12-May-95	DAY	0	0	0	0	0	0	0	0	0	0	0	0
				15-May-01	DAY	1+2 TO 3		0	0	0	0	0	0	0	0	0	0
				16-Jun-01	DAY	(+)	1	0	1+	0	0	0	0	0	0	0	0
				16-Jun-01	NIGHT	21+	0	11+	1	0	0	0	0	0	0	0	0
				2-Mar-02	EGG MASS	0	0	0	0	1	0	0	0	0	0	0	0
				8-May-02	NIGHT	11	1	0	0	0	0	0	0	0	0	0	0
50	B(N)	C - 4	Small ephemeral spring-fed pond														
				12-May-95	DAY	0	0	0	0	0	0	0	0	0	0	0	0
				15-May-01	DAY	2 TO 38 TO 9		0	0	0	0	0	0	0	0	0	0
				16-Jun-01	DAY	0	0	0	0	0	0	0	0	0	0	0	0
				16-Jun-01	NIGHT	4	0	5	0	0	0	0	0	0	0	0	0
				2-Mar-02	EGG MASS	0	0	0	0	0	0	0	0	0	0	0	0
				8-May-02	NIGHT	3	1	0	0	0	0	0	0	0	0	0	0
54		C - 2	Small vernal pool & medium temporary wetland														
				6-Mar-01	NIGHT	3+	0	0	0	0	0	0	0	0	0	0	0
58		C - 3	Gravel pit														
				22-May-95	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				22-May-95	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0
				22-Aug-95	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0
				4-Jun-96	TRAPPING	1	0	0	1	0	0	0	0	0	0	0	0
				5-Jun-96	TRAPPING	1	0	0	0	0	0	0	0	0	0	0	0
				18-Apr-99	NIGHT	3	0	0	0	0	2	(+)	0	0	0	0	0
60		C - 3	Lake in steep canyon														
				15-Aug-95	DAY	0	0	38	0	0	0	0	0	0	0	0	0
				16-Aug-95	TRAPPING	0	0	39+	47	0	0	0	0	0	0	0	0
				17-Aug-95	TRAPPING	0	0	6+	26	0	0	0	0	0	0	0	0
				18-Aug-95	TRAPPING	0	0	0	13	0	0	0	0	0	0	0	0

SITE	SUB	MAP	DESCRIPTION	DATE	SURVEY	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL
81				3-Aug-95	NIGHT	0	3	0	0	0	0	0	0	0	0	0	0
			(surveyed from bridge only)	7-Oct-02	NIGHT	1	0	0	0	0	0	0	0	0	0	0	0
				23-Oct-02	NIGHT	1	0	1	0	0	1	0	0	0	0	0	0
85		C - 2	Permanent marsh in canyon	22-Aug-95	TRAPPING	0	0	0	4	0	0	0	0	0	0	0	0
				22-Aug-95	NOTES	0	0	4	0	0	0	0	0	0	0	0	0
87		C - 4	Spring-fed large pond	13-Sep-95	NIGHT	2	0	30	0	0	0	0	0	0	0	0	0
				9-Mar-02	EGG MASS	(+)	0	0	0	0	7	0	0	0	0	0	0
				30-Apr-02	NIGHT	20	0	0	0	0	0	0	0	0	0	0	0
				21-Aug-02	NIGHT	63	0	1	0	0	0	0	0	0	0	0	0
				30-Sep-02	DAY	0	0	0	0	0	0	0	0	0	0	0	0
				30-Sep-02	NIGHT	94	0	10	0	0	0	0	0	0	0	0	0
91		C - 2	Permanent/semi-permanent dune swale pond	2-Feb-97	EGG MASS	0	0	0	0	0	17	0	0	0	0	0	0
				11-Feb-97	EGG MASS	0	0	0	0	0	0	0	0	0	0	0	0
				21-Jun-97	TRAPPING	0	0	0	29	0	0	0	0	0	0	0	0
				12-Jul-97	TRAPPING	0	0	0	46	0	0	0	0	0	0	0	0
				12-Jul-97	NOTES	~8	0	0	0	0	0	0	0	0	0	0	0
				25-Jul-97	NIGHT	18+	0	1	0	0	0	0	0	0	0	0	0
				25-Jul-97	TRAPPING	0	0	0	16	0	0	0	0	0	0	0	0
				13-Sep-97	NIGHT	(+)	0	12	0	0	0	0	0	0	0	0	0
				19-Sep-97	NIGHT	(+)	0	15	0	0	0	0	0	0	0	0	0
				23-Sep-97	NIGHT	21	0	9	0	0	0	0	0	0	0	0	0
				25-Nov-97	NIGHT	7+	0	0	0	0	0	0	0	0	0	0	0
				7-Dec-97	NIGHT	5	0	0	0	0	0	0	0	0	0	0	0
				7-Jan-98	EGG MASS	(+)	0	0	0	0	2	0	0	0	0	0	0
				15-Feb-98	EGG MASS	0	0	0	0	0	0	0	0	0	0	0	0
				18-Jul-98	NIGHT	2	0	5	0	0	0	0	0	0	0	0	0
				5-Aug-98	NIGHT	17	0	14	0	0	0	0	0	0	0	0	0
				18-Aug-98	NIGHT	8+	0	7	0	0	0	0	0	0	0	0	0
				10-Sep-98	NIGHT	5+	0	11	0	0	0	0	0	0	0	0	0
				24-Sep-98	NIGHT	5+	0	12	0	0	0	0	0	0	0	0	0
				10-Aug-01	NIGHT	15+	12+	4	0	0	0	0	0	0	0	0	0
				29-Aug-02	NIGHT	64+	6	169+	COUPLE	0	0	0	0	0	0	0	0

SITE	SUB	MAP	DESCRIPTION	DATE	SURVEY	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL
116		C - 2	Permanent/semi-permanent dune swale pond	1-Jun-01	NIGHT	14	18	3	0	0	0		0	0	0	0	0
120 B(NW)		C - 2	Permanent/semi-permanent dune swale pond	25-Jul-01	NIGHT	15+	1	0	0	0	0	0	0	0	0	0	0
				1-Aug-01	NIGHT	14+	2	2	0	0	0	0	0	0	0	0	0
				11-Oct-02	NIGHT	21+	11	7	0	0	0	0	0	0	0	0	0
123		C - 2	Permanent dune swale pond	25-Aug-01	NIGHT	41+	14	0	0	0	0	0	0	0	0	0	0
				13-Mar-02	EGG MASS	0	0	0	0	0	0	0	0	0	0	0	0
				14-May-02	NIGHT	7+	4+	0	7+	0	0	0	0	0	0	0	0
				15-Aug-02	NIGHT	61+	17	4	2-3(+)	0	5 TO 6	0	0	0	0	0	0
128		C - 2	Permanent dune swale pond w/ extensive open water	25-Feb-02	EGG MASS	0	0	0	0	0	4	0	0	0	0	0	0
				30-May-02	NIGHT	30+	8+	0	0	0	0	0	0	0	0	0	0
				26-Aug-02	NIGHT	70	17	90	0	0	0	0	0	0	0	0	0
130		C - 2	Semi-permanent dune swale pond	25-Feb-02	EGG MASS	11	1	0	0	0	28	0	0	0	0	0	0
				20-Mar-02	EGG MASS	3	0	0	0	0	4	0	0	0	0	0	0
				26-Mar-02	NIGHT	16+	1	0	0	0	0 COUPLE	0	0	0	0	0	0
				30-May-02	NIGHT	17+	8+	0	MANY	0	0	0	0	0	0	0	0
			(dried to stream)	10-Aug-02	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0
			(dried to stream)	7-Sep-02	DAY	0	0	0	0	0	0	0	0	0	0	0	0
140		C - 3	Permanent large pond in drainage blocked by road	22-Aug-95	NOTES	2	0	0	0	0	0	0	0	0	0	0	0
			Mosquitofish	22-Dec-96	NOTES	0	0	0	0	0	3	0	0	0	0	0	0
				5-Mar-99	CALLING	4+	0	0	0	0	6	1	0	0	0	0	0
				6-Mar-99	CALLING	5+	0	0	0	0	9	1+	0	0	0	0	0
				31-Mar-99	CALLING	0	0	0	0	0	(+)	0	0	0	0	0	0
				4-Apr-99	CALLING	1+	0	0	0	0	5+	(+)	0	0	0	0	0
				10-Apr-99	EGG MASS	0	0	0	0	0	0	(+)	0	0	0	0	0

SITE	SUB	MAP	DESCRIPTION	DATE	SURVEY	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL	BULLFROGS	#ADULTS	#JUV	#META	#LARV	#EGG MS	#CALL
151				8-Aug-00	NIGHT	1	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				2-Oct-00	DAY	0	0	15	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				23-Oct-01	NIGHT	2+	0	0	5	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				15-Mar-02	EGG MASS	0	0	0	0	0	5	0	0	0	0	0	0		0	0	0	0	0	0
				9-May-02	NIGHT	13	1	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
			(dried to puddle)	4-Aug-02	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
			(dried to puddle)	6-Sep-02	DAY	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
			Permanent pond in unnamed drainage																					
155		C - 2		30-Mar-01	NIGHT	1+	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				28-May-02	NIGHT	16	2	0	MANY	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				22-Nov-02	NIGHT	10	2	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
			Large vernal pool																					
157				14-Jan-01	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				21-Jan-01	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				14-Feb-01	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				28-Feb-01	NIGHT	1	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				11-May-01	TRAPPING	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				30-Aug-01	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				8-Dec-01	NIGHT	1	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				15-Mar-02	EGG MASS	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				16-Apr-02	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
171 A(E)		C - 4	Channelized stream																					
				30-Mar-00	NIGHT	5+	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				20-Apr-00	EGG MASS	(+)	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				20-Apr-00	NIGHT	5+	(+)	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				21-Apr-00	NIGHT	7+	1	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				14-Jan-01	CALLING	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				29-Jan-01	NIGHT	4	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				12-Mar-01	NOTES	2	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				26-Jun-01	NOTES	1	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				13-Nov-01	DAY	(+)	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				19-Dec-01	CALLING	(+)	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				29-Apr-02	NIGHT	0	1	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				7-Jul-02	NIGHT	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				10-Nov-02	NIGHT	3	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
179		C - 3	Large semi-permanent pond																					
				14-Feb-01	NIGHT	11	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				30-Aug-01	NIGHT	13+	1	5	3	0	0	0	0	0	0	0	0		0	0	0	0	0	0
				20-Feb-02	EGG MASS	(+)	0	0	0	0	18	0	0	0	0	0	0		0	0	0	0	0	0

Appendix F

Metamorph Data from Chapter 2, Study 2

Date	Pond	Perim (m)	RAAU meta	RAAU adlt	RACA juv	RACA ad	UnID	Time (h)	Observer
5-Jul-97	30	496	1	NR	NR	NR	NR	1:30	SVC/SSC
6-Jul-97	30		9	NR	NR	NR	NR	NR	SVC/SSC
7-Jul-97	30		3	NR	NR	NR	NR	NR	SVC/SSC
1-Sep-97	36	753	0	NR	NR	NR	NR	0:24	SSC
10-Sep-97	36		0	1	8	8	0	0:30	SVC
21-Sep-97	36		0	2	6	2	5	0:22	SSC
2-Sep-97	39	977	6	NR	NR	NR	NR	2:12	SSC
11-Sep-97	39		1	NR	NR	NR	NR	2:00	SSC
18-Sep-97	39		1	15	0	1	0	1:10	SVC
13-Sep-97	77	463	103	NR	NR	NR	NR	2:40	SSC
19-Sep-97	77		96	NR	NR	NR	NR	2:12	SSC
23-Sep-97	77		112	32	0	0	0	2:26	SSC
15-Aug-97	79	459	255	5	0	0	0	2:35	SVC
31-Aug-97	79		282	NR	NR	NR	NR	3:43	SSC
10-Sep-97	79		257	NR	NR	NR	NR	2:47	SSC
13-Sep-97	91	382	12	NR	NR	NR	NR	1:20	SSC
19-Sep-97	91		15	NR	NR	NR	NR	1:42	SSC
23-Sep-97	91		9	21	0	0	0	1:26	SSC

Notes:

Perim. = Pond perimeter

RAAU = *Rana aurora*, California red-legged frog

RACA = *Rana catesbeiana*, bullfrog

NR = Not recorded

Unid = Number of ranid frogs not identified to species

Time = Amount of time for each survey

SVC = Susan V. Christopher

SSC = Steve S. Collie

Appendix G
Data from Chapter 2, Experiment III

TAD- POLE #	TREATMENT	# CROSSES	IN REFUGE (of 19)	LENGTH (MM TL)	WEIGHT (G)	STAGE
1	CONTROL	1	15	103	11.1	41
1	BULLFROG	2	18			
1	TREEFROGS	1	0			
1	RED-LEGGED	0	0			
2	CONTROL	6	9	103	12.3	41
2	TREEFROGS	10	13			
2	RED-LEGGED	6	4			
2	BULLFROG	14	9			
3	CONTROL	0	19	104	11.5	42
3	RED-LEGGED	0	19			
3	TREEFROGS	0	0			
3	BULLFROG	0	19			
4	BULLFROG	5	10	111	11	42
4	TREEFROGS	4	12			
4	CONTROL	1	8			
4	RED-LEGGED	0	19			
5	CONTROL	1	8	101	10.2	42
5	RED-LEGGED	1	3			
5	BULLFROG	0	19			
6	BULLFROG	1	7	110	12.4	42
6	RED-LEGGED	3	14			
6	CONTROL	7	13			
7	CONTROL	0	19	105	9.8	42
7	RED-LEGGED	1	19			
7	BULLFROG	2	12			
8	RED-LEGGED	2	7	100	10	43
8	CONTROL	0	19			
8	BULLFROG	1	2			
9	RED-LEGGED	2	0	84	7.7	43
9	BULLFROG	13	2			
9	CONTROL	1	0			

Appendix G (Continued)

TAD- POLE #	TREATMENT	# CROSSES	IN REFUGE (of 19)	LENGTH (MM TL)	WEIGHT (G)	STAGE
10	RED-LEGGED	0	19	101	9.6	42
10	CONTROL	0	19			
10	BULLFROG	1	18			
11	BULLFROG	3	1	104	10.2	41
11	CONTROL	9	4			
11	RED-LEGGED	15	8			
12	CONTROL	2	17	97	9.2	41
12	BULLFROG	6	14			
12	RED-LEGGED	0	19			

Appendix H
Sites Surveyed in Chapter 3 Study 1
And Maximum Number of California Red-legged
Frogs & Bullfrogs Seen During Any One Survey

SITES WITHOUT FISH:

CO ¹	AREA ²	SITE	LOCALITY	RLF	BF	DATE	CF ³
SB		GAVIOTA CR	MOUTH TO JUST ABOVE CG RD XING	7	0	24MAR1997	
SB		REFUGIO CR	1ST XING N OF HWY 101	98 ⁴	0	14APR1994	
SB		TECOLOTE CR	MOUTH TO 1ST RD N OF HWY 101	2	0	16JAN1997	
SB	LPNF	ALDER CR	DOWNSTREAM FROM CAR PARK	2	0	28JUL1996	
SB	LPNF	ALDER CR	CAR PARK TO WATERFALL	3	0	11JUL1996	
SB	LPNF	FOX CR	SANTA YNEZ TO WATERFALL	1	0	1APR1996	
SB	LPNF	JAMESON LAKE	N SHORE	4	20	28MAY1996	X
SB	LPNF	MANZANA CR	NEAR NIRA CG	2	0	16APR1996	
SB	LPNF	MONO CR	BTW 1ST & 3RD XING OGILVY RD	19	0	16AUG1996	
SB	LPNF	MONO CR	BTW 4TH & 6TH XING OGILVY RD	17	0	16AUG1996	
SB	LPNF	SANTA YNEZ R	DOWNSTREAM FROM JUNCAL CG	6	0	24JUL1996	
SB	LPNF	SANTA YNEZ R	UPSTREAM FROM JUNCAL CG	14	0	19JUL1996	
SB	VAFB	26		4	0	11FEB1995	
SB	VAFB	27		8	0	10JUL2001	
SB	VAFB	30		0	3	22JUN1995	
SB	VAFB	30		9	0	22AUG2001	
SB	VAFB	36		3	0	19FEB1995	
SB	VAFB	36		1	11	26JUL1995	
SB	VAFB	39		1	2	23OCT1996	
SB	VAFB	39		75	1	27SEP1997	
SB	VAFB	48 (04)	WATERFOWL PONDS	94	3	17SEP2000	
SB	VAFB	48 (04)	WATERFOWL PONDS	51	8	21AUG1999	
SB	VAFB	48 (05)	WATERFOWL PONDS	0	12	26MAY1995	
SB	VAFB	48 (05)	WATERFOWL PONDS	40	0	20AUG1999	
SB	VAFB	50A		21	0	16JUN2001	
SB	VAFB	58		3	?	18APR1999	
SB	VAFB	61		2	1	10AUG1995	X
SB	VAFB	61		0	4	21FEB1997	X
SB	VAFB	71		5	0	3JUL2001	
SB	VAFB	72		12	0	27JUN2001	
SB	VAFB	77		8	0	16AUG1997	
SB	VAFB	78		65	0	1AUG2001	
SB	VAFB	81	LOWER OCEAN AVE DITCH	1	0	23OCT2002	X

Appendix H (Continued)

SITES WITHOUT FISH:

CO ¹	AREA ²	SITE	LOCALITY	RLF	BF	DATE	CF ³
SB	VAFB	87		65	0	21AUG2002	
SB	VAFB	91		21	0	23SEP2002	
SB	VAFB	92		11	0	5AUG1998	
SB	VAFB	120B		21	0	11OCT2002	
SB	VAFB	123		61	0	15AUG2002	
SB	VAFB	128		70	0	26AUG2002	
SB	VAFB	140		55	8	23AUG2002	
SB	VAFB	150	SLC-6 WASTEWATER POND (N)	43	0	21APR2000	
SB	VAFB	155	TITAN GATE DRAINAGE	16	0	28MAY2002	
SB	VAFB	280		18	0	26MAR02	
SB	VAFB	HONDA CR	MOUTH TO WATERFALL	14	0	11OCT2001	
SB	VAFB	HONDA CR	1ST XING TO 3RD XING OF OLD RD	1	0	24AUG1995	
SB	VAFB	HONDA CR	WOODEN BRIDGE TO POWERLINE	1	0	28JUL1995	
SB	VAFB	OCEAN AVE DITCH		2	0	4AUG1997	X
SB	VAFB	JALAMA CR	MOUTH TO 150 M UPSTREAM UPRR	18	0	5JUL1995	
SB	VAFB	MONROE ST (171)	DITCH AT JCT MONROE ST X SWEENEY	7	0	21APR2000	X
SB	VAFB	SAN ANTONIO CR	SIDE CHANNELS AT EL RANCHO RD	4	1	5MAR1999	
SB	VAFB	SHUMAN CR	MOUTH	5	0	18JUL1995	
SB	VAFB	SHUMAN CR	AT JCT CASMALIA CR	1	0	2SEP1995	
SC		BIG CR	SWANTON RD TO SCOTT CR	2	0	12MAR1997	
SLO		ARROYO LAGUNA	MOUTH UPSTREAM ~1 MI	13	0	22SEP1994	
SLO		LITTLE PICO CR	MOUTH UPSTREAM ~1 MI	5	0	23APR1996	
SLO		PICO CR	MOUTH UPSTREAM ~1 MI	7	0	24SEP1994	
SLO	SAN SIM- EON	SAN SIMEON CR	MOUTH UPSTREAM ~1 MI	36	0	23SEP1994	
SLO	GUAD	A8 (S)		10	0	14MAR1999	
SLO	GUAD	L11		10	0	5MAY1999	
SLO	GUAD	M12		9	0	18APR1999	
SLO	GUAD	POND A	JUST N SANTA MARIA RIVER MOUTH	28	0	19JUN1996	
SLO	GUAD	POND B		2	0	14MAR1999	
SLO	GUAD	TB8	RETENTION PONDS	7	0	15APR1999	
VEN	LPNF	AGUA BLANCA CR	NEAR DEVIL'S GATEWAY	0	1	25MAY1996	
VEN	LPNF	AGUA BLANCA CR	NEAR RANCH	0	2	3AUG1994	
VEN	LPNF	N FORK MATILIJA	WHEELER GORGE	0	0	MAR 1999	
VEN	LPNF	TULE CR	JCT. SESPE CR TO ~0.5 MI UPSTREAM	0	0	1997, 1999	

Appendix H (Continued)

SITES WITH FISH:

CO ₁	AREA ₂	SITE	LOCALITY	RLF	BF	DATE	FISH SPECIES ⁵	CF ³
SB	VAFB	38	EL RANCHO LATERAL POND	2	4	21SEP1997	AMNE, GAAC, GAAF, LECY, LEMA, MISA	X
SB	VAFB	45A	LOWER-MOST PINE CYN. LAKE	0	9	18FEB1995	GAAF, MISA	X
SB	VAFB	45B	MIDDLE PINE CYN. LAKE	0	10	18AUG1995	GAAF, PONI	X
SB	VAFB	45C	UPPER PINE CYN. LAKE	0	4	22SEP1999	GAAF, MIDO, PONI	X
SB	VAFB	46	PUNCHBOWL LAKE	9	0	13OCT2002	GAAF, LEMA, LEMI, MIDO, MISA, PONI	X
SB	VAFB	46	PUNCHBOWL LAKE	0	1	19OCT1999	GAAF, LEMA, LEMI, MIDO, MISA, PONI	X
SB	VAFB	SAN ANTONIO CR	LAGOON	27	0	19JUL1995	AMME, ECNE, GAAC, COAS, LEAR, PLST	
SB	VAFB	SAN ANTONIO CR	AT UPRR	6	0	7JUL1995	COAS, CYCA, GAAC, EUNE, GIOR, LECY	
SB	VAFB	SAN ANTONIO CR	AT LOMPOC-CASMALIA RD.	21	0	5JUL2001	AMNE, COAS, ECNE, GAAC, GAAF	X
SB	VAFB	SAN ANTONIO CR	AT LOMPOC-CASMALIA RD.	3	5	31MAY1996	AMNE, COAS, ECNE, GAAC, GAAF	X
SB	VAFB	SAN ANTONIO CR	UPSTREAM LOMPOC-CASMALIA RD	34	0	24APR2002	AMME, COAS, GAAC, GAAF, GIOR, ICNE, LECY, PIPR	X
SB	VAFB	SAN ANTONIO CR	AT SAN ANTONIO RD WEST	3	0	8APR2002	AMNE, GIOR	
SB	VAFB	SAN ANTONIO CR	AT HWY. 1	9	3	23AUG1995	AMNE, GIOR	
SB	VAFB	SANTA YNEZ R	DOWN-STREAM 13TH ST TO LAGOON	22	21	24JUL2001	AMME, COAS, GAAC, GAAF, GIOR, EUNE, LEAR, LECY, MISA, PLST, PIPR	X
SB	VAFB	SANTA YNEZ R	AT 13TH ST	1	0	29OCT2002	AMNE, EUNE, GAAC, GAAF, GIOR, LEAR, LECY, PLST	X
SB	VAFB	SANTA YNEZ R	UPSTREAM 13TH ST TO PENITENTIARY	1	7	29AUG1995	AMNE, EUNE, GAAC, GAAF, GIOR, PLST	X
SB	VAFB	SANTA YNEZ R	UPSTREAM 13TH ST TO PENITENTIARY	0	12	17JUL1995	AMNE, EUNE, GAAC, GAAF, GIOR, PLST	X

Appendix H (Continued)

SITES WITH FISH:

CO ₁	AREA ₂	SITE	LOCALITY	RLF	BF	DATE	FISH SPECIES ⁵	CF ³
SB	GOLTA	LOS CARNEROS LAKE		0	14	9NOV1996	BASS AND SUNFISH SP.	?
SB	LPNF	MONO CR	DEBRIS DAM TO SANTA YNEZ R	19	2	2AUG1996	CAAU, GAAF, GIOR, LECY, ONMY, PIPR	X
SB	LPNF	SANTA YNEZ R	CONFL MONO CR TO GIBRALTAR RES	6	3	27JUN1996	GAAF, GAAC, GIOR, LECY, ONMY, PIPR	X
SB	LPNF	SANTA YNEZ R	CONFL MONO CR TO GIBRALTAR RES	3	20	5 SEP1997	GAAF, GAAC, GIOR, LECY, ONMY, PIPR	X
SB	LPNF	SANTA YNEZ R	ABOVE BLUE CYN	7	0	18JUL1996	GAAC, GIOR, LECY, ONMY, PIPR	X
SLO	AG	ARROYO GRANDE CR	LAGOON	0	1	14JUN1996	GAAC, LEMA, MISA	X
SLO	AG	ARROYO GRANDE CR	TRIBUTARY NEAR OCEAN	0	2	14JUN1996	GAAC, GAAF, DOWN-STREAM OF RESERVIOR THAT IS STOCKED W/ FISH	
SLO	AG	ARROYO GRANDE CR	SLOUGH	0	2	14JUN1996	GAAC, MISA, DOWN-STREAM OF RESERVIOR THAT IS STOCKED W/ FISH	X
SLO	AG	ARROYO GRANDE CR	TOWN PARK	0	1	14JUN1996	DOWN-STREAM OF RESERVIOR THAT IS STOCKED W/ FISH	
SLO	AG	ARROYO GRANDE CR	BIDDLE PARK	0	3	13JUN1996	DOWN-STREAM OF RESERVIOR THAT IS STOCKED W/ FISH	
SLO	AG	ARROYO GRANDE CR	CECCHETTI RD XING	1	0	13JUN1996	DOWN-STREAM OF RESERVIOR THAT IS STOCKED W/ FISH	
SLO	AG	ARROYO GRANDE CR	POND BELOW LOPEZ DAM	1	1	13JUN1996	GAAC, DOWN-STREAM OF RESERVIOR THAT IS STOCKED WITH FISH	X

Appendix H (Continued)

SITES WITH FISH:

CO ₁	AREA ₂	SITE	LOCALITY	RLF	BF	DATE	FISH SPECIES ⁵	CF ³
SLO	PASO ROBL ES	FRANKLIN LAKES	CRESTON RD. BIG POND.	0	81	13OCT1999	GAAF, ICPU, LEMA, MISA	?
SLO	PASO ROBL ES	FRANKLIN LAKES	CRESTON RD. SMALL POND	0	42	13OCT1999	GAAF, ICPU, LEMA, MISA	?
SLO	PASO ROBL ES	PASO ROBLES HOT SPRINGS		0	30	9AUG1999	GAAF, CENTRAR-CHIDS	
SLO	MORRO BAY	CHORRO CR	AT S BAY BLVD	3	0	9JUL1996	GAAC, PTGR, SCULPIN SP.	X
SLO	MORRO BAY	CHORRO CR	AT S BAY BLVD	1	1	9JUL1996	GAAC, PTGR, SCULPIN SP.	X
VEN	FILL-MORE	SESPE CR	AT OLD TELEGRAPH RD	0	2	4AUG1999	GAAF, LEMA, BULLHEAD SP.	
VEN	LPNF	SESPE CR	AT LION CG	0	0	21JAN1995	GAAC, GIOR, LECY, ONMY, PATR, SAFO, BULLHEAD SP.	
VEN	LPNF	SESPE CR	AT BEAVER CG	0	TADS	3SEP1997	GAAC, GIOR, LECY, ONMY, AMEIRUS SP.	
VEN	LPNF	PIRU CR	BLUE PT CG TO AGUA BLANCA	0	MAN Y	3AUG1994	LEMA, MISA, ONMY, PONI, SATR, SCULPIN SP, CATFISH SP., SUNFISH SP.	X

Appendix H (Continued)

¹County

²LPNF = Los Padres National Forest; VAFB = Vandenberg Air Force Base (Maps of sites are given in App. C); GUAD = Unocal's Guadalupe Former Oil Field

³Crayfish: "X" = present, blank = not detected

⁴Tadpoles

⁵Fish Species:

AMME	<i>Ameiurus melas</i>	Black bullhead	Introduced
AMNE	<i>Ameiurus nebulosus</i>	Brown bullhead	Introduced
CAAU	<i>Carassius auratus</i>	Goldfish	Introduced
COAS	<i>Cottus asper</i>	Prickly sculpin	Native
CYCA	<i>Cyprinus carpio</i>	Carp	Introduced
ECNE	<i>Eucyclogobius newberryi</i>	Tidewater goby	Native
GAAC	<i>Gasterosteus aculeatus</i>	Three-spine stickleback	Native
GAAF	<i>Gambusia affinis</i>	Western mosquitofish	Introduced
GIOR	<i>Gila orcutti</i>	Arroyo chub	Translocated at VAFB
ICPU	<i>Ictalurus punctatus</i>	Channel catfish	Introduced
LATR	<i>Lampetra tridentata</i>	Pacific lamprey	Native
LEAR	<i>Leptocottus armatus</i>	Pacific staghorn sculpin	Native
LECY	<i>Lepomis cyanellus</i>	Green sunfish	Introduced
LEMA	<i>Lepomis macrochirus</i>	Bluegill	Introduced
LEMI	<i>Lepomis microlophus</i>	Redear sunfish	Introduced
MIDO	<i>Micropterus dolomieu</i>	Smallmouth bass	Introduced
MISA	<i>Micropterus salmoides</i>	Largemouth bass	Introduced
ONMY	<i>Oncorhynchus mykiss</i>	Rainbow trout	Native
PLST	<i>Platichthys stellatus</i>	Starry flounder	Native
PONI	<i>Pomoxis nigromaculatus</i>	Black crappie	Introduced
PIPR	<i>Pimephales promelas</i>	Fathead minnow	Introduced
PTGR	<i>Ptychocheilus grandis</i>	Sacramento squawfish	Translocated in central coast
SAFO	<i>Salvelinus fontinalis</i>	Brook trout	Introduced
SATR	<i>Salmo trutta</i>	Brown trout	Introduced

Appendix I
Physical Characteristics of Ponds
In Chapter 3, Study 2

Pond	Surface area (m ²)	Perimeter (m)	Maximum depth (m)	Shore & emergent vegetation
37	6,401	407	0.7	Dense bulrushes (<i>Scirpus</i> sp.) around entire perimeter, with some willows (<i>Salix</i> sp.).
38	6,692	443	1.4	Dense bulrushes and some cattails (<i>Typha</i> sp.) around perimeter.
46	178,480	2,714	5.4	Dense bulrushes and some cattails (<i>Typha</i> sp.) around perimeter.
77	10,087	463	1.8	Cattails and some patches of bulrushes and willow around entire perimeter. Mats of marsh pennywort (<i>Hydrocotyle</i> sp.).
79	8,708	459	1.35	Cattails around some of perimeter, with some open shore and a small clump of willows. Extensive mats of marsh pennywort.
91	7,483	382	1.6	Cattails around entire perimeter with some patches of bulrushes and willow. Some mats of marsh pennywort.

Appendix J

Metamorph Data from Chapter 3, Study 2

Date	Pond	Perim (m)	RAAU meta	RAAU ad	RACA juv	RACA ad	UnID	Time (h)	Obs.
3-Sep-97	37	585	1	NR	NR	NR	NR	2:24	SSC
12-Sep-97	37		0	25	0	1	0	2:00	SSC
22-Sep-97	37		0	27	0	2	0	2:15	SSC
8-Sep-97	38	443	0	NR	NR	NR	NR	0:57	SSC
11-Sep-97	38		0	NR	NR	NR	NR	1:28	SSC
21-Sep-97	38		0	2	0	4	0	1:22	SSC
12-Sep-97	46	2714	0	NR	NR	NR	NR	1:06	SSC
22-Sep-97	46		0	0	0	1	0	1:25	SSC
27-Sep-97	46		0	0	0	0	0	1:00	SVC
13-Sep-97	77	463	103	NR	NR	NR	NR	2:40	SSC
19-Sep-97	77		96	NR	NR	NR	NR	2:12	SSC
23-Sep-97	77		112	32	0	0	0	2:26	SSC
15-Aug-97	79	459	255	5	0	0	0	2:35	SVC
31-Aug-97	79		282	NR	NR	NR	NR	3:43	SSC
10-Sep-97	79		257	NR	NR	NR	NR	2:47	SSC
13-Sep-97	91	382	12	NR	NR	NR	NR	1:20	SSC
19-Sep-97	91		15	NR	NR	NR	NR	1:42	SSC
23-Sep-97	91		9	21	0	0	0	1:26	SSC

Notes:

Perim. = Pond perimeter

RAAU = *Rana aurora*, California red-legged frog

RACA = *Rana catesbeiana*, bullfrog

NR = Not recorded

Unid = Number of ranid frogs not identified to species

Time = Amount of time for each survey

Obs. = Observer

SVC = Susan V. Christopher

SSC = Steve S. Collie