MICROHABITAT USE AND REPRODUCTIVE SUCCESS OF THE CALIFORNIA RED-LEGGED FROG (*RANA AURORA DRAYTONII*) AND BULLFROG (*RANA CATESBEIANA*) IN AN EPHEMERAL MARSH

by

David Cook

A thesis submitted to
Sonoma State University in partial fulfillment of the requirements
for the degree of

MASTERS OF ARTS

in

Biology

Dr. Philip T. Northen

Dr. J. Hall Cushman

Dr. Nathan Rank

Dr. Mark R. Jennings

12/05/97

Date

Copyright 1997

By David Cook

AUTHORIZATION FOR REPRODUCTION
OF MASTER'S THESIS/PROJECT

I grant permission for the reproduction of this thesis in its entirety without further authorization from me, on the condition that the person or agency requesting reproduction absorb the cost and provide proper acknowledgment of authorship.

Date: 12/5/98

MICROHABITAT USE AND REPRODUCTIVE SUCCESS OF THE CALIFORNIA RED-LEGGED FROG (*RANA AURORA DRAYTONII*) AND BULLFROG (*RANA CATESBEIANA*) IN AN EPHEMERAL MARSH

Thesis by
David Cook

ABSTRACT

I undertook a study of the habitat use, distribution, and factors influencing the reproductive success of the threatened California red-legged frog (*Rana aurora draytonii*) and introduced bullfrog (*Rana catesbeiana*) at Ledson Marsh, Sonoma County, California. Ledson Marsh is a seasonal marsh encompassing approximately 11 ha at its maximum size and is typically dry by late fall. This human-constructed marsh supports on abundant population of red-legged frogs and has been invaded by non-native bullfrogs. The bullfrog has been implicated as a predator and competitor of native amphibians, including the red-legged frog.

The availability of microhabitats and their locations in the marsh changed markedly with the seasons, and frogs were associated with microhabitats at each season. Both species of frog showed distribution patterns in the marsh that were related to seasonal changes in habitat and their social behavior, and both were most active during their respective breeding periods. Important microhabitat features for all seasons included vegetative cover at the water's surface and water depth. Dead spikerush in shallow water (mean=39 cm) was the primary microhabitat used by frogs early in the season but it only covered 13.7% of the marsh in the winter of 1996. In spring through fall, frogs were most associated with smartweed, a dominant microhabitat type in the marsh. Frogs typically avoided open water and occasionally used bulrush, but both microhabitat types became more important late in the season.

Water depths used by both species of frog did not differ significantly throughout the year, except during spring, but the marsh water levels changed substantially. The marsh water depths were highest in the winter and rapidly receded in summer. Maximum water depth of the marsh was approximately 150 cm. Both species were distributed in vegetative cover usually with depths between 30-40 cm, but spring was the exception when bullfrogs used deeper water for breeding. In summer, smartweed was a dominant microhabitat type used by frogs, and it occurs in the deepest remaining water.

The breeding schedule, egg mass locations, and microhabitat used at oviposition sites differed substantially between species of frog. Resource partitioning of microhabitat types between the red-legged frog and bullfrog was evident during their breeding periods, although substantial habitat overlap occurred during all seasons. Habitat types used by one species where generally unavailable during the breeding period of the other species. The breeding periods of the two species were separated by approximately two months. Red-legged frog egg masses were significantly associated with dead spikerush in shallow water (mean=32.8 cm), while bullfrog egg masses were significantly associated with smartweed in deeper water (mean=63.1 cm). There was no significant evidence that temperature differences were responsible for the selection of shallow water for ovipostion sites by the red-legged frog. Dead spikerush and cattail were common attachment sites for red-legged frog egg masses, while bulrush was never used.

The relative successes of the red-legged frog and bullfrog are largely related to their strategies for reproduction and how well these match the ephemeral nature of Ledson Marsh. The seasonality of the marsh limits the possible duration of breeding and requires a high rate of embryonic development and tadpole metamorphosis prior to the marsh drying. Only post-metamorphic frogs can survive the fall dry period. Red-legged frog tadpoles metamorphosed by mid-summer, several months before the marsh dried in mid-October. Most bullfrog tadpoles were unable to metamorphose prior to the dry-down. The survival rate of red-legged frog eggs to metamorphosis was estimated at 1.9%, while the bullfrog rate was 0.0001%.

The dry-down of the marsh by a third of its area in the summer and the observed concentration of both species suggests that the rate of predation by bullfrogs on red-legged frogs is highest during summer from the increased chance of interspecific encounters. The remains of three red-legged frog tadpoles were found in the stomachs of eight bullfrogs examined in the spring and summer.

The ephemeral nature of Ledson Marsh favors the reproductive success of red-legged frogs, while hindering tadpole survival of bullfrogs. Designing and maintaining ephemeral habitats is an important consideration in managing populations of red-legged frogs. However, other factors should be examined, such as local climatic conditions, proximity to bullfrog source populations and frog dispersal rates, and the susceptibility of habitats to invasion by other non-native predators.

Chair:

M.A. Program: Biology Sonoma State University

Date: 12/05/97

TABLE OF CONTENTS

APPENDIX A: LIST OF TABLES

APPENDIX B: LIST OF FIGURES

MICROHABITAT USE AND REPRODUCTIVE SUCCESS OF THE CALIFORNIA RED-LEGGED FROG (*RANA AURORA DRAYTONII*) AND BULLFROG (*RANA CATESBEIANA*) IN AN EPHEMERAL MARSH

I. INTRODUCTION

A main goal in conservation biology is to enhance populations of rare or declining species and to minimize or eliminate exotic species that have a detrimental effect on those species targeted for conservation (Meffe & Carroll 1994). What is often needed for conservation planning is good ecological information on both the rare and exotic species. Specific habitat requirements, overlap in ecological niches, and competitive and predatory relationships between target and invasive species are important considerations (Meffe & Carroll 1994). In addition, a practical approach to conservation of a species may include identifying conditions that influence or allow for the survival or stable coexistence of rare and exotic species. Unfortunately, this information is often not available. Amphibians are one such group of concern because of their importance as indicators of the health of environmental systems (Heyer et al. 1994).

The decline of amphibian populations is a recent global phenomenon (Blaustein & Wake 1995). Many frogs and toads of western North America (Class Amphibia, Order Anura) have experienced reductions in their ranges and declines in population size in the past decade. All native frogs of California (Family Ranidae) have shown dramatic population declines during the past 25 years (Hayes & Jennings 1986; Hayes & Kremples 1986; Jennings & Hayes 1994; Drost & Fellers 1996; Fisher & Shaffer 1996). One of these native frogs, the California red-legged frog (*Rana aurora draytonii*), has undergone such an extensive decline in distribution in the state that it was recently listed as threatened by the U. S. Fish and Wildlife Service (Miller et al. 1996). Because of the many current threats and continued decline of the species in California, resources agencies are particularly interested in ecological information about the California red-legged frog. Such information will hopefully result in better knowledge about this frog and lead to the eventual recovery of the species.

In 1990, the California red-legged frog was discovered in Ledson Marsh, an artificial, ephemeral marsh of 11 ha located in Annadel State Park, Sonoma County, California, and initial studies showed that a substantial breeding population of frogs existed (Northen 1993). Since little is known about the ecology of this subspecies, I undertook an 18 month study of its ecology. One important factor in Ledson marsh and for many declining frogs in the western United States is the negative effect of non-native bullfrogs (*Rana catesbeiana*) on native frog populations (e.g., see Moyle 1973; Bury & Whelan 1984, Nussbaum et al. 1983). The marsh with co-occurring populations of red-legged frogs and bullfrogs, therefore, provided a good opportunity for analysis of interactions of these taxa.

Factors influencing the decline of ranids in the west are numerous, likely have synergistic effects, and are not well documented (Hayes & Jennings 1986). The primary factors suspected of having major impacts on amphibian populations are habitat alteration and predation by exotic species (Hayes & Jennings 1986). These two factors often result in changes in resource partitioning among species (Hayes & Jennings 1986; Blaustein et al. 1996). Other hypotheses for decline include commercial overharvest, air and water pollution, solar radiation, pathogens and parasites, and mortality due to catastrophe.

Resource partitioning, or how species differ in their use of resources, can be subdivided into three basic categories: habitat, food, and time. These dimensions were refined by Schoener (1974) to include macrohabitat, microhabitat, food type, food size, and seasonal and daily activity periods. In general, habitat type for amphibians (and most animals in general) is the first resource to be partitioned, while daily time is the least important dimension (Toft 1985). One exception to the primacy of habitat type in resource partitioning is the seasonal partitioning of the growth periods of tadpoles (Toft 1985). This importance of seasonality for tadpoles is primarily due to their need to exploit an ephemeral food source and habitat, and to avoid periods of high predator densities. This study focuses on seasonal habitat requirements and unique environmental conditions that influence the coexistence of the native California red-legged frog and the introduced bullfrog.

Bullfrogs have been implicated as a predator and competitor of native ranids (Bury & Whelan 1984; Hayes & Jennings 1986; Hayes & Jennings 1988; Jennings & Hayes 1985; Licht 1974; Moyle 1973; Nussbaum et al. 1983). Hayes & Jennings (1988) found a positive correlation between extant California red-legged frog populations and three habitat variables, including aquatic habitat that is ephemeral, drainages having small area, and lack of introduced bullfrogs. Bullfrogs are known to take large prey of various forms, including other species of *Rana* (McAlpine & Dilworth 1989). Moyle (1973) examined suitable habitats for the California red-legged frog in the San Joaquin Valley but found only bullfrogs and suggested that competition and predation were responsible for elimination of the native species. Twedt (1993) found a significant difference in habitat use between *R. a. aurora* (northern red-legged frog) and bullfrog and showed that bullfrogs prey upon juvenile red-legged frogs. Hayes and Jennings (1986) discussed the hypothesis that bullfrogs are the cause of decline of the red-legged frog population. They suggested that habitat alteration favors the establishment of bullfrogs through resource partitioning (e.g., change in hydrology from an ephemeral to permanent water source, removal of emergent vegetative cover, higher water temperatures from increased solar exposure, etc.), and that interspecific competition and predation, although poorly documented, are of secondary importance in the survival of native frogs.

Bullfrogs are known to suppress resource use and restrict population size of *Rana* species. McAlpine (1989) studied distinct microhabitat features of three sympatric species of *Rana* and their predatory relationships. He suggested that interspecific predation contributed to patterns of resource use between the bullfrog and green frog (*Rana* *clamitans*) and suppressed the green frog population. Avoidance of bullfrogs may have restricted the use of habitat by the green frog. The California red-legged frog and green frog have similar behaviors and use of habitats but differ in their ranges. Hecnar & M'Closkey (1997) found a significant increase in the relative abundance of green frogs following the local extinction of bullfrogs. The red-legged frog may not have the adaptive capabilities (e.g., competitive and anti-predator behaviors) that the green frog has developed to survive with its natural neighbor, the bullfrog. *Rana aurora* may be naive to exotic species and lack antipredator behavior necessary for survival with bullfrogs (Kiesecker & Blaustein 1997). The long-term coexistence (= decades) of red-legged frogs and bullfrogs is contrary to many studies (see above), although there are other possible factors contributing to their decline. For this reason, the Ledson Marsh, which contains populations of both species, is an important system to study to better understand conditions that allow for their coexistence. Specifically, I address the following questions: 1) Is microhabitat use by red-legged frogs and bullfrogs simply correlated with abundance of different habitat types or do the frog species exhibit habitat preferences?; 2) Do both species of frog exhibit spatial and temporal differences in the patterns of microhabitat use?; and 3) What biotic and abiotic factors influence survival and reproductive success of both species?

II. NATURAL HISTORY AND SITE DESCRIPTION

Natural History

Rana aurora is the largest native frog in California, while the larger bullfrog was introduced in 1896 as a human food source (Jennings & Hayes 1985), and is now widespread and common throughout most of the state below elevations of 1,800 m. The bullfrog naturally occurs east of the Rocky Mountain crest. *Rana aurora* historically occurred from southwest British Columbia to northwestern Baja California, west of the Cascade and Sierra Nevada crests (Stebbins 1985). In California, the northern red-legged frog occurs in coastal drainages from Marin County to the Oregon border (Jennings & Hayes 1994), while the southern subspecies, the California red-legged frog, occurred historically from the vicinity of Redding throughout the Central Valley and Sierra Nevada foothills and along the Coast Ranges from Sonoma County to the Mexican border.

The California red-legged frog and bullfrog are both pond inhabitants. Also, the red-legged frog occurs in slack water segments of streams with adequate cover. The California red-legged frog requires cooler water temperatures to reproduce and is more tolerant of ephemeral water sources than the bullfrog, largely because the larval state of the bullfrog requires more than one year to reach metamorphosis (Bury & Whelan 1984). The California red-legged frog requires only 4-5 months to reach metamorphosis (Storer 1925). California red-legged frog breeding occurs from winter to early spring, while the bullfrog breeds locally from spring to summer.

There are substantial differences between the red-legged frog subspecies, and findings in the northern form may not apply to conservation of the southern form. The two subspecies differ substantially in morphology and behavior, which, combined with geography, have been the basis of subspecific designation. There is mounting evidence that they represent distinct species. Green (1985) and Hayes and Miyamoto (1984) indicated that a substantial genetic difference exists between the two subspecies, and both papers suggest that a transition zone occurs approximately from Sonoma to Del Norte counties. Hayes and Tennet (1985) and Hayes and Kremples (1986) further studied size, vocal sac variation, and behavioral differences and found vocal sac variation within the transition zone suggesting secondary contact and hybridization between the northern and southern forms. The northern red-legged frog typically is smaller in size, has no vocal sacs, has males that predominantly vocalize underwater, is terrestrial during non-breeding periods, and deposits eggs below the water surface. In contrast, the California red-legged frog is generally 30-40 mm larger than its northern relative, has paired vocal sacs, has males that vocalize in the air, is largely aquatic, and typically lays its eggs at the water surface (Hayes & Miyamoto 1984; Jennings & Hayes 1994; Licht 1969a; Licht 1969b; Nussbaum et al. 1983; Storm 1960). Red-legged frogs at the study site exhibit all the characteristics of *R. a. draytonii* described above, including visible paired vocal sac skin folds observed on several captured males. A few egg masses were found in 1996 and 1997 below the water's surface, but these were probably deposited at the surface and then later covered due to rising water levels of the marsh following rain.

Study Site

I conducted my study at Ledson Marsh located in Annadel State Park, Sonoma County. Ledson Marsh is a seasonal marsh encompassing approximately 11 ha at its maximum size and is situated at an elevation of 476 m (Figure 1). Typically, the marsh is dry by late fall, and it hydrates during the rainy season, usually beginning in late November or early December. Maximum water depth of the marsh is approximately 150 cm. During the study, the marsh was dry by November 30, 1995 and October 19, 1996. The primary outlet is over an earthen dam constructed in 1930, and during high water periods some flow exits through a small channel at the opposite end of the marsh. In winter, the marsh is dominated by open water and large stands of bulrush (*Scirpus californicus*) and cattail (*Typha latifolia*). The appearance and growing period for most common plants is during the spring and summer; these included spikerush (*Eleocharis macrostachya*), smartweed (*Polygonum hydropiperoides*), aquatic buttercup (*Ranunculus lobbii.*), and water plantain (*Alisma plantago-aquatica*). See Table 1 for a description of the characteristics of these dominant plants of Ledson Marsh.

III. METHODS

The seasonal changes in habitat types and frog behavior at the study site required a sampling scheme that would reflect these conditions. I conducted day and night sampling at Ledson Marsh on a weekly to monthly basis from January 1996 to March 1997. Preliminary field studies were done from May to December 1995. Because the marsh is intermittent, surveys ended when the marsh was entirely dry (late fall) and resumed with the first heavy winter rains. Both *R. a. draytonii* and *R. catesbeiana* are highly aquatic, so I restricted my surveys to areas of the marsh with standing water. Also, it is impractical to walk through the large, dense stands of bulrush and cattail that occur in the marsh so I used only the edges of these stands. All red-legged frog field studies were conducted under the authorization of California Department of Fish and Game Scientific Collectors Permit (801063-09) and U.S. Fish and Wildlife Service Incidental Take Permit (PRT-816187).

Seasonal Habitat Use and Distribution of Frogs

Using methods detailed below, I collected data on microhabitat at the location of egg masses, sites where frogs were captured or observed, and at a randomly selected set of sampling points. In all instances, the study feature (e.g., frog, egg mass) was used as the center of a plot of one m radius. Variables included percent cover of vegetation or habitat feature (e.g., open water, stump), temperature, and water depth. Typically, the entire marsh would be systematically surveyed in one or two consecutive sampling periods by one or two investigators. One systematic coverage of the marsh constituted a "survey."

I recorded air and surface water temperatures using a Digi-Sense® thermometer or glass thermometer. Temperature data were taken during day and evening field visits, and for statistical comparison of species' habitat only temperatures taken during the same time of day were comparable. For example, temperature data on both species of frog were sampled during evening surveys and represent relative temperature preferences between species, however, sampling at permanent points was conducted during daytime visits and temperatures are not comparable to frog temperature data. In addition, I used two HOBO® temperature data loggers to record daily temperatures at frog breeding sites. During the spring and summer of 1996, data loggers were placed near two bullfrog breeding sites. During the winter of 1997 one data logger was placed at a red-legged frog oviposition site and the other near a bullfrog oviposition site from the previous year, which typified deep, open water habitat in the central portion of the marsh. I suspended the devices 15 cm below the water surface and situated them in sites with solar exposure.

Night surveying focused on capturing frogs and sampling their microhabitat use. Night sampling was done by slowly walking through shallow portions of the marsh or by poling a three-person inflatable boat. Sampling began when headlamps (Justrite No. 1904) were effective in seeing frog eye shine. Assistants and I attempted to capture all observed ranids. Captured frogs were identified to species, and adults were sexed, as indicated by the presence of nuptial thumb pads on males. I measured each captured frog for snout to vent length (SVL) using a hand ruler and weighed it using a hand-held Pesola® 1000 g or 300 g scale. Frogs were then released at the point of capture.

During the observed breeding periods of each species, surveys were conducted approximately once or twice a week for red-legged frogs and twice a month for bullfrogs. In shallow areas, I slowly walked transects spaced five to ten meters apart depending on water visibility. In deeper water, surveys were conducted on foot or by boat.

I established 34 permanent plots in the marsh using a stratified random sampling method. The marsh was sectioned into 50-m wide segments running perpendicular from the marsh edge toward its center. Using the random function of a hand held calculator, I established a single transect per segment. At 40-m intervals along each transect and ending at the approximate center of the marsh, plots were marked with stakes. The first plot of each segment was placed a random distance between 0 and 20 m from the shoreline. I collected microhabitat data, including bottom temperature, from each plot on a monthly basis from February 1996 to March 1997. Specific microhabitat data were collected at all sample plots containing standing water. Plots with no water, regardless of actual vegetative cover, were recorded as "dry" microhabitat.

Analysis consisted of statistical evaluation of sampled microhabitat data, and mapping of the marsh habitats and sample site locations. Since the habitat features change with seasonal growth of plants and availability of water, I compared microhabitat use of red-legged frogs and bullfrogs by the following seasons: 1) Winter of 1996, red-legged frog breeding period and marsh fully hydrated (February 11 to March 25, 1996); 2) Spring of 1996, bullfrog breeding period and marsh nearly hydrated (March 26 to June 9, 1996); 3) Summer of 1996, bullfrog breeding period and marsh levels begin to drop (June 10 to August 14, 1996); 4) Fall - limited frog activity and marsh nearly or completely dry (August 14 to December 5, 1996); and Winter of 1997, red-legged frog breeding period and marsh fully hydrated (January 19 to March 9, 1997).

Between fall of 1996 and winter of 1997, as defined above, the marsh was either dry or contained very low water levels from early rains. Typically, amphibians are inactive during cold, winter periods. None or very few frogs were active during this time period, and therefore it was not included in the analysis.

All microhabitat samples for a given variable in a given season (e.g., water depth of red-legged frogs in the winter of 1996) were averaged to produce mean values. Mean percent cover calculations from permanent sample point data were used to estimate the proportion of microhabitat types present in the marsh. The mean percent cover of microhabitats used by both species of frog were compared with marsh values to determine the association of microhabitats. I used analysis of variance, using DataDesk 4.0®, to evaluate associations among microhabitat values of the marsh and species of frog. Mean values are important statistical comparisons of microhabitat use, however many variables are correlates of one another. For example, water temperature and vegetation type are directly related to water depth. I used a principal components analysis (SAS, release 6.10) to better understand the importance of microhabitat variables and to further evaluate microhabitat types used by both species of frog.

I mapped field sample sites and habitats using aerial photographs and a global positioning system (GPS). Each observed frog location and egg mass location was marked by a Trimble Navigation GeoExplorer GPS or on an aerial photograph and later digitized in a geographic information system (GIS). Marsh perimeter and habitat features were delineated four times during 1996. I corrected GPS files for selective availability error using base station files from Sonoma State University. Using ArcView 3.0 and ARC/INFO 7.1 programs, I prepared figures indicating seasonal habitat types and ranid observation sites.

Since vegetation and water levels in the marsh changed continuously, I prepared vegetation maps that best characterized the marsh during the four specified seasons. The smallest mapping unit for delineating marsh habitat was approximately 9 m^2. Consequently, the actual habitat located at frog and egg mass sites, and mapped vegetation types may differ when compared together.

Factors Influencing the Survival of Frogs

Evaluating factors that may influence the survival of each species of frog required estimating the numbers of frogs at several life stages, identifying potential predators and their effects, and identifying environmental conditions that effect reproductive success.

I determined the numbers of both species of frog at the egg, juvenile frog (newly metamorphosed tadpole), and adult frog life stages. Egg masses and adult frogs were found during surveys discussed above. I measured the height and two perpendicular width dimensions of each egg mass, which was used to calculate the volume of each mass. I estimated the egg population size of red-legged frogs for the 1996 and 1997 breeding season by counting the total number of eggs within a sampling of masses. The number of eggs per mass for the remaining masses was then interpolated using the calculated volume of each mass. To count eggs, I photographed egg masses, *in situ.* A white tray was placed below the mass to illuminate individual eggs. Then a slide photograph of the mass was taken and the projected image was used to count embryos. This counting method worked especially well with older masses that were near hatching because: 1) masses tended to flatten into a cylindrical shape with eggs only a few layers thick, and 2) embryos are elongated and are easily distinguished from other overlapping embryos. This method allowed counting of eggs at leisure and minimized disturbance to masses.

Bullfrog egg masses were amorphic and a population estimate based on mass volume could not be done. A subjective but moderate number of 10,000 eggs per mass was used to estimate the annual total egg count. The number of eggs per mass can vary from about 1,000 to 25,000 (Bury & Whelan 1984).

Each subadult and adult frog was uniquely marked for future identification by a toe-clipping system devised by Hero (1989). Population estimates using a mark and recapture method was attempted using Petersen Estimate and the Bailey's Modification, when required (Donnell & Guyer 1994). The low recapture rate throughout the duration of the study suggested that the typical capture of about 12 frogs per survey was inadequate of a sample size to estimate the true number of red-legged frogs at the marsh. Bullfrogs proved difficult to capture, resulting in a low mark and recapture number. Consequently, population estimates using surveys during an entire season were grouped and used as a high end range value. For each species, I used their respective breeding period and following season as comparative groups in the Peterson Estimate formula. The actual number of frogs uniquely marked in 1996 was used as the low end range value.

Ranid tadpoles were sampled by placing plastic or nylon (5 mm) mesh minnow traps near permanent plot sites in the late spring and summer of 1996. I placed traps along the marsh bottom for periods between 2 and 8 hours in water that was at least 15 cm deep. Caught tadpoles were identified to species, and their developmental stage was determined using Gosner (1960). I immediately released tadpoles at the point of capture. Only large ranid tadpoles were caught due to the mesh size of the traps. Trapping data for tadpoles was used to characterize seasonal timing of development and transformation to terrestrial life stage. This information was then used to indicate optimal survey periods for juvenile frogs.

I conducted juvenile red-legged frog surveys to determine their numbers. Surveys were done on August 22 and September 8, 1996. At this time, red-legged frog tadpoles were no longer caught in traps. I conducted surveys by slowly walking 10 m transects through the marsh on sunny, late afternoons when juvenile frogs are most active and visible. Surveys did not include capturing juvenile frogs, which would have been a monumental task given the large number of sightings. If juvenile frogs were able to flee before a positive identification could be made, they were recorded as red-legged frogs. Although, these frogs could have been juvenile bullfrogs or adult Pacific treefrogs (*Hyla regilla*), in all likelihood they were juvenile red-legged frogs because 1) out of over 500 confirmed juvenile red-legged frog sightings only one adult treefrog was observed, and 2) bullfrogs had only been observed as tadpoles (I first observed juvenile bullfrogs more than a month later, on October 12, 1996).

Because of the legal protection provided to the California red-legged frog, the analysis of stomach contents was restricted to bullfrogs. To identify food sources, I flushed the stomach of each captured adult bullfrog and examined its contents. I used a large syringe (turkey baster) for flushing. Each bullfrog was flushed at least three times to dislodge all material in the stomach. Stomach contents were identified in the field. Contents potentially containing red-legged frog remains were preserved in 70 percent ethanol for later identification. Bullfrogs were then released at the point of capture.

IV. RESULTS

Seasonal Habitat Use and Distribution of Frogs

Winter - Red-legged Frog Breeding Period

In late winter, Ledson Marsh is fully hydrated, temperatures begin to rise, red-legged frogs appear in large numbers, and bullfrogs are occasionally seen. This is the normal breeding period for the red-legged frog. While I occasionally heard vocalizing bullfrogs, no choruses or egg masses were found until spring. The growing season for most plants had not begun, and deep water areas were primarily unvegetated (open water). Mid-level depths were dominated by large stands of bulrush and, in shallow water, dead spikerush and cattail stands (Table 2). Other microhabitat types present, but in small coverage, included living spikerush, smartweed, and algae. Figures 4 and 5 show the winter distribution of microhabitats and frogs in the marsh. Both red-legged frogs and bullfrogs were distributed along the margins of the marsh, although few bullfrogs were active. The association of red-legged frogs and bullfrogs with microhabitat types is discussed below.

I observed similar microhabitat use by both species of frog during the red-legged frog breeding season of the winters of 1996 and 1997. In general, frogs were negatively associated with deep, open water and positively associated with dead spikerush in shallow water (Table 3). Open water occurs in large central portions of the marsh, while dead spikerush is restricted to its margins. Similar trends occurred in both winters, and for simplicity, data are discussed below only for winter of 1996. Also, the number of bullfrog samples (n=4) in the winter of 1997 was too small to evaluate trends. Open water was the dominant habitat of the marsh (65.9% mean cover at 66.6 cm depth) but red-legged frogs and bullfrogs had significantly lower coverage use for this microhabitat type (Table 4). I observed red-legged frogs and bullfrogs most frequently in the shallow waters of the marsh with a dense surface cover of dead spikerush. Dead spikerush covers a small portion of the marsh (13.7% mean cover) but the mean cover in plots containing red-legged frogs and bullfrogs was nearly five times the mean of the marsh. The mean depth at frog sites was similar to the dead spikerush mean depth of 39.1 cm. The mean water depth in the marsh was 63.0 cm with a maximum on about 150 cm. Both frog species were associated with shallower waters of the marsh (RLF mean=39.5 cm and BF mean=37.7 cm) and depths did not differ significantly between species.

Surface water temperatures for both species of frog were similar. Also, temperatures at the marsh have substantial daily, seasonal, and site-specific fluctuations (e.g., at different water depths and degrees of shading from emergent and submergent vegetation). Evening surface water temperatures taken at red-legged frog sample sites had a mean temperature of 14.4 °C and bullfrogs had a mean temperature of 14.1 °C in 1996. These did not differ significantly between species (Table 4).

Red-legged frogs and bullfrogs differed significantly in their use of bulrush and cattail microhabitats. Bulrush and cattail are structurally similar and are unique in that they are substantially taller (> 1 m) than other emergent plant species in the marsh, but the two plant species differ in hydrologic distribution in the marsh (Figure 4). Bulrush cover varied little in the marsh throughout the 1996 year and in winter was the deepest emergent plant in the marsh (mean depth=76.5 cm, see Table 2). Cattail occurred in water nearly half the depth of bulrush and was restricted to the margins of the marsh, while bulrush occurred predominantly in the center. Cattail cover gradually decreased to zero by late summer due to receding marsh water levels. In other words, marsh sample points containing cattail had no standing water and were recorded as "dry" cover late in the season. Bullfrogs were positively associated with bulrush and cattail in the winter of 1996 but this was not statistically significant (Table 4). Red-legged frogs rarely occurred in bulrush and cattail habitats during this season (Tables 3 and 4). However, cattail is an important microhabitat type for red-legged frog oviposition and is further discussed below.

The principal component analysis supports the association of red-legged frogs and bullfrogs with specific microhabitats, particularly open water, dead spikerush, and water depth, but also identified water temperature and cattail as important characteristics (Figure 3). These variables had heavy loadings on the first two principal components and cumulatively explained 70.0% of the standard variance (Table 5). The first component accounts for 46.2% of the variation and describes the inverse relationship between dead spikerush cover and open water habitat with water depth, where dead spikerush is correlated with shallow water and open water is related to deeper waters. The second component represents the positive correlation between water temperatures and cattail. This relationship is counterintuitive because tall emergent vegetation, such as cattail, would be expected to shade and cool water temperatures. Both species of frog are associated with dead spikerush in shallow water and sparse cattail with cool water (Figure 3A) and have similar sample point distributions (Figure 3B). Also, most outlier values were bullfrog sample points and this probably relates to behavioral differences between breeding red-legged frogs in dead spikerush and bullfrogs beginning to emerge from hibernation. The principal component analysis for winter of 1997 were similar to 1996, however, PC2 had heavy loadings on algae, dead spikerush, and bulrush. Algal plumes occurred in dead spikerush beds where decomposing material was high.

Red-legged frog breeding activity was first observed on February 11, 1996 and January 19, 1997, and frog choruses were in similar locations each year (Figures 4 and 5). Most red-legged frog egg masses were found near two of the four choruses. In 1996, 19 of the 20 masses where deposited in or near the two choruses, and in 1997, 60 of the 62 masses were deposited in the same areas. The exceptions were one mass in 1996 and two masses in 1997 which were located on the eastern side of the marsh. Frogs observed in the marsh were primarily medium to large sized frogs. Red-legged frogs are sexually dimorphic and these two size categories probably consisted of sexually mature frogs. Reproductive success of male red-legged frogs varied from one chorus to another. One possibility is that smaller males were excluded from the best areas by social interaction with larger males. Male red-legged frogs in the west side choruses were slightly larger and weighed more (West side: mean_{SVL}=101.6 mm, SD=31.5, mean_{wt}=108.7 mm, SD=7.9; East side: mean_{SVL}=97.6 mm, SD=8.1, mean_{wt}=101.7 mm, SD=29.0), but there was no significant difference between the successful west side and predominantly unsuccessful east side breeding choruses (ANOVA SVL: $\text{F-ratio}_{(df=1,\ 12)} = 0.87$, $p = 0.3784$; weight: $\text{F-ratio}_{(df=1,\ 12)} = 0.19$, $p = 0.6726$).

As Table 3 shows, egg masses were found almost exclusively in shallow water associated with dead spikerush. In 1996, I found all red-legged frog egg masses (n=20) associated with dead spikerush. The mean cover of dead spikerush in the marsh was 13.7% at a mean water depth of 34.5 cm, but red-legged frog egg masses had a mean dead spikerush cover of 86.8% at a mean water depth of 32.8 cm. Attachment type in 1996 for red-legged frog egg masses was 95% "dead spikerush" or "unattached" but surrounded by dead spikerush vegetation. One mass (5%) was attached to a cattail stalk.

In 1997, dead spikerush remained the dominant oviposition and egg attachment site for red-legged frogs, but other attachment sites were used. Forty-one of 62 masses (66.1%) were attached to or surrounded by dead spikerush. Other egg attachment sites included cattail (19.4%) , old inflorescences of water plantain (11.3%), and living spikerush (3.2%). Cattail may not represent a large portion of microhabitat used by breeding frogs but it is important as an egg attachment site. In both 1996 and 1997 red-legged frogs were negatively associated with cattail (Table 3) and the variation was significant in 1996 (Table 4). However, the principal component analysis for the winter of 1996 identified cattail as an important habitat component for the red-legged frog. (See PC2, Figure 3A). This phenomenon is probably due to frogs depositing eggs in open (as opposed to dense) stands of cattail, which resulted in cattail having a small cover value within the sampling plot. In 1996, cattail had a mean cover of 7.1% of the marsh, and for red-legged frog egg sites it had a mean cover of 1.1%. Differences between years of mean water depths at egg mass sites, as well as percent cover of dead spikerush and open water, is likely a result from water level fluctuations due to sporadic heavy rains in 1997.

Water temperatures appear to have little influence on selection of sites for oviposition by the red-legged frog. Surface water temperatures at a red-legged frog egg mass site were slightly higher than temperatures in deep, open water, common in the central portion of the marsh, but there was no significant difference (ANOVA F-test$_{(df=1, 960)}$ = 1.2, p = 0.27). Temperature recordings included values from January 19 to February 12, 1996, when embryos were observed. The station located in open water had a mean temperature of 9.9° C and a range from 7.2. to 14.0° C. The station in dead spikerush near a red-legged frog egg mass had a mean temperature of 10.0° C and a range from 7.5 to 13.7° C. Water temperatures at the two stations during the period that eggs were hatching (February 1 through 21) differed significantly at a slightly higher p value (ANOVA F-test = 3.54, p = 0.0605). The mean temperatures at the two stations were 10.0° C (range 7.5 to 13.7°C) in dead spikerush and 10.2°C (range 8.0 to 13.7° C) in open water. Newly hatched tadpoles often stay near the mass for a day or more. Higher temperatures during this time period may be an advantage to the developmental rates of tadpoles.

Bullfrog Breeding Period

Because of the long bullfrog breeding period and changing habitat conditions at Ledson Marsh, the bullfrog breeding period was separated into spring and summer seasons. Microhabitats available in the marsh and those used by frogs are summarized in Table 6. Both red-legged frogs and bullfrogs remained highly active during the spring, and bullfrogs began breeding in late April and continued through July. Most marsh plant species began to grow during the spring, and water levels began to slowly recede. Open water cover in the marsh had decreased since winter, due primarily to lower water levels and the emergence of smartweed. Living spikerush replaced most of the dead spikerush and much of the marsh edge was dry. The mean cover of bulrush in the marsh remained close to the winter coverage during spring and summer. By summer, the rainy season is over and the water level of the marsh had begun to drop dramatically. Smartweed emerged in most open water areas and most of the once shallow areas were dry.

Frog distribution patterns during the spring and summer were characterized by both species being distributed closer to the center of the marsh (Figures 7 and 8). In spring, both species continued to use vegetated margins of the marsh as observed in winter. Although, the marsh edge had advanced toward its center and the vegetation composition was changed from dead spikerush to predominantly spikerush and smartweed. Few red-legged frogs were found in the areas where winter breeding occurred. In summer, both species congregated in remaining wet and relatively deep portions of the marsh. The deepest parts of the marsh were on the western side, in smartweed, adjacent to bulrush and at a channel that bisects the marsh (see Figure 10 for the location of this channel).

The pattern of microhabitat use of open water and dead spikerush was similar to the previous winter, but habitat types in the marsh had changed. During spring, smartweed was the dominant microhabitat type in the marsh followed by open water and spikerush. While dead spikerush remained an important microhabitat for frogs, its living component was negatively associated with both species (Table 6). Smartweed covered more than a third of the marsh at a water depth above the marsh average and there was no significant trend in the use of smartweed by either species of frog (Tables 6 and 7). The cover of open water in spring was less than half of that in winter and both species maintained a strong negative association with this microhabitat.

Water depth was an important aspect of habitat used by frogs. The mean water depth of the marsh during the spring was 54.4 cm with a maximum of about 136 cm.

Mean water depths for the red-legged frog were significantly less (mean=36.8 cm), while the bullfrog used deeper water (mean=54.6 cm) that was close to the marsh mean. Water depths at red-legged frog sample sites were most similar to emergent plants that occurred in relatively shallow water along the margins of the marsh (cattail, living and dead spikerush), while bullfrog depths were most similar to mid-level plants (smartweed, see Figure 7). Interestingly, the mean water depth for spikerush (37.8 cm) and red-legged frog were similar but had a negative association, although the frog was closely associated with dead spikerush. Water depth differed significantly between the two species of frog (Table 7). The variation in water depths used by both species is probably related to their different breeding schedules and use of deeper water for oviposition sites by bullfrogs, and is further discussed below.

In spring, the principal components analysis indicated a separation in habitat used by red-legged frogs and bullfrogs that is probably related to the breeding behavior of bullfrogs (Figure 9). The first component accounts for 32.5% of the variation and describes the inverse relationship of dead spikerush cover with smartweed cover and water depth (Table 8). The second component is the inverse relationship between open water cover with water temperature and aquatic buttercup cover. Figure 9B shows a similar distribution of sample points for both species, indicating that red-legged frogs and bullfrogs had a similar range of habitat use. However, red-legged frogs were more associated with shallow dead spikerush, while bullfrogs occurred in deeper water with smartweed (see PC1, Figure 9A).

The first bullfrog egg masses were found in late April, and breeding continued through the end of July and was associated with smartweed in deep water (Table 6). Thirteen bullfrog egg masses were found during the spring and an additional seven masses in the summer. In spring, bullfrog egg masses, as well as chorusing male bullfrogs, were aggregated near the dam and in the middle of the western side of the marsh in deep water vegetated with smartweed (Figure 7). Bullfrog activity was reduced in summer, and bullfrog vocalizations consisted of choruses of a few frogs or of individuals located throughout the marsh (Figure 8). The few bullfrog egg masses deposited in the summer of 1996 were in more central portions of the marsh in habitat similar to that of spring. Egg masses were most often located in smartweed adjacent to the deepest open water habitat in the marsh.

Water depth and smartweed were important factors in selection of oviposition sites by bullfrogs in spring and summer (Table 6). Water depth at mass sites varied little between the two seasons, although water depths in the marsh dropped substantially from spring to summer. The mean depth of bullfrog egg masses was 63.1 cm in the spring and 60.0 in the summer, while the marsh average was 55.0 cm in the spring and 23.7 cm in the summer. Smartweed had a mean cover of 80.4% at bullfrog egg mass sites in the spring and 52.1% in summer. In comparison, smartweed in the marsh had a mean cover of 36.1% in spring and 31.0% cover in summer and was a dominant vegetation type in the marsh (Table 6). The consistent use of similar water depths at mass sites, regardless of substantial water level decreases in the marsh, suggests that water depth is a primary factor in the selection of oviposition sites by bullfrogs.

In summer, red-legged frogs and bullfrogs continued to use similar microhabitats but there was a change in habitat used from the previous spring season (Table 6). This shift in microhabitat use is likely due to the substantial drop in the marsh's water level and the congregation of frogs in remaining areas with standing water. Approximately a third of the marsh was dry and the mean depth was 23.8 cm with a maximum of 87.0 cm. Summer marked the first time that both species were positively associated with water depths significantly deeper than the marsh's mean (Table 7). Red-legged frogs were associated with a mean water depth of 41.3 cm and bullfrogs 47.4 cm. Also, both species were positively associated with open water for the first time. Vegetation occurring in the deepest water of the marsh usually included smartweed, aquatic buttercup, or bulrush. Both species of frog were positively associated with all three of these vegetation types. Aquatic buttercup occurs in small isolated sites covering only 2.5% of the marsh. This emergent plant grows in near homogeneous patches prostrate to the waters surface, similar to the structure of dead spikerush. Bulrush cover at the marsh varied little during the entire year, but red-legged frogs only began to use bulrush significantly during the summer season. The use of similar water depths throughout the year suggest that both species of frog select habitats primarily by water depth and secondarily by cover type.

As seen in the previous principal components analysis, red-legged frogs and bullfrogs used similar microhabitat types. The first component accounted for 27.0% of the variability and was the inverse relationship of smartweed and water temperatures with aquatic buttercup, while the second component was primarily the inverse relationship between bulrush and water depth (Table 8). Species of frog differed in relation to the two principal component themes, but this trend was not significant (Figure 9A). As seen in winter and spring, the distribution of sample points of each species of frog had similar ranges in microhabitats used (Figure 9B).

Fall - Non-breeding Period

The water levels of the marsh had dramatically receded by late summer, and by early fall the marsh was completely dry in 1996. The marsh began to hydrate with late fall rains that started in November. Few frogs were observed when the marsh was dry or during the cool early winter, but the frogs that were present used similar habitats (Table 9). Most of the remaining water was located in small depressions in the marsh and was dominated by smartweed and/or adjacent to bulrush. During this season all sample plots went completely dry but small puddles of standing water remained until mid-October. The mean cover of dry microhabitat for the marsh was 69.5%. The remaining dominant aquatic microhabitat had mean covers of open water (13.3%), smartweed (8.6%), and bulrush (5.2%).

Frog activity during this season was very low and no breeding activity occurred. Because of the small sample of frogs in the fall (n=24), a principal component analysis was not conducted. Most of the persisting aquatic habitat occurred along a channel extending from the dam into the center of the marsh (Figure 10). Frog activity was highest in the channel. Both red-legged frogs and bullfrogs were positively associated with open water, smartweed, and bulrush microhabitats. Habitat used by frogs in the marsh was restricted to available water sources, and there was no significant difference between species and microhabitats used (Table 10). The lack of habitat variation between what was available in the marsh and used by species of frog is probably due to the restriction of frogs to the very few aquatic habitat types available at the marsh.

Factors Influencing the Survival of Frogs

Population Estimates

Population estimates of red-legged frogs and bullfrogs are summarized in Table 11. In 1996, 127 adult red-legged frogs and 27 bullfrogs were uniquely marked and are the most conservative population estimates for the year. Twenty-two bullfrog egg masses were found in 1996 and the total number of eggs was approximately 220,000. Twenty red-legged frog egg masses were found in 1996 and 62 in 1997. The total number of red-legged frog eggs was approximately 46,000 in 1996 and 123,000 in 1997. The size of masses between breeding years had a similar frequency distribution (Figure 18; ANOVA F-ratio$_{(df=1,\ 80)}$= 0.754; p = 0.388). Egg masses large in size contributed a disproportionate number of eggs to the annual production. For example, the largest mass in 1996 contained an estimated 8,181 eggs and accounted for 5.0% of the masses deposited during the year, but contributed 17.6% to the total egg count. Consequently, a small number of productive females could have a substantial effect on the reproductive success for an entire year.

Field counts of juvenile frogs were used as an estimate and are undoubtedly underestimates of their true numbers. A total of 805 juvenile red-legged frogs in the summer of 1996 and 12 juvenile bullfrogs in early fall were found.

Predation

Of particular interest in this study was the predation on red-legged frogs by bullfrogs and how this relationship influences the survival of the red-legged frog. The diet of bullfrogs varied, but consisted primarily of amphibians and aquatic invertebrates (Table 12). The small sample size of bullfrogs examined (n=15) makes evaluating the predatory relationship of red-legged frogs and bullfrogs difficult. However, the preferences of prey items and their life stage when consumed are worth mentioning. All three native amphibians known to occur at Ledson Marsh were prey items of the bullfrog, including the California newt (*Taricha torosa*), Pacific treefrog (*Hyla regilla*), and red-legged frog. Of the bullfrogs examined, 47% contained the remains of Pacific treefrogs, and of these treefrogs 96% were newly metamorphosed individuals. The largest prey taken were adult California newts, which were found in 27% of the bullfrogs examined. The remains of three red-legged frog tadpoles were found in 20% (two out of eight) bullfrogs sampled in the spring and summer when tadpoles were present in the marsh. At least two of the consumed tadpoles were near metamorphosis (stage 37-39, Gosner 1960) when tadpoles are acutely vulnerable to predation (Formanowicz 1986). Evidence of the bullfrog's indiscrimant foraging behavior was the presence of dried bulrush stem segments in the stomachs of two frogs.

Reproductive Success

The seasonal supply of water at Ledson Marsh is an important environmental condition influencing survival of tadpoles. The marsh dry-down in mid-October of 1996 provided adequate time for red-legged frog tadpoles to metamorphose but marginal time for the transformation of bullfrog tadpoles. Red-legged frog egg masses were first observed in early-February of 1996 and juvenile frogs were first found in mid-July, a period of five months. No red-legged frog tadpoles were found during tadpole trapping surveys after June 23 and all tadpoles probably transformed by mid-summer. However, the period of metamorphosis probably fluctuates from year to year. Red-legged frogs began breeding one month earlier in 1997 and in 1990 red-legged frog tadpoles were present in mid-September (P. Northen, Sonoma State University, pers. com.). The annual dry-down date of the marsh, obviously, fluctuates from year to year and is primarily related to the duration, intensity, and timing of rainfall. Ledson Marsh probably remains wet well into fall in years with high rainfall and heavy rains late in the season, while in drought years with rain early in the season the marsh may be dry by summer. It is probably only in drought years, and early drying of the marsh, that desiccation of red-legged frog tadpoles is a substantial contributor to mortality. The number of eggs surviving to the terrestrial life stage for the red-legged frog in 1996 was at a rate of 1.9%. This survival rate estimate is probably at the low end range, because the juvenile red-legged frog count is probably an underestimate of the true number present at the marsh.

Bullfrog tadpoles usually over winter and typically take a year or more to metamorphose, but in California, under favorable conditions, they can transform within six months (Cohen & Howard 1958). This study indicates that bullfrog tadpoles can transform in as short as 5.5 months. Bullfrog egg masses were first found on April 28 and were probably deposited three days before. Eggs hatched within a week and juvenile bullfrogs were first found on October 12. The previous visit on October 2 found no juvenile bullfrogs and tadpole mortality from desiccation had begun. By mid-October, the marsh was completely dry and all tadpoles had perished. Only a few bullfrogs produced that year survived the fall dry period, a survival rate to metamorphosis of 0.0001%.

V. DISCUSSION

Habitat Use and Distribution of Frogs

This study indicates that resource partitioning between species of frog was most evident during breeding periods, although there was considerable overlap in habitats used by both species for frog. In addition, microhabitats used by frogs differed proportionately from those available in the marsh. Important microhabitat features for all seasons included vegetative cover at the water's surface, water depth, and water temperature. Dead spikerush in shallow water was used by frogs in the winter and spring but occurred in a small portion of the marsh. In spring through fall, frogs were most associated with smartweed, a dominant microhabitat type in the marsh. Frogs typically avoided open water and occasionally used bulrush, but both microhabitat types became more important late in the season.

Water depths used by both species of frog remained similar throughout the year, but the marsh levels changed dramatically. The marsh water depths were highest in the winter and rapidly receded in summer. Water depths for red-legged frogs were highest during the summer. This is not surprising considering that adequate cover is an important habitat factor. Dead spikerush in the winter and spring occurs in shallow water and both species of frog were highly associated with this microhabitat type. In summer, smartweed was a dominant microhabitat type used by frogs, and it occurs in relatively deep water. Water depths between species of frog were similar, but spring was the exception. This variation in habitat used is likely related to bullfrog breeding behavior where deeper water was used for oviposition sites.

Hayes and Jennings (1988) reviewed habitat characteristics of *R. a. draytonii* populations in the Central Valley of California and indicated that bulrush (*Scirpus* spp.) was an important habitat correlate. In this study, bulrush was generally avoided by red-legged frogs and was only used when aquatic habitats were in limited supply late in the season. Bulrush may be an indicator of other important conditions that are within tolerable limits of the red-legged frog. Aquatic habitat with "water at least 0.7 m deep" has been identified as an important habitat characteristic of the red-legged frog (Hayes & Jennings 1988), where deeper waters are probably used for escape. Red-legged frogs at Ledson Marsh consistently used water depths half this deep throughout the year when deeper vegetated habitats were available. In the winter and spring of 1996, bulrush was associated with mean water depths of 76.5 and 69.1 cm, respectively, but was rarely used by red-legged frogs. Bulrush only became used substantially by red-legged frogs in the summer and fall when mean water depths at bulrush were similar to depths used by frogs throughout the year. This suggests that red-legged frogs prefer shallow (31-42 cm deep) vegetated habitats over deeper vegetated habitats. However, hydrologic conditions that allow for the survival of bulrush may be a good indicator of the duration of ponding water required for tadpole transformation (i.e. late summer). Bulrush had the deepest water levels late in the season (Table 2), past mid-summer when most red-legged frog tadpoles had transformed. In addition, the terrestrial habits of the red-legged are poorly known and dry stands of bulrush occurring in the fall may provide important habitat for cover, aestivation, or hibernation.

There was no evidence that temperature differences were responsible for the selection of shallow water for ovipostion sites by the red-legged frog. However, selection of oviposition sites by anurans is often correlated with higher water temperatures. Olson (1991) observed that the western toad (*Bufo boreas*) and Cascades frog (*Rana cascadae*) selected oviposition sites in shallow waters that warmed quickly during the day and that the insular properties of woody debris contributed to higher water temperatures. Warmer water temperatures increase embryonic development of several species of *Rana* in North America (Moore 1939; Moore 1942). Mean values at the two temperature stations (located in shallow dead spikerush and deep open water) differed by only 0.1°C. Also, the range in values at the stations were similar (6.3°C in dead spikerush and 6.8°C in open water). Slightly warmer waters did occur at the dead spikerush station from the time of egg hatching through the first few weeks of tadpole development. The small but statistically significant difference in water temperature between stations of 0.2°C may be an advantage to developing tadpoles. Embryonic development rates of several species of *Rana* native to North America are temperature correlated and are highest near a species critical thermal maximum (Moore 1942). The red-legged frog's critical thermal maximum is not known, but laboratory experiments by Jennings and Hayes (1990) indicate that it is at least 23°C. The recorded temperature high of 13.7°C during egg deposition at the dead spikerush station is well below the critical thermal maximum. Most eggs hatched, indicating that temperature requirements for normal embryonic development were met. This suggests that red-legged frog oviposition site selection for embryonic development is not influenced by variation in water temperatures of the marsh, but may be attributed to temperature requirements of newly hatched tadpoles, suitability of available egg attachment sites, and water depth.

Dead spikerush and cattail were common attachment sites for red-legged frog egg masses, while bulrush was never used. The stalks of bulrush differ from dead spikerush and cattail in texture and occurrence in water depth. Bulrush has a similar structure to cattail, but its stalks are smooth and may provide a poor cohesive surface for eggs. Also, the selection of shallow water for egg deposition would preclude oviposition on bulrush, which occurs in nearly twice the depth as dead spikerush and cattail.

Mate selection in ranids typically consists of females choosing a calling male from a chorus. Red-legged frog choruses at Ledson Marsh were all observed in shallow water characteristic of oviposition sites. The traditional use of specific sites for both male choruses and female oviposition sites suggests that exposed dead spikerush beds are used for both breeding behaviors (see Figures 4 and 5). Most eggs were laid in or near two choruses located on the western side of the marsh, while the two choruses on the eastern side had few associated masses. Why were two chorus of male red-legged frogs, located in the east side of the marsh, consistently unsuccessful in breeding with females? Vegetation types and topography are similar on both sides of the marsh. Dead spikerush beds on the west side of the marsh are similar to beds on the east side. Given that the location of calling males and those of egg masses are very similar, it is reasonable to conclude that females deposit their eggs near where they have selected a mate. Interestingly, females selected specific choruses for egg deposition. I have several working hypotheses to explain this phenomenon, which are outlined below.

Avoidance of predation by bullfrogs is a possible explanation for the selection of oviposition sites by red-legged frogs. The number of bullfrogs active at the marsh began to increase at the end of the red-legged frog breeding period. In 1996, bullfrogs were primarily distributed along the eastern margin of the marsh near the unsuccessful choruses. However, in 1997 very few bullfrogs were active during the winter and the same oviposition pattern was observed. This suggests that oviposition site selection is not substantially influenced by the presence of bullfrogs. The Cascades frog and foothill yellow-legged frog (*Rana boylii*) are ranids native to the Pacific Northwest that are philopatric (Kupferberg 1996; Olson 1991) and the red-legged frog may also be. However, breeding in the same location does not explain why female selection of oviposition sites varies from male chorus locations when both occur in the same microhabitat type.

Another possible reason for the red-legged frog egg laying pattern is related to the fitness of males among choruses. Male red-legged frogs arrive at breeding sites before females. Preferred chorus sites may be occupied by dominant males, which would be evident by their relative size and weight differences. However, there was no significant difference in body size (SVL) or weight between successful and unsuccessful breeding choruses.

The effects of wind and wave action in the marsh are a reasonable explanation for the oviposition site distribution of red-legged frog egg masses. The prevailing winds at Ledson Marsh blow from the northwest. I observed reduced winds and less accumulation of debris from the effects of waves on the western side of the marsh, where the successfully breeding choruses were located. On the western side, the dead spikerush beds are sheltered by several small stands of cattail, which reduce wind speeds and minimize the formation of waves. In contrast, on the eastern side winds blow across the central open water portion of the marsh and few cattail and bulrush stands occur between the prevailing winds and the dead spikerush beds. The avoidance of areas disturbed by wind and wave action and the presence of tall emergent vegetation may be important contributing factors for the selection of ovipostion sites by breeding females.

Factors Influencing the Survival of Frogs

The relative successes of the red-legged frog and bullfrog are largely related to their adaptive strategies for reproduction and the ephemeral nature of Ledson Marsh. The seasonality of the marsh limits the possible duration of breeding and requires a rate of embryonic and tadpole development that allows for transformation prior to the marsh drying. Only post-metamorphic frogs can survive the fall dry period. Also, the marsh's seasonality influences the predator composition and predation pressure on frogs.

The reproductive strategy of the bullfrog is poorly adapted to the environmental conditions at Ledson Marsh. Embryos have a high critical thermal maximum (32°C) and a narrow range of temperature tolerance (Moore 1942). These physiological factors suit the bullfrog to breed late in the season when water temperatures are high and temperature variation is low. Not surprisingly, bullfrogs have the latest breeding schedule of any ranid of North America. The bullfrog's late breeding schedule and physiological constraints are a strong disadvantage in attempting to reproduce in an ephemeral system. Bullfrog tadpoles at Ledson Marsh required at least 5.5 months to metamorphose. Most eggs laid by Ledson Marsh bullfrogs have little chance of transforming before the marsh dries.

The available information suggests that a sizable population of red-legged frogs is maintained at Ledson Marsh. A breeding population of red-legged frogs has been present for at least seven years (since 1990). Size distribution of red-legged frogs from the winter of 1990 and 1993 suggests that potentially breeding frogs have been present during this interval and breeding was observed during this study. In addition, during three fall seasons (1990 - 1992) newly metamorphosed red-legged frogs were found at the marsh (P. Northen, Sonoma State University, pers. com.) and during this study were observed in abundance in 1995 and 1996. The early 1990s were the end of a regional drought that had lasted for several years. This suggests that the population of red-legged frogs at Ledson Marsh were able to reproduce during drought and wet years. In addition, sexually mature frogs may not return to breed every year. Olson (1991) found that the western toad (*Bufo boreas*) and Cascades frog (*Rana cascadae*) skip one or more years before returning to traditional breeding sites.

Anecdotal evidence suggests that the bullfrog population has increased at Ledson Marsh. The number of adult bullfrogs appeared larger in 1996 than in 1990 (P. Northen, Sonoma State University, pers. com.). This increase may have been caused by a reduced carrying capacity during the drought in the late 1980s and early 1990s. The size distribution of bullfrogs in the summer of 1995 and 1996 indicate that most frogs were medium to large adults. There were few small bullfrogs, which probably represent 1- and 2-year old subadults. The absence of large numbers of subadult bullfrogs and the large annual tadpole mortality, suggests that the bullfrog population is largely dependent on the movement of frogs to the marsh. Probably no bullfrog tadpoles transform in years with moderate to low rainfall. Also, a decrease of water in drainages surrounding Ledson Marsh during periods of drought may reduce the potential duration of bullfrogs moving to the marsh.

The environmental conditions at Ledson Marsh not only influence reproduction of red-legged frogs and bullfrogs but also the predator assemblage. Potential predators on both species of frog include several terrestrial and aquatic species, but given the highly aquatic nature of both species of frog they are probably more susceptible to aquatic predators at least during the egg and tadpole life stages. The annual drying of the marsh precludes the establishment of predatory fish and aquatic invertebrates that overwinter. Native California ranids may have evolved under conditions of limited fish predation (Hayes & Jennings 1986). The bullfrog is adapted to aquatic systems with fish, and tadpoles have a low palatability to many species of fish. Werner & McPeak (1994) studied predation by bullfrogs on green frogs in permanent and temporary ponds, with and without fish. Bullfrog tadpoles had the lowest survival in permanent ponds without fish and they were most successful in permanent ponds with fish. Aquatic invertebrates were the dominant predators on bullfrog tadpoles in ponds without fish. The green frog, which inhabits a similar ecological niche as the red-legged frog, was most successful in temporary ponds without fish. In temporary ponds the number of aquatic invertebrate predators was reduced but adequate to substantially reduce the bullfrog tadpole population. Werner & Peak's (1994) study suggests that where the red-legged frog and bullfrog occur the relative population size of red-legged frogs can be maximized in ephemeral systems, where the dominant suite of predators are aquatic invertebrates that favor bullfrog tadpole prey.

Important determinants in predation pressure are numbers of predators in relation to prey and the vulnerability of prey. Prey are often subject to increased predation during different developmental stages or sizes. Formanowicz (1986) studied ranid tadpole predation by the predaceous diving beetle larvae (*Dytiscus verticalis*) in semi-permanent ponds. Tadpole vulnerability was correlated with the relative size of predator and prey. Calef (1973) concluded that the 95% tadpole mortality of *R. a. aurora* was due to predation, and the rate of predation was highest when tadpoles were small. Seasonal abundance and composition of predators would differ between the permanent lake that

Calef studied and the ephemeral Ledson Marsh. The abundance of predators at Ledson Marsh is probably reduced due to the seasonal water supply. Aquatic invertebrate predators typically breed in the spring so their densities are low in winter and those present have just begun to grow and are small. Werner & McPeak (1994) found fewer aquatic invertebrate predators in ephemeral ponds than in permanent ponds. In addition to fewer and smaller potential predators during the winter season at Ledson Marsh, red-legged frogs presumably have anti-predator characteristics to survive interactions with native predators.

At Ledson Marsh, bullfrogs are primarily inactive during the red-legged frog breeding period and the frogs that are present are spatially distributed apart from areas with red-legged frogs (i.e. breeding sites). In the winter of 1997, the diet of the bullfrog consisted mostly of subadult Pacific treefrogs and no red-legged frogs (Table 12). Surprisingly, red-legged frogs and bullfrogs are highly associated with dead spikerush but bullfrogs do not appear to congregate where there are large numbers of red-legged frogs (Figure 4), a potential prey item.

The dry-down of the marsh of its area by a third in the summer and the observed concentration of both species of frog (Figure 8) suggests that the rate of predation by bullfrogs on red-legged frogs is highest during summer from the increased chance of interspecific encounters. The generalized population estimates of both species and the small number of bullfrog stomachs analyzed makes an evaluation of predation rate on red-legged frogs by adult bullfrogs difficult. The close proximity of bullfrog predators to potential red-legged frog prey, from a receding marsh, suggests that predation, particularly on tadpoles during their vulnerable stage of transformation, is highest during the summer. Adult ranids are typically sit-and-wait foragers that discriminate poorly among prey items, where prey size dictates those attacked. In this study, adult bullfrogs were found to prey on red-legged frog tadpoles near transformation, and in a field experiment adult bullfrogs were found to prey on *R. a. aurora* tadpoles (Kiesecker & Blaustein 1997). However, the high fecundity of the red-legged frog and relatively small population of adult bullfrogs suggests that predation by adults is not a major factor in the reproductive success of red-legged frogs. The Ledson Marsh survival rate of red-legged frogs to the juvenile frog stage (1.9%) is similar to other survivorship studies of *R. a. aurora* (Calef 1973; Licht 1974). Also, no juvenile red-legged frogs were found in the bullfrog diet when juveniles were abundant in the marsh, but this may be related to small sample size. In an analysis of 22 bullfrogs, Twedt (1993) found 9.1% of the prey items were juvenile northern red-legged frogs. It is important to stress that predation pressure is largely a function of the relative population sizes of predators and prey, and bullfrog population changes at Ledson Marsh could have dramatic effects on red-legged frog numbers. The diurnal behavior of juvenile red-legged frogs may subject them more to other predators, such as garter snakes (*Thamnophis* spp.), then to the primarily nocturnal adult bullfrogs.

Interspecific competition between species of frog in their larval stage may influence red-legged frog survival. Algae is probably an important part of the diet of tadpoles of both species (Kupferberg 1997; Jennings & Hayes 1994). Lawler (Univ. Calif. Davis Department of Entomology, unpubl. data) in an experimental study with artificial pools vegetated with cattail, showed that bullfrog tadpoles reduced the survival of *R. a. draytonii* tadpoles to less than 5% and suggested that competition was the reason. Kupferberg (1997) showed that bullfrog tadpoles out competed native yellow-legged frog tadpoles for algal resources. There was significant mortality in foothill yellow-legged frog tadpoles when interacting with bullfrog tadpoles that were large, over-wintered individuals and small, young-of-the-year. Both studies by Kupferberg and Lawler where conducted in systems with substantially less vegetative biomass found in typical marsh systems. Limited food resources resulting in competition among tadpoles may only occur in depauperate systems. Calef (1973) studied the survival rate of *R. a. aurora* in an oligotrophic lake and commented that this nutrient low system was capable of supporting tadpoles at least 100 times more than what naturally occurred. Competition between species at Ledson Marsh is questionable because the marsh contains an abundance of potential food material, including algae, marsh vegetation, and detritus. Ledson Marsh is a eutrophic system with a dense cover of emergent vegetation present throughout the marsh beginning in spring, when tadpoles are abundant. Also, the amount of food consumed by tadpoles is related to their size. Large red-legged frog tadpoles are abundant in the early to mid-summer when bullfrog tadpoles are relatively small. The temporal partitioning of large tadpoles of both species and the abundance of vegetative biomass in the marsh suggests that competition for food resources is low.

Implications for Management

The red-legged frog and bullfrog used similar habitat types with variation during the bullfrog breeding period. Consequently, habitat suitable for breeding red-legged frogs will be suitable for bullfrog survival. However, the reproductive success of the bullfrog is marginal in ephemeral systems. Habitat enhancement for the red-legged frog can be maximized in ephemeral systems while providing only marginal habitat requirements of the bullfrog.

Bullfrogs are naturalized in the state and occur in most suitable water bodies west of the Sierra Nevada Crest below 2,000 m. Barring geographically isolated populations of red-legged frogs, the acknowledgment and preparation of the eventual colonization of bullfrogs to much of the remaining red-legged frog habitat is essential for a successful red-legged frog conservation program.

This study has shown how an ephemeral marsh favors the reproductive success of red-legged frogs, while hindering tadpole survival of bullfrogs. Designing and maintaining ephemeral habitats is an important consideration in managing populations of red-legged frogs, although other conditions should be examined. The proximity to and likelihood of bullfrog dispersal to an ephemeral site must be evaluated or the benefits of an ephemeral system may be thwarted by continual recolonization by bullfrogs. Also, cool climatic conditions may reduce bullfrog survival making an ephemeral habitat unnecessary. Many permanent ponds in Pt. Reyes, Marin County, are inhabited by both red-legged frogs and bullfrogs (G.Fellers, Pt. Reyes National Shoreline, pers. com.). Cool year-round coastal temperatures are suspected of reducing the recruitment of juvenile bullfrogs into the population (M. Jennings, National Biological Service, pers. com.). Permanent aquatic systems run the risk of other non-native species preying on or competing with red-legged frog frogs, such as warm water fish (Centrarchidae and Ictaluridae).

Bullfrog removal at Ledson Marsh would be a labor intensive venture with complete eradication unlikely, given the size of the marsh and extensive vegetative cover. Also, bullfrogs probably move to Ledson Marsh from surrounding aquatic sites and an effective removal program would have to include aquatic sites that are topographically open to frog movement to the marsh. At other locations bullfrog removal may be effective when approached from a topographically isolated (e.g., watershed-based) plan.

A particular concern at Ledson Marsh are significant changes in its hydrology. In exceptionally wet years, where the marsh remains hydrated the entire year, a large number of bullfrog tadpoles could overwinter and metamorphose the following year. This could significantly increase the bullfrog population and predation pressure on the red-legged frog. If the dam at Ledson Marsh were to fail during the red-legged frog breeding period complete reproductive failure may occur. Females deposit eggs in shallow water and a drop in the water level by greater than 0.5 m could result in high mortality of eggs due to desiccation.

Little is known about population dynamics of amphibians in fluctuating environments and long-term studies would be useful. Also, little is known of the terrestrial habitat requirements and movement of the red-legged frog, particularly juvenile frogs, and additional studies are essential for appropriate management. For example, I observed numerous juvenile red-legged frogs in the summer of 1996 but few were seen the following winter. Calef (1973) suggested a 95% mortality rate of juvenile *R. a. aurora* in his study population during their first year. Further studies of terrestrial escape cover, aestivation, and dispersal requirements is warranted.

APPENDIX A: TABLES

Table 1. Characteristics of dominant plants at Ledson Marsh.

Species	*Ht. (m)**	*Growth and Structure*
Scirpus californica (Bulrush)	2 to 4	Grows in dense stands in deep, central areas of the marsh. Stalks are erect and perennial, creating large, impenetrable stands.
Typha latifolia (Cattail)	1 to 2	Grows in dense to open stands along margins of the marsh in shallow water or moist soils. Stalks and tall linear leaves are erect. Plants often die back to rhizome in fall and winter. Dead stalks often remain through winter.
Eleocharis macrostachya (Spikerush)	0.5	Grows in shallow zones of the marsh, often terrestrial by summer. Thin, round stalks die back to rhizome by fall. During winter, dead stalks occur in dense mats at the water surface in shallow water.
Polygonum hydropiperoides (Smartweed)	0.2	Grows erect or ascending throughout the marsh in deeper water. Submergent or emergent stems and broad leaves grow through the water column and appear in spring and summer. Plants die back to rhizome in fall and winter.
Ranunculus lobbii (Aquatic buttercup)	<0.1	Floating aquatic plant. Small dense mats appear in late spring and summer in moderately deep water.
Alisma plantago-aquatica (Water plantain)	<1	Large spoon-shaped leaves arise from corms in shallow water. Plants appear in spring and summer. Tall, open infloresences dry and remain through winter.

*Typical height above water at Ledson Marsh.

Table 2. Mean water depths for prominent microhabitat types at Ledson Marsh. Values based on permanent sampling points.

	Mean Depth (cm)				
	1996				*1997*
Microhabitat	*Winter*	*Spring*	*Summer*	*Fall*	*Winter*
Open Water	66.6	60.4	48.7	22.6	59.3
Bulrush	76.5	69.1	36.4	26.7	68.0
Cattail	40.9	38.7	15.7	*	39.3
Spikerush	17.0	37.8	17.0	5.5	*
Dead Spikerush	39.1	40.4	*	*	29.7
Smartweed	33.0	57.0	36.5	7.9	*
Algae	62.0	70.8	45.2	12.0	45.3
Aquatic Buttercup	*	40.7	52.6	*	*

*Not detected at sample points.

Table 3. Winter - Means and SD for microhabitat variables, red-legged frog breeding period. Data collected from red-legged frog and bullfrog sites, egg mass sites, and permanent marsh sample points.

	Winter 1996				*Winter 1997*			
Microhabitat[1]	*Marsh* *n=34*	*RLF* *n=82*	*RLF Mass* *n=20*	*BF* *n=14*	*Marsh* *n=34*	*RLF* *n=106*	*RLF Mass* *n=62*	*BF* *n=4*
Open Water	65.9 (37.4)	32.0 (37.4)	12.1 (9.8)	12.3 (19.6)	65.0 (35.1)	23.6 (28.4)	55.9 (35.0)	8.3 (14.4)
Bulrush	4.8 (12.7)	0.37 (3.3)	0	14.6 (27.9)	6.8 (16.6)	0.95 (7.4)	0	3.3 (5.8)
Cattail	7.1 (22.0)	0.98 (6.2)	1.1 (4.6)	8.5 (17.2)	6.1 (20.8)	3.8 (14.4)	6.7 (16.9)	21.6 (37.5)
Spikerush	1.2 (6.6)	0	0	0	1.2 (4.3)	0.24 (2.4)	0.1 (0.7)	0
Dead Spikerush	13.7 (26.7)	65.1 (39.0)	86.8 (9.5)	64.6 (44.8)	11.2 (20.5)	52.2 (34.5)	36.1 (35.7)	51.6 (36.9)
Smartweed	1.8 (10.4)	0	0	0	0	0.57 (3.6)	0.1 (0.6)	0
Dead Swartweed	3.7 (15.2)	0	0	0	0	0	0	0
Algae	0	0	0	0	3.9 (10.3)	14.8 (21.9)	0.7 (4.0)	13.3 (11.5)
Aq. Buttercup	0.44 (2.7)	0	0	0	0	0	0	0
Water Plantain	0	0	0	0	0.91 (4.8)	1.3 (6.0)	0.2 (0.9)	0
Grasses	0	0	0	0	1.7 (8.7)	1.0 (6.0)	0	1.7 (2.9)
Mares tail	0	0	0	0	0	0	0	0
Other	0	0	0	0	1.6 (8.7)	0.67 (4.2)	0.3 (1.5)	0
Dry land	0	1.4 (6.2)	0	0.71 (2.7)	1.3 (6.9)	0	0	0
Water Depth	63.0 (27.8)	39.5 (13.1)	32.8 (12.5)	37.7 (14.9)	54.5 (27.7)	35.8 (15.8)	44.4 (14.7)	34.8 (5.9)
Air Temp.[2]	13.6 (12.2)	9.7 (2.2)	15.5 (4.7)	9.16 (1.6)	11.0 (6.4)	8.3 (1.7)	10.8 (2.6)	9.5 (1.7)
Water Temp.[2]	14.8 (5.5	14.4 (1.0)	19.6 (3.6)	14.1 (1.5)	10.5 (1.0)	11.3 (1.6)	12.9 (11.4)	13.3 (1.9)

[1] includes Bulrush (*Scirpus californicus*), Cattail (*Typha latifolia*), Spikerush (*Eleocharis macrostachya*), Smartweed (*Polygonum hydropiperoides*), filamentous Algae, Aquatic buttercup (*Ranunculus lobbii*), Water plantain (*Alisma plantago-aquatica*), and Mare's-tail (*Hippuris vulgaris*).

[2] Temperatures at marsh, frog, and egg mass were taken at different times and are not comparable.

Table 4. Winter - ANOVA of microhabitat variables, red-legged frog breeding period. Data collected from red-legged frog and bullfrog sites, egg mass sites, and permanent marsh sample points. F-test values for each paired comparison are shown in the table with p values.

Microhabitat	*df*	*Marsh/RLF*	*df*	*Marsh/BF*	*df*	*Marsh/RLF Egg Mass*	*df*	*RLF/BF*
				Winter 1996				
Open Water	1,114	23.8, ***	1,46	40.0, ***	1,52	63.9, ***	1,94	22.7, p=0.056
Bulrush	1,114	8.7, **	1,46	2.6, p=0.13	1,52	2.9, p=0.098	1,94	18.8, ***
Cattail	1,114	5.8, *	1,46	0.01, p=0.94	1,52	1.6, p=0.21	1,94	7.9, *
Dead Spikerush	1,114	51.9, ***	1,46	31.2, ***	1,52	201.6, ***	1,94	0.01, p=0.91
Depth	1,114	39.9, ***	1,46	10.8, **	1,52	22.7, ***	1,94	0.2, p=0.65
Surf. Temp.		#		#		#	1,94	1.6, p=0.22
				Winter 1997				
Open Water	1,138	44.6, ***	1,36	9.7, **	1,94	0.8, p=0.38	1,108	1.5, p=0.23
Bulrush	1,138	8.0, **	1,36	0.3, p=0.62	1,94	10.3, **	1,108	0.2, p=0.67
Cattail	1,138	0.5, p=0.45	1,36	3.8, p=0.058	1,94	0.02, p=0.88	1,108	10.4, **
Dead Spikerush	1,138	43.8, ***	1,36	12.0, **	1,94	13.4, **	1,108	0.02, p=0.89
Algae	1,138	4.2, *	1,36	0.3, p=0.58	1,94	6.2, *	1,108	0.8, p=0.71
Depth	1,138	24.8, ***	1,36	2.0, p=0.16	1,94	5.5, *	1,108	0.02, p=0.90
Surf. Temp.		#		#		#	1,108	5.1, *

#Temperature data collected at different time and are not comparable.

*Significance between 0.01 and 0.05.

**Significance between 0.01 and 0.0001.

***Significance $p \leq 0.0001$.

Table 5. Winter - Correlations between red-legged frog and bullfrog microhabitat variables, principal component analysis. Red-legged frog breeding period. Corresponding eigenvalues account for 70.0% of the variance in winter of 1996 and 50.9% in winter of 1997.

	Winter 1996		*Winter 1997*	
Variables	*PC1*	*PC2*	*PC1*	*PC2*
Open Water	0.497	-0.309	0.568	-0.143
Bulrush	0.094	-0.366	-0.041	0.408
Cattail	0.320	0.594	0.161	0.188
Dead Spikerush	-0.552	0.291	-0.545	-0.454
Algae	-	-	0.011	0.631
Water Temp.	0.260	0.576	-0.255	0.380
Water Depth[1]	0.519	0.018	0.536	-0.169

[1] Logarithm values used.

Table 6. Spring/Summer - Means and SD for microhabitat variables, bullfrog breeding period. Data collected from red-legged frog and bullfrog sites, egg mass sites, and permanent marsh sample points.

	Spring 1996				*Summer 1996*			
Microhabitat [1]	*Marsh* *n=34*	*RLF* *n=93*	*BF* *n=63*	*BF Mass* [2] *n=12*	*Marsh* *n=34*	*RLF* *n=37*	*BF* *n=28*	*BF Mass*[2] *n=7*
Open Water	28.6 (29.0)	15.7 (20.2)	21.0 (24.7)	2.1 (7.2)	8.3 (14.1)	11.4 (12.4)	22.7 (23.2)	35.7 (20.9)
Bulrush	4.5 (11.0)	2.8 (12.1)	6.0 (17.0)	0.8 (2.9)	4.4 (10.8)	15.0 (23.2)	9.6 (20.4)	0
Cattail	7.3 (23.4)	2.1 (9.4)	1.9 (10.2)	3.8 (9.3)	4.1 (13.2)	0	0	0
Spikerush	10.8 (19.6)	7.7 (15.4)	2.3 (5.8)	2.1 (5.8)	15.6 (23.4)	0.54 (2.6)	3.6 (7.7)	0.7 (1.9)
Dead Spikerush	3.1 (7.3)	28.9 (37.0)	23.1 (35.9)	0	0.22 (1.3)	0	0	0
Smartweed	36.1 (30.3)	27.9 (33.1)	35.5 (34.8)	80.4 (18.1)	31.0 (32.6)	52.6 (25.7)	46.1 (33.5)	52.1 (32.5)
Dead Swartweed	0	0	0	0	0	0	0	0
Algae	1.8 (8.0)	6.0 (13.8)	2.3 (8.2)	0	1.7 (5.9)	5.9 (13.2)	0	0
Aq. Buttercup	1.4 (5.4)	4.7 (14.5)	7.6 (18.3)	5.8 (17.3)	2.5 (5.5)	10.1 (18.4)	15.5 (20.8)	4.3 (7.9)
Water Plantain	1.8 (4.6)	0.27 (1.9)	0.32 (2.5)	1.7 (5.8)	1.5 (6.5)	0.41 (2.5)	0	0
Grasses	2.9 (16.5)	1.1 (8.4)	0	0	0	0	0	0
Mares tail	0	0	0	0	0	2.2 (7.1)	0.71 (2.2)	7.1 (15.0)
Other	0	0	0	0	0.5 (3.1)	0	0	0
Dry land	2.5 (10.3)	2.5 (10.0)	0	3.3 (7.8)	29.4 (35.1)	1.9 (8.8)	1.8 (9.4)	0
Water Depth	54.4 (27.4)	36.8 (18.5)	54.6 (26.9)	63.1 (12.5)	23.8 (22.2)	41.3 (18.6)	47.4 (22.0)	60.0 (12.5)
Air Temp.[3]	17.3 (1.6)	11.5 (3.1)	13.1 (4.0)	15.0 (2.9)	*	17.0 (2.4)	15.6 (2.4)	20.9 (4.2)
Water Temp.[3]	20.7 (1.4)	18.3 (2.5)	19.7 (2.2)	18.1 (2.1)	*	20.0 (1.6)	20.0 (2.1)	23.2 (3.0)

[1] Includes Bulrush (*Scirpus californicus*), Cattail (*Typha latifolia*), Spikerush (*Eleocharis macrostachya*), Smartweed (*Polygonum hydropiperoides*), Aq. buttercup (*Ranunculus lobbii*), Water plantain (*Alisma plantago-aquatica*), and Mare's-tail (*Hippuris vulgaris*).

[2] Microhabitat data missing for one bullfrog mass in the spring and two masses in the summer.

[3] Temperatures at marsh, frog, and egg mass were taken at different times and are not comparable.

*Water temperature data incomplete due to dry sample plots.

Table 7 - Spring/Summer - ANOVA of microhabitat variables, bullfrog breeding period. Data collected from red-legged frog and bullfrog sites, egg mass sites, and permanent marsh sample points. F-test values for each paired comparison are shown in the table with p value.

Microhabitat	*df*	*Marsh/RLF*	*df*	*Marsh/BF*	*df*	*Marsh/BF Egg Mass*	*df*	*RLF/BF*
				Spring 1996				
Open Water	1,125	8.5, **	1,95	2.0, p=0.16	1,44	10.2, **	1,154	2.2, p=0.14
Spikerush	1,125	0.9, p=0.35	1,95	10.8, **	1,44	2.4, p=0.13	1,154	7.4, *
Dead Spikerush	1,125	15.0, **	1,95	9.5, **	1,44	2.2, p=0.15	1,154	0.8, p=0.38
Smartweed	1,125	1.5, p=0.23	1,95	0.01, p=0.94	1,44	23.4, ***	1,154	0.9, p=0.52
Depth	1,125	17.9, ***	1,95	0.001, p=0.97	1,44	1.1, p=0.31	1,154	25.3, ***
Water Temp.		#		#		#	1,154	12.3, **
				Summer 1996				
Open Water	1,69	1.1, p=0.30	1,60	9.4, **	1,39	19.0, ***	1,63	6.4, *
Bulrush	1,69	6.1, *	1,60	1.8, p=0.19	1,39	1.1, p=0.30	1,63	0.9, p=0.33
Smartweed	1,69	10.5, **	1,60	3.6, p=0.063	1,39	2.7, p=0.11	1,63	0.8, p=0.38
Aq. Buttercup	1,69	5.5, *	1,60	12.5, **	1,39	0.6, p=0.45	1,63	1.2, p=0.27
Depth	1,69	13.1, **	1,60	17.5, ***	1,39	17.3, **	1,63	1.4, p=0.24
Water Temp.		#		#		#	1,63	0.05, p=0.82

#Temperature data collected at different time and are not comparable.
*Significance between 0.01 and 0.05.
**Significance between 0.01 and 0.0001.
***Significance $p \leq 0.0001$.

Table 8. Spring/Summer - Correlations between red-legged frog and bullfrog microhabitat variables, principal component analysis. Bullfrog breeding period. Corresponding eigenvalues account for 50.7% of the variance in spring of 1996 and 49.2% in summer of 1997.

	Spring 1996		*Summer 1996*	
Variables	*PC1*	*PC2*	*PC1*	*PC2*
Open Water	0.096	-0.549	0.222	-0.032
Bullrush	-	-	0.203	-0.646
Spikerush	-0.335	0.233	0.203	-0.024
Dead Spikerush	-0.515	0.055	-	-
Smartweed	0.507	-0.013	-0.621	0.343
Aq. Buttercup	0.237	0.481	0.488	0.370
Water Temp.	0.122	0.638	-0.460	-0.167
Water Depth[1]	0.534	-0.050	0.180	0.547

[1] Logarithm values used.

Table 9: Fall - Means and SD for microhabitat variables, frog non-breeding season. Data collected from red-legged frog and bulllfrog sites, and permanent marsh sample points.

	Fall 1996		
Microhabitat [1]	*Marsh* *n=34*	*RLF* *n=19*	*BF* *n=5*
Open Water	13.3 (21.1)	25.5 (27.6)	20.0 (15.8)
Bulrush	5.2 (12.5)	8.2 (17.3)	23.0 (32.7)
Cattail	0	0	0
Spikerush	0.53 (2.4)	6.3 (16.4)	0
Dead Spikerush	0.63 (2.5)	0	0
Smartweed	8.6 (15.2)	46.1 (32.9)	49.0 (38.5)
Dead Smartweed	0.97 (5.7)	0	0
Algae	1.5 (4.5)	7.1 (11.2)	8.0 (11.0)
Aq. Buttercup	0	0	0
Water Plantain	0	0	0
Grasses	0	0	0
Mares tail	0	1.1 (4.6)	0
Other	0	0	0
Dry land	69.5 (43.8)	5.8 (17.4)	0
Water Depth	6.4 (10.5)	31.0 (14.0)	30.8 (13.2)
Air Temp.[2]	*	13.1 (3.6)	13.8 (3.4)
Water Temp.[2]	*	15.8 (2.7)	16.8 (1.1)

[1] includes Bulrush (*Scirpus californicus*), Cattail (*Typha latifolia*), Spikerush (*Eleocharis macrostachya*), Smartweed (*Polygonum hydropiperoides*), filamentous Algae, Aquatic buttercup (*Ranunculus lobbii*), Water plantain (*Alisma plantago-aquatica*), and Mare's-tail (*Hippuris vulgaris*).

[2] Temperatures at marsh, frog, and egg mass were taken at different times and are not comparable.

*Temperature data incomplete due to dry sample plots.

Table 10. Fall - ANOVA of microhabitat variables, frog non-breeding period. Data collected from red-legged frog and bullfrog sites, and permanent marsh sample points. F-test values for each paired comparison are shown in the table.

Microhabitat	*df*	*Marsh/RLF*	*df*	*Marsh/BF*	*df*	*RLF/BF*
Open Water	1,51	9.4, **	1,37	3.1, p=0.39	1,22	0.2, p=0.68
Bulrush	1,51	1.0, p=0.32	1,37	7.0, *	1,22	2.0, p=0.17
Smartweed	1,51	2.9, p=0.094	1,37	1.4, p=0.24	1,22	0.03, p=0.86
Depth	1,51	1.6, p=0.21	1,37	0.5, p=0.49	1,22	0.001, p=0.97
Water Temp.		#		#	1,22	0.6, p=0.45

#Temperature data collected at different time and are not comparable.
*Significance between 0.01 and 0.05.
**Significance between 0.01 and 0.0001.
***Significance $p \leq 0.0001$.

Table 11. Population Estimates.

	Winter 1996				*Winter 1997*
Species	*Adult*[1]	*Egg Mass*	*Egg*	*Juv. Frog*[2]	*Egg Mass*
Red-legged frog	127 - 179	20	46,000	805	62
Bullfrog	27 - 39	23	220,000[3]	12	N/A

---

[1] Range of estimate values. Low range vales are actual numbers of frogs uniquely marked during the entire year. High end values were calculted using the Peterson Estimate.

[2] Actual number of juvenile frogs observed during a survey.

[3] One egg mass deposited in the spring was removed from the marsh and was not included in the egg count.

Table 12. Summary of Bullfrog Stomach Contents.

Season	*SVL (mm)*	R. a. draytonii	Hyla regilla	*Odonate*	Taricha torosa	*Other*
1996						
Spring	65			3 nymphs		1 aquatic snail
Spring	174			1 nymph		1 unknown spine, 8cm of bulrush
Summer	183				1 adult	Filamentous algae
Summer	Large*		2 subadults			
Summer	Large*	2 tadpoles				1 undigested spine
Summer	Large*		3 subadults		2 adults	
Summer	185	1 tadpole	1 tadpole			
Summer	141			1 nymph	1 larvae	
Fall	140					Stomach empty
Fall	210					Stomach empty
Fall	122				1 larvae	
1997						
Winter	147		6 subadult			4 cm of cattail, possible *Taricha* sp.
Winter	152		4 subadults			1 Coleopteran
Winter	142		4 subadults			1 Aquatic snail
Winter	163		6 subadults			

*Size visually estimated

APPENDIX B: FIGURES

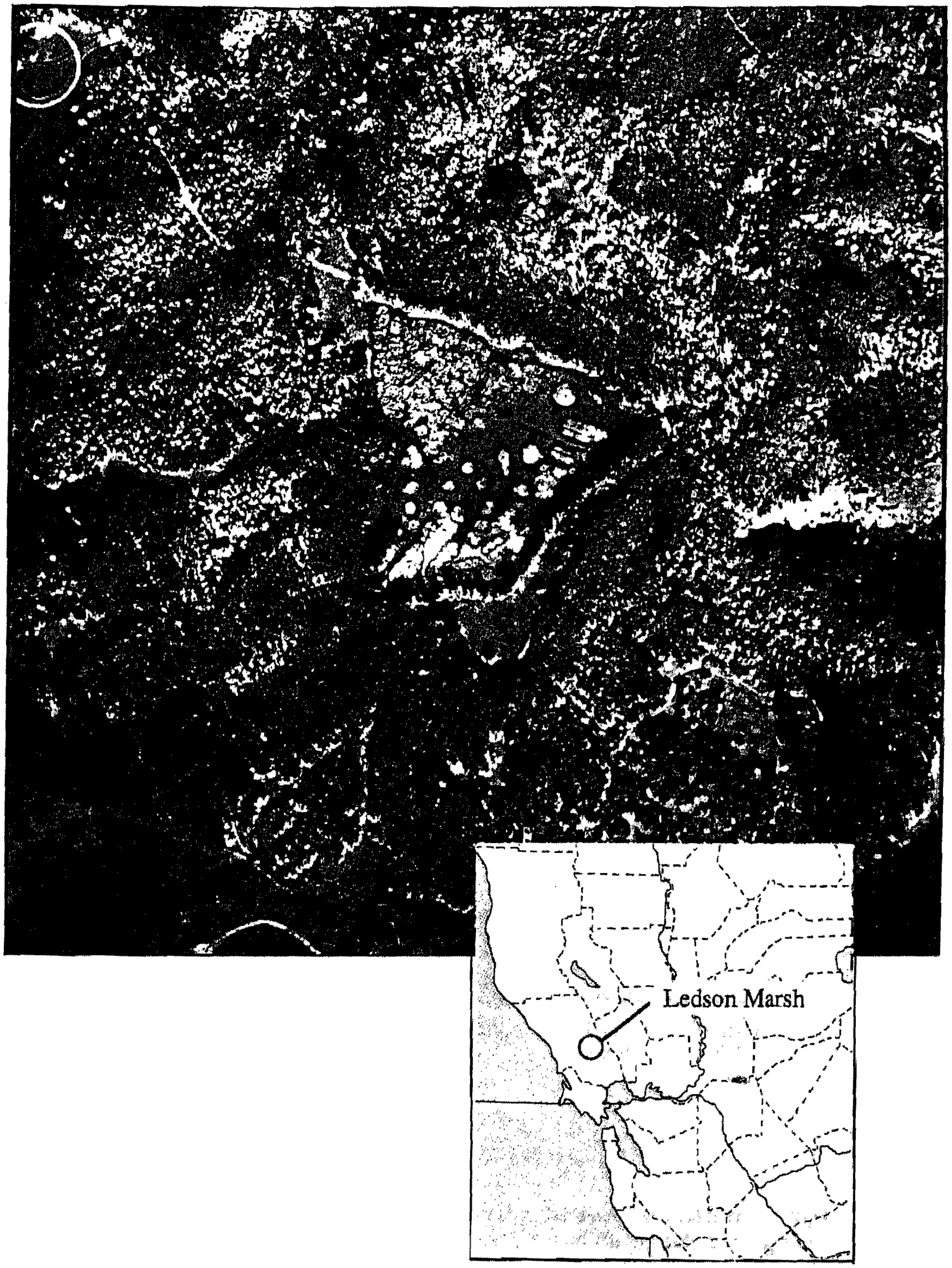


Figure 1. Aerial photograph of Ledson Marsh. Cartwright Aerial Surveys Inc., CA number 2476-3, 17 December 1968, magnified 1.33X to show Ledson Marsh. North is verticle. Scale: 1 in = 750 ft.

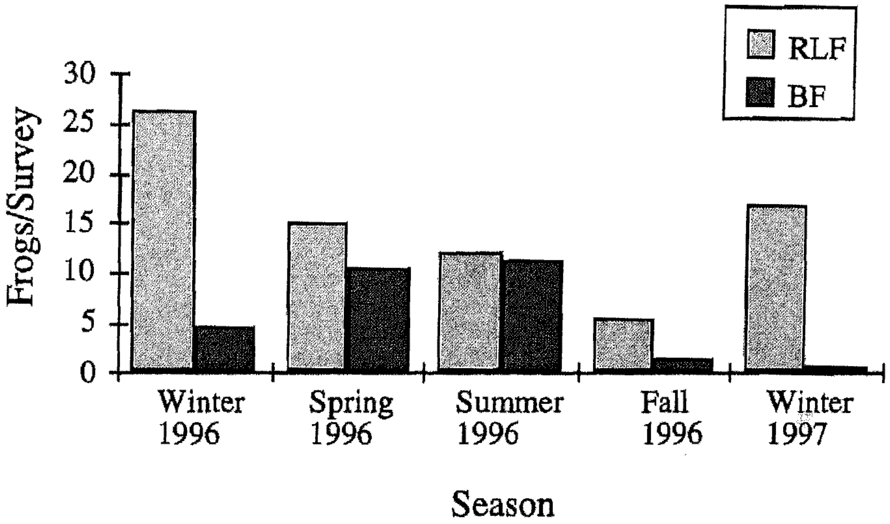


Figure 2. Frog activity patterns. Values are the average number of frogs captured or observed during systematic surveys of the marsh, for a given season.

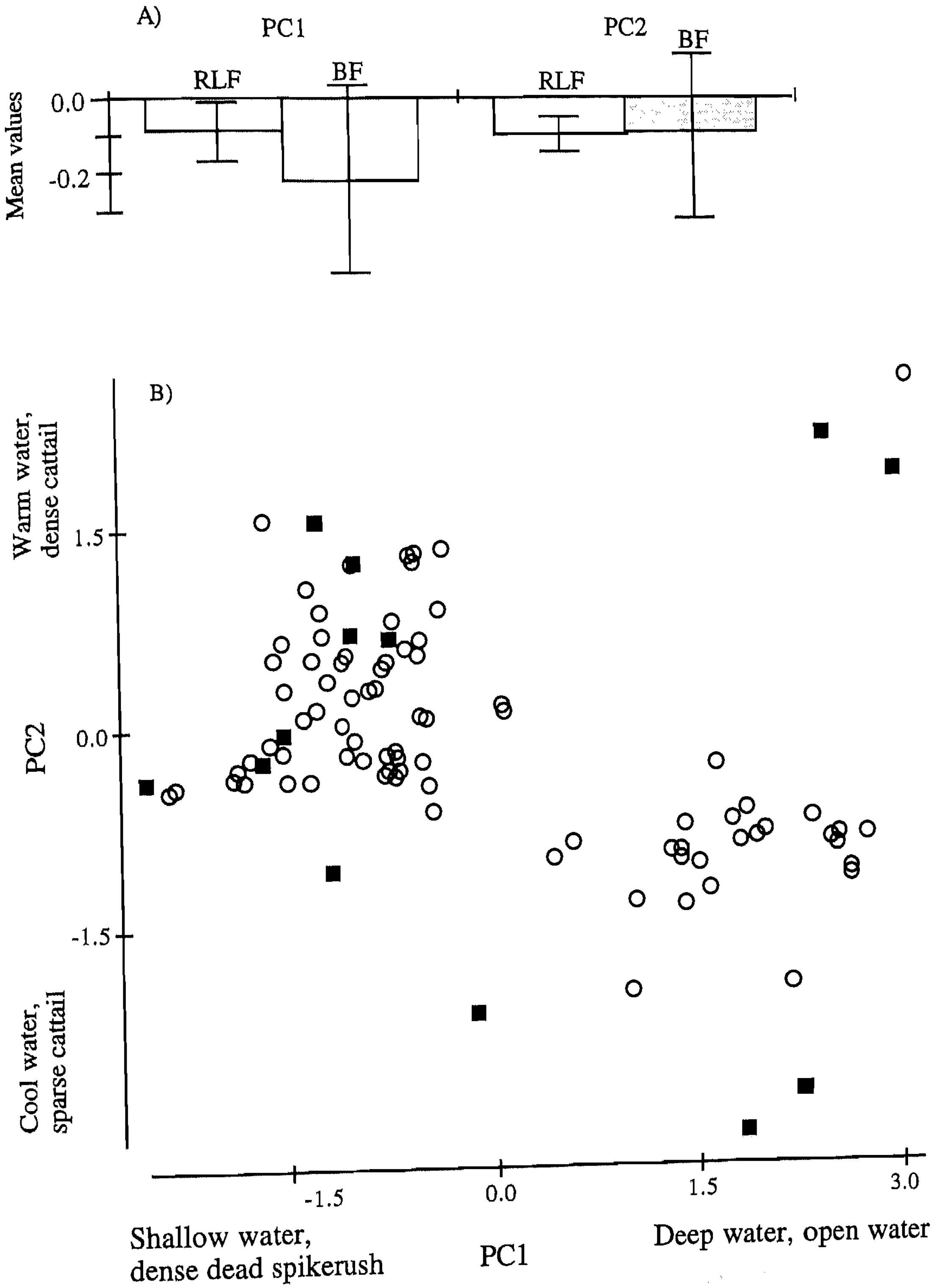


Figure 3. Winter of 1996 - Principal components of frog microhabitat use. A) Mean values of PC1 and PC2 by species of frog (n=96, alpha=0.05; PC1: T-test = 0.30, p=0.76 and PC2: T-test = -0.01, p=0.99); B) plot of principal component themes. Red-legged frog values are represented by open circles and bullfrogs by filled squares.

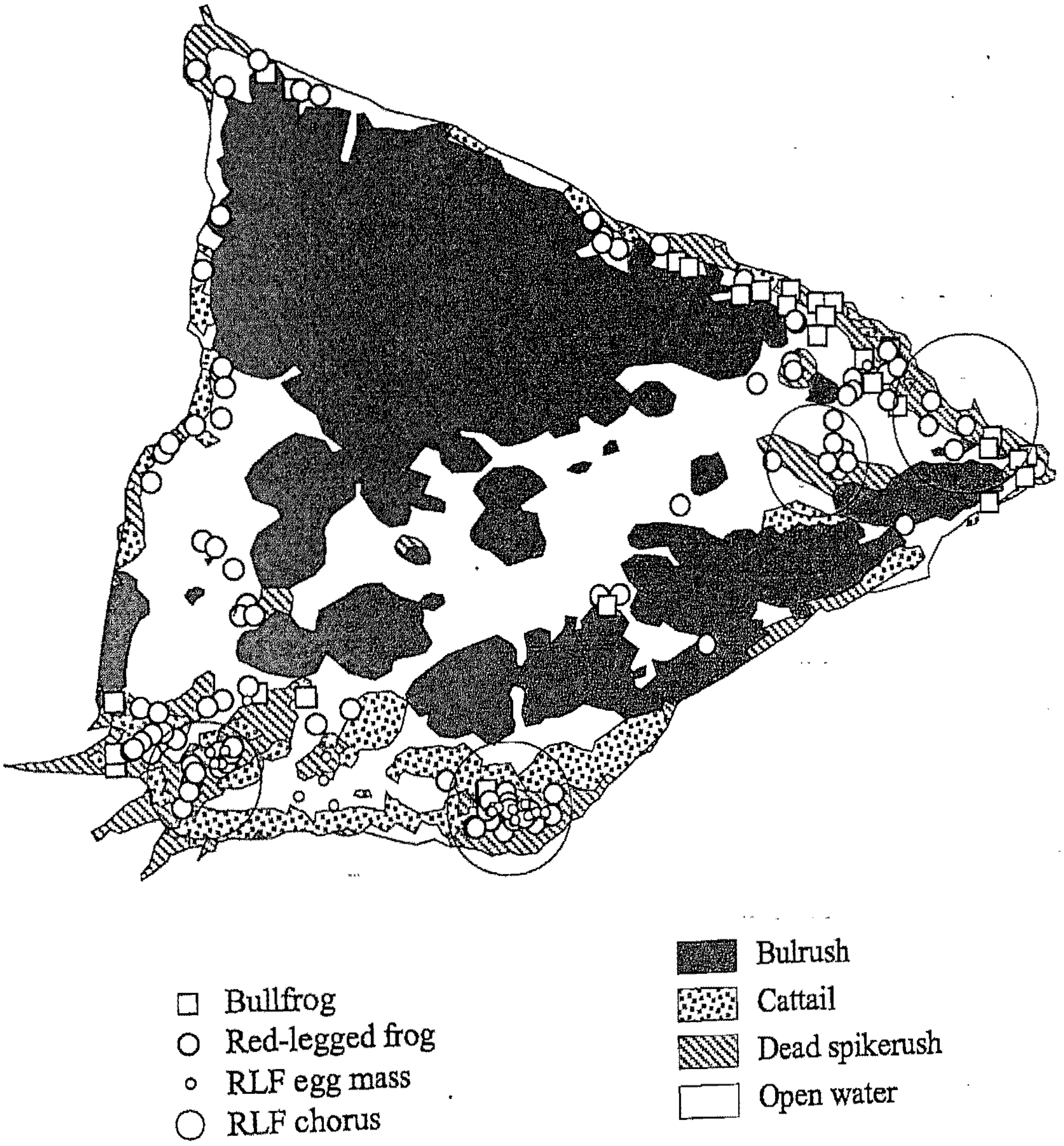


Figure 4: Winter of 1996 - Frog locations and habitat.

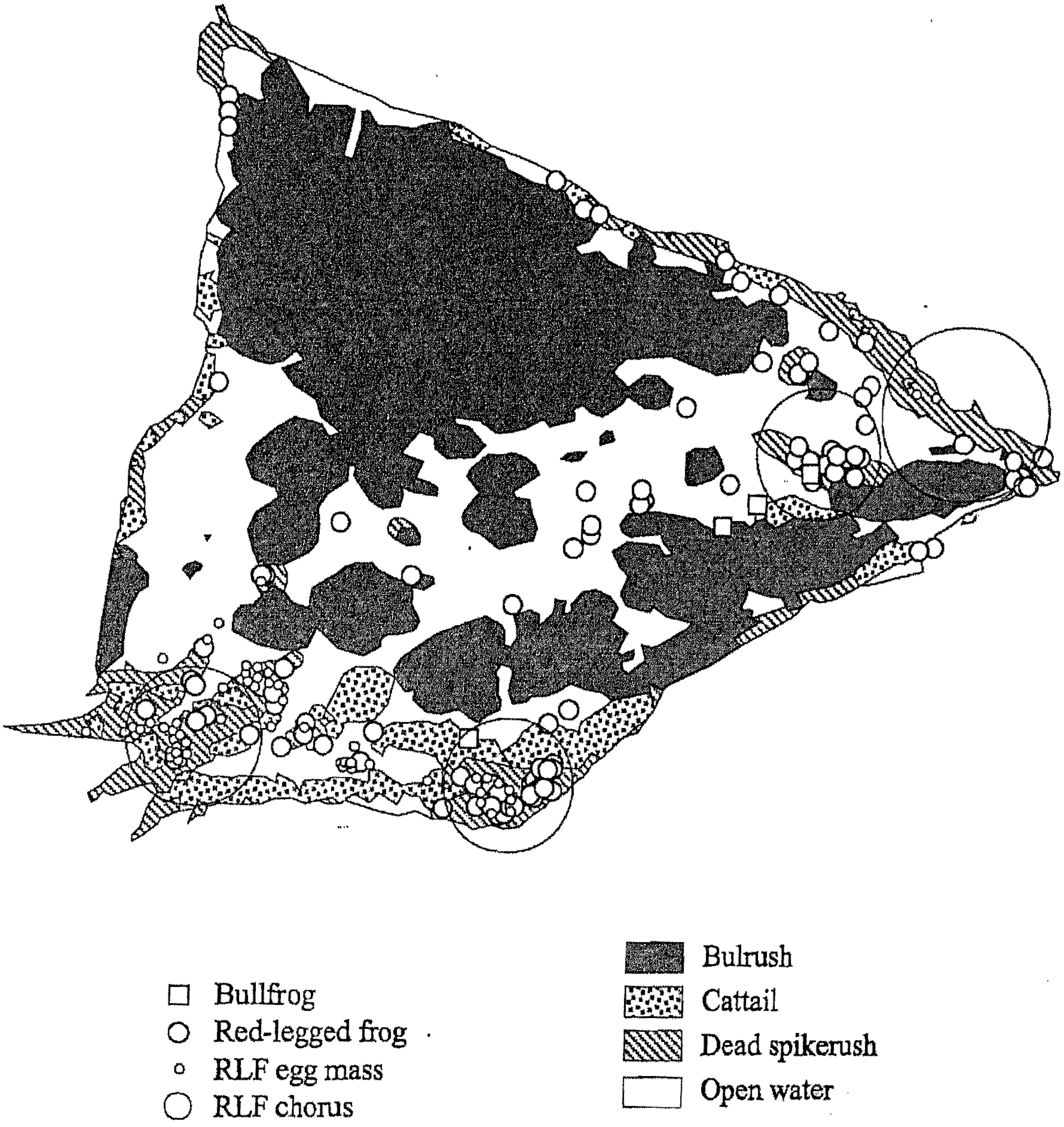


Figure 5: Winter of 1997 - Frog locations and habitat.

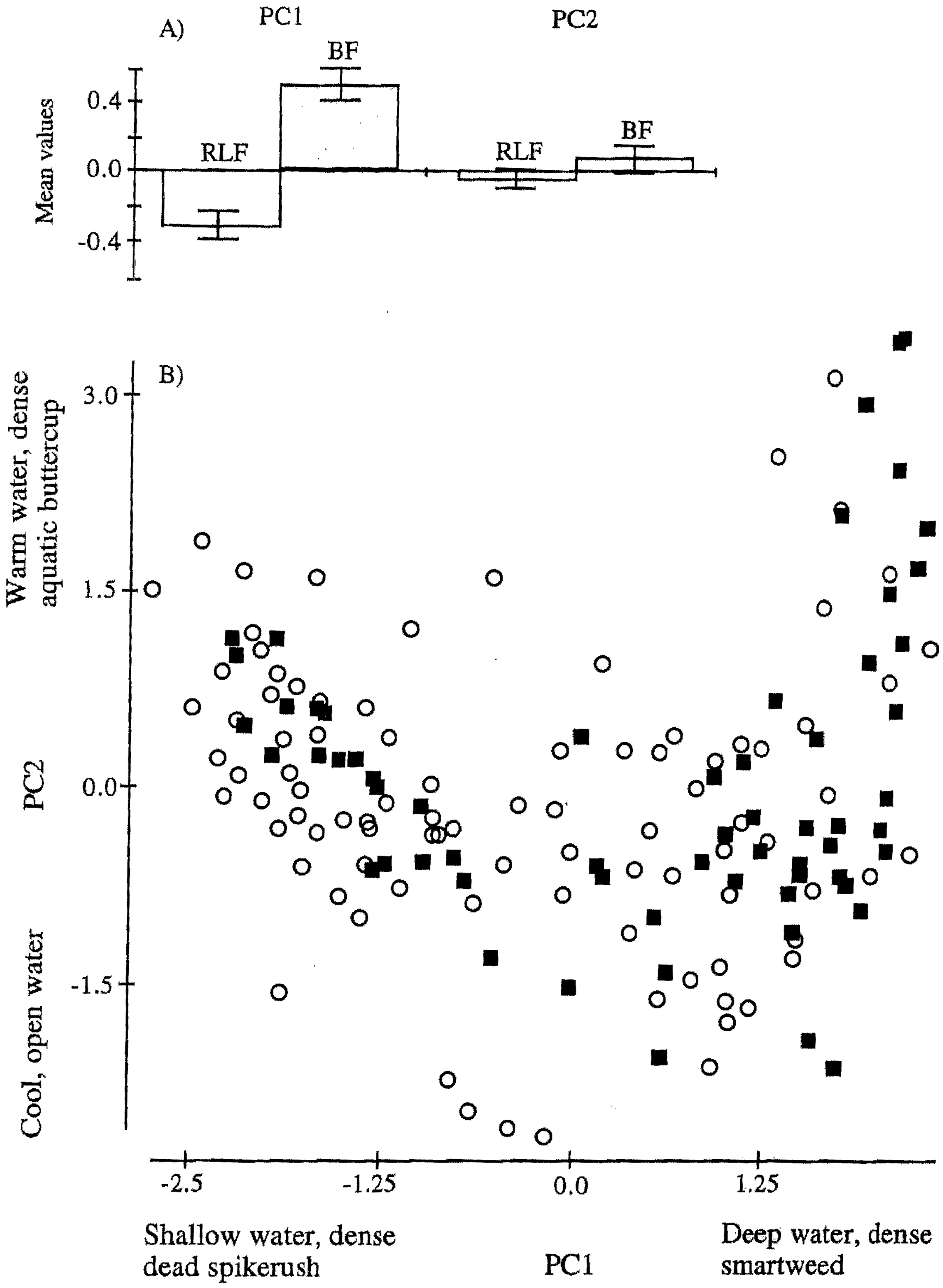


Figure 6. Spring of 1996 - Principal components of frog microhabitat use. A) Mean values of PC1 and PC2 by species of frog (n=154, alpha=0.05; PC1: T-test = -3.5, p=0.0005 and PC2: T-test = -0.81, p=0.42); B) plot of principal component themes. Red-legged frog values are represented by open circles and bullfrogs by filled squares.

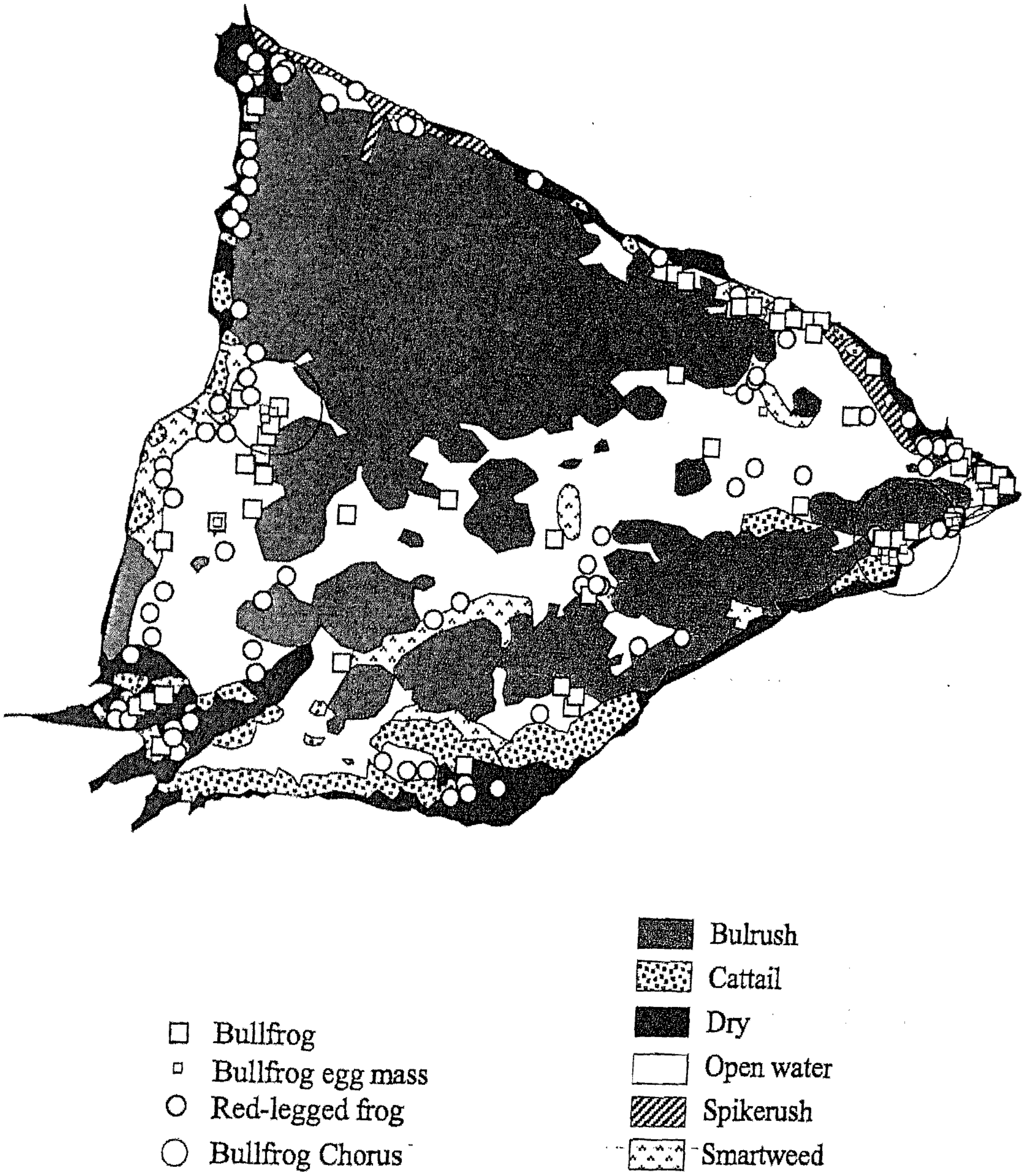
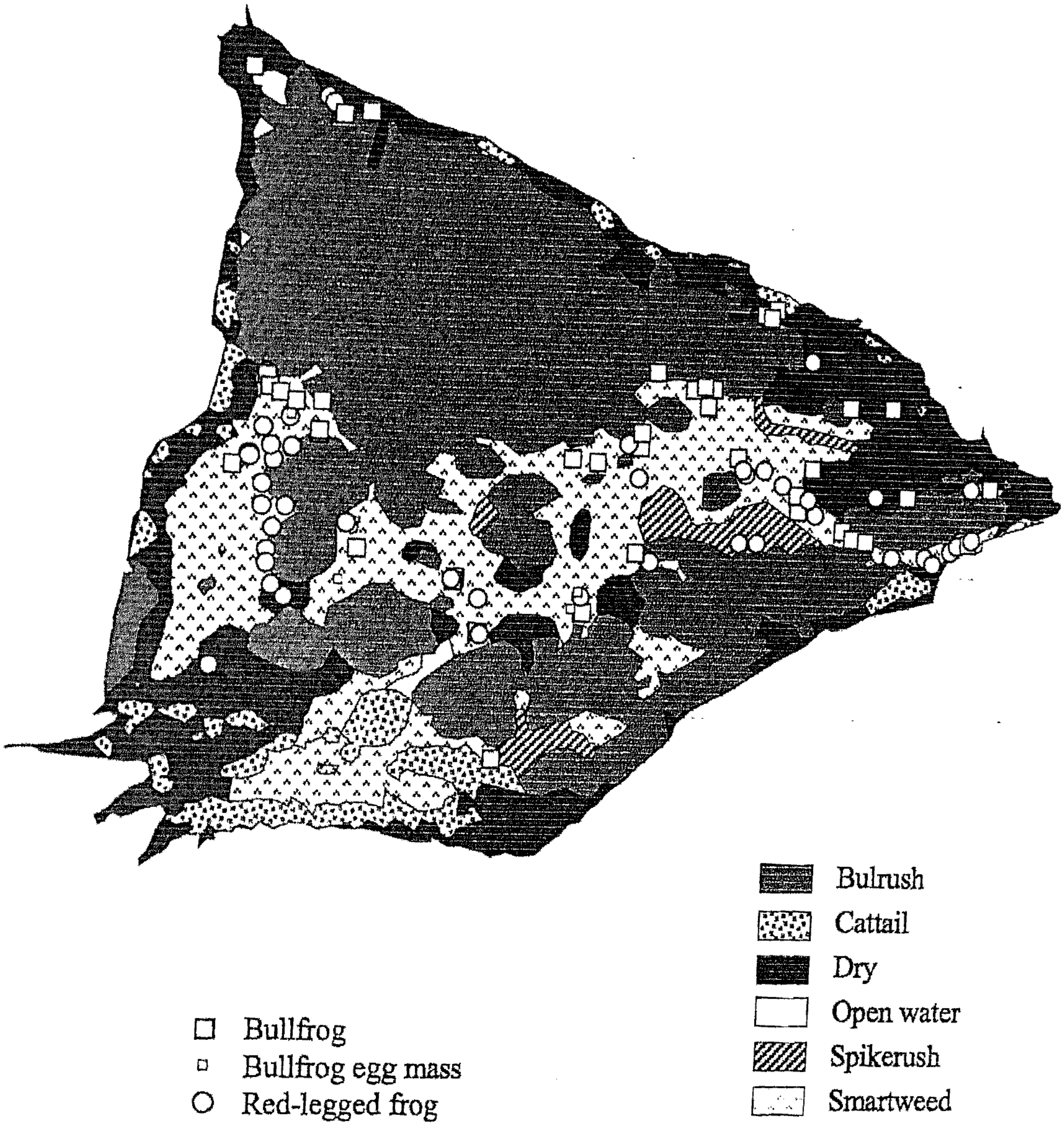


Figure 7: Spring of 1996 - Frog locations and habitat.



Note - Juvenile red-legged frog observations are underrepresented. Juveniles are primarily diurnal and surveys were conducted in the evening when adult frogs are most active.

Figure 8: Summer of 1996 - Frog locations and habitat.

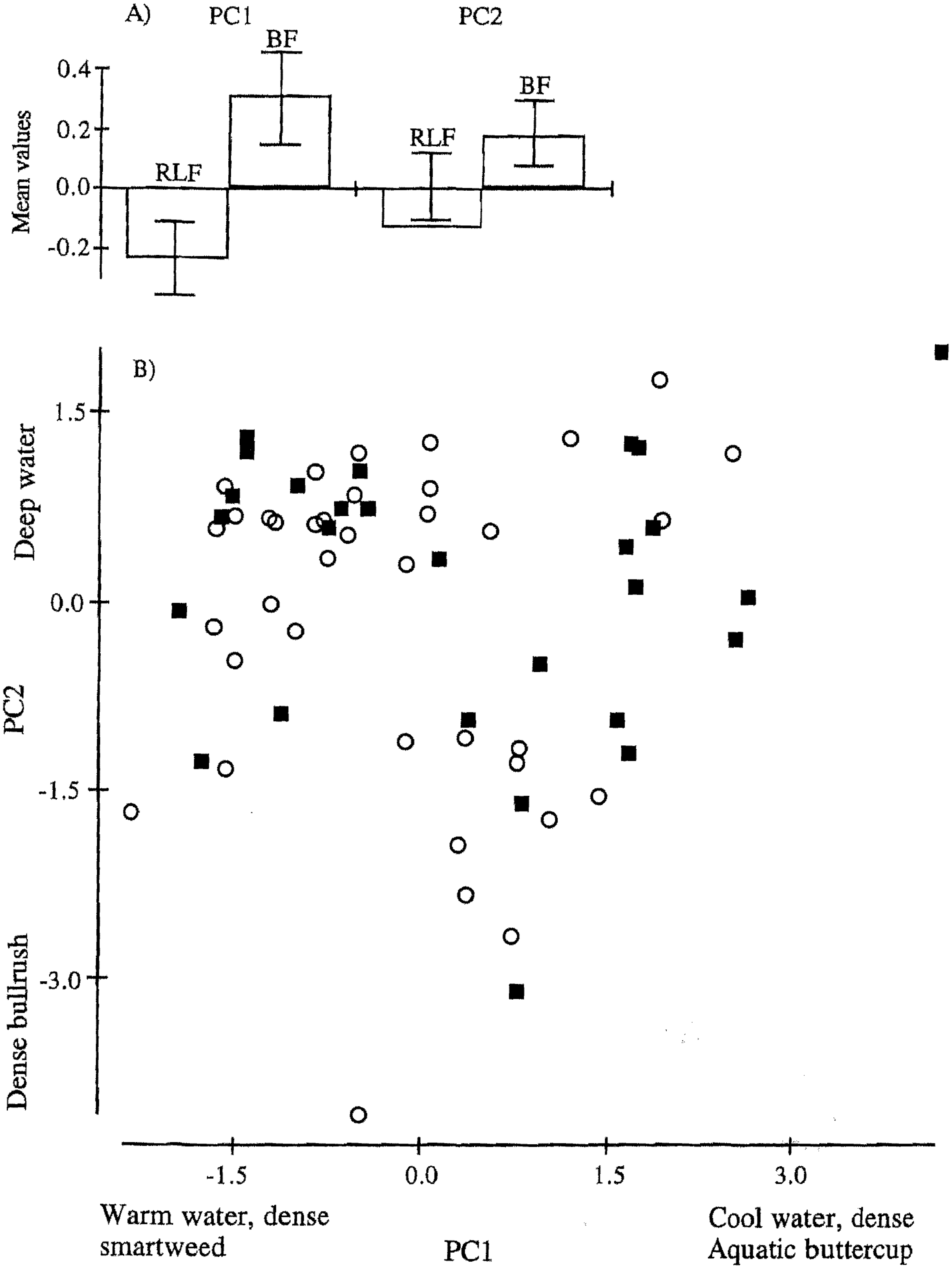
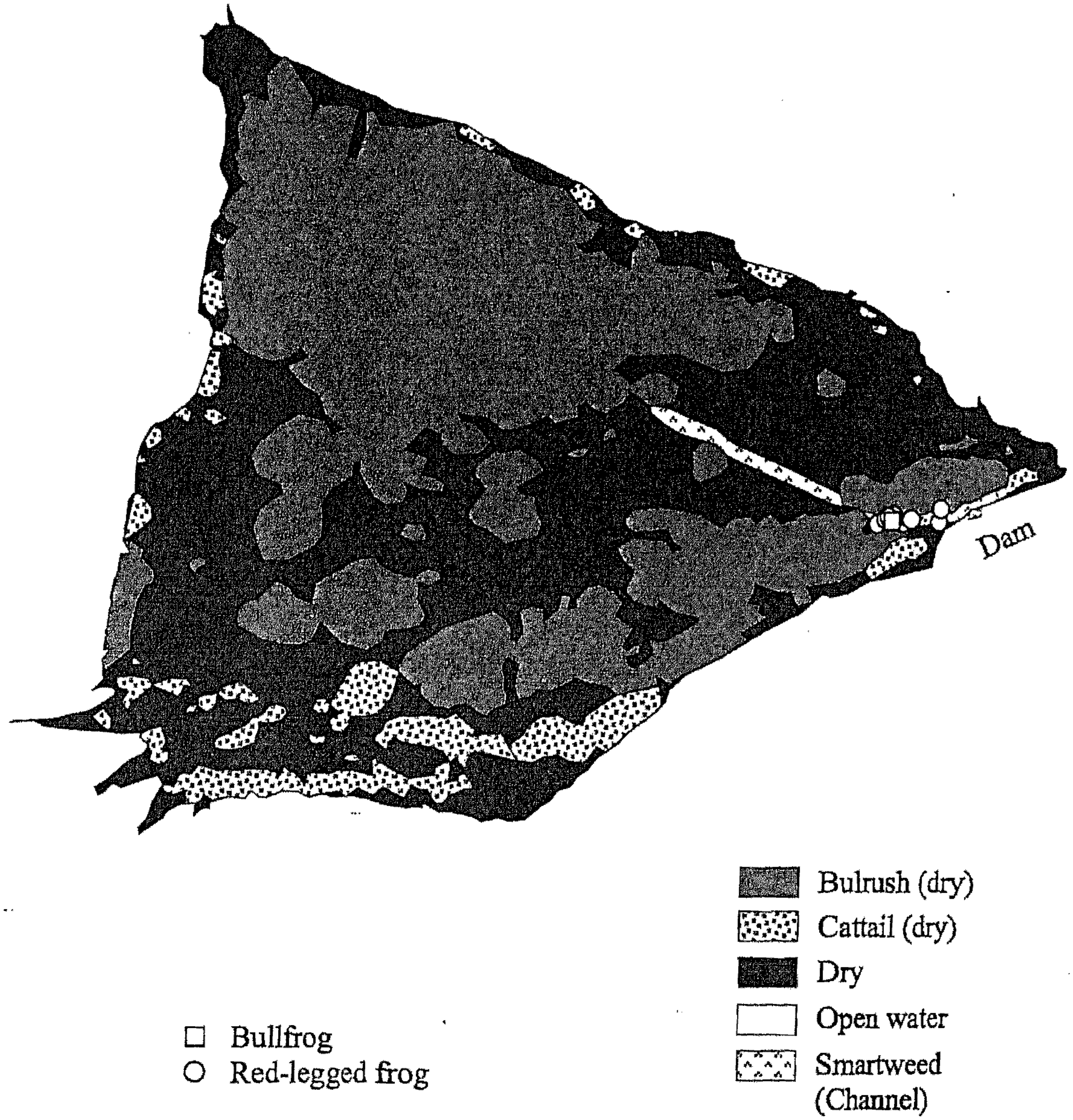


Figure 9. Summer of 1996 - Principal components of frog microhabitat use. A) Mean values of PC1 and PC2 by species of frog;.(n=65, alpha=0.05; PC1: T-test = -1.6, p=0.11 and PC2: T-test = -0.99, p=0.33); B) plot of principal component themes. Red-legged frog values are represented by open circles and bullfrogs by filled squares.



Note - Juvenile red-legged frog observations are underrepresented. Juveniles are primarily diurnal and surveys were conducted in the evening when adult frogs are most active.

Figure 10: Fall of 1996 - Frog locations and habitat.

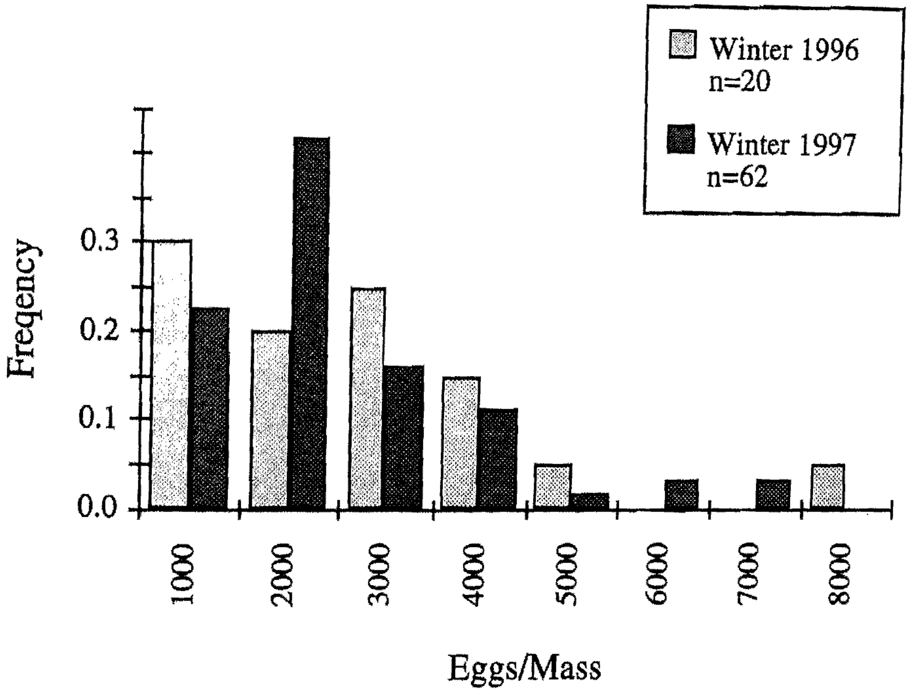


Figure 11. Freqency of red-legged frog eggs per mass.

LITERATURE CITED

Bury, R. B., and J. A. Whelan. 1984. Ecology and management of the bullfrog. U.S. Fish and Wildlife Service, Resource Publication (155):1-23.

Blaustein, A. R., P. D. Hoffman, J. M. Kiesecker, and J. B. Hays. 1996. DNA repair activity and resistance to solar UV-B radiation in eggs of the red-legged frog. Conservation Biology 10:1398-1402.

Blaustein, A. R., and D. B. Wake. 1995. The puzzle of declining amphian populations. Scientific American 272(4):52-57.

Calef, G. W. 1973. Natural mortality of tadpoles in a population of *Rana aurora*. Ecology 54:741-758.

Cohen, N. W., and W.E. Howard. 1958. Bullfrog food and growth at the San Joaquin Experimental Range, California. Copeia 1958:223-225.

Cunningham, J. D. 1952. Notes on abnormal *Rana aurora draytonii*. Herpetologica 11:149.

Donnelly, M. A., and C. Guyer. 1994. Estimating population size. In: Heyer et al. 1994. 183-200 p.

Drost, C. A., and G.M. Fellers. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. Conservation Biology 10:414-425.

Fisher, R. N., and H. B. Shaffer. 1996. The decline of amphibians in California's Great Central Valley. Conservation Biology 10:1387-1397.

Formanowicz, D. R. Jr. 1986. Anuran tadpole/aquatic insect predator-prey interactions: tadpole size and predator capture success. Herpetologica 42:367-373.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16:183-190.

Green, D. M. 1985. Differentiation in amount of centromeric heterochromatin between subspecies of the red-legged frog, *Rana aurora*. Copeia 1985:1070-1074.

Hayes, M. P., and M. M. Miyamoto. 1984. Biochemical, behavioral and body size differences between *Rana aurora aurora* and *R. a. draytonii*. Copeia 1984:1018-1022.

Hayes, M. P., and R. Tennent. 1985. Diet and feeding behavior or the California red-legged frog, *Rana aurora draytonii* (Ranidae). The Southwestern Naturalist 30:601-605.

Hayes, M. P., and M. R. Jennings. 1986. Decline of ranid frog species in western North America: are bullfrogs (*Rana catesbiana*.) responsible? Journal of Herpetology 20:490-509.

Hayes, M. P. and D. M. Kremples. 1986. Vocal sac variation among frogs of the genus *Rana* from Western North America. Copeia 1986:927-936.

Hayes, M. P., and M. R. Jennings. 1988. Habitat correlates of distribution of the California red-legged frog (*Rana aurora draytonii*) and the foothill yellow-legged frog (*Rana boylii*): implications for management. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. General Technical Report (RM-166): 144-158.

Hays, M. R. 1955. Ultragulosity in the frog *Rana aurora draytoni*. Herpetolgica 11:153.

Hecnar, S. J., and R. T. M'Closkey. 1997. Changes in the composition of a ranid frog community following bullfrog extinction. American Midland Naturalist 137:145-150.

Hero, J. M. 1989. A simple code for toe clipping anurans. Herpetological review 20:66-67.

Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, editors. 1994. Measuring and monitoring biodiversity, standard methods for amphibians. Washington: Smithonian Institution Press. 3 p.

Jennings, M. R., and M. P. Hayes. 1985. Pre-1900 Overharvest of California red-legged Frog (*Rana aurora draytonii*): the inducement for bullfrog (*Rana catesbiana*) introduction. Herpetologica 41:94-103.

Jennings, M. R. 1988. Natural history and decline of native Ranids in California. In: De Lisle, H.F., P. B. Brown, B. Kaufman, and B. M. McGurty, editors. Southwestern Herpetologists Society, Special Publication (4):61-72.

Jennings, M. R., and M. P. Hayes. 1990. Status of the California red-legged frog *Rana aurora draytonii* in the Pescadero Marsh Natural Preserve. Sacramento, California Department of Parks and Recreation, Resource Division, Natural Heritage Section.

Jennings, M. R., and M. P. Hayes. 1994. Amphibian and reptile species of special concern in California. Rancho Cordova: California Department of Fish and Game, Inland Fisheries Division.

Kupferberg, S. J. 1996. Hydrologic and geomorphic factors affecting conservation of a river-breeding frog (*Rana boylii*). Ecological Applications 6:1332-1344.

Licht, L. E. 1969a. Comparative breeding behavior of the red-legged frog (*Rana aurora aurora*) and the western spotted frog (*Rana pretiosa pretiosa*) in southwestern Bristish Columbia. Candian Journal of Zoology 47:1287-1299.

Licht, L. E. 1969b. Unusual aspects of anuran sexual behavior as seen in the red-legged frog, *Rana aurora aurora*. Canadian Journal of Zoology 47:505-509.

Licht, L. E. 1974. Survival of embryos, tadpoles, and adults of the frogs *Rana aurora aurora* and *Rana pretiosa pretiosa* sympatric in southwestern British Columbia. Canadian Journal of Zoology 52:613-627.

Meffe, G. K., and C. R. Carroll. 1994. Principles of conservation biology. Sunderland, Massachusetts: Sinauer Associates, Inc. 209-236 and 307-335 p.

McAlpine, D. F., and T. G. Dilworth. 1989. Microhabitat and prey size among three species of *Rana* (Anura: Ranidae) sympatric in eastern Canada. Canadian Journal of Zoology 67:2244-2252.

Miller, K. J., A. Willy, S. Larsen, and S. Morey. 1996. Endangered and threatened wildlife and plants; determination of threatened status for the California red-legged frog. Federal Register 61:25813-25833.

Moore, J. A. 1939. Temperature tolerance and rates of development of the eggs of amphibia. Ecology 20:459-477.

Moore, J. A. 1942. Embryonic temperature tolerance and rate of development in *Rana catesbeiana.* Biol Bulletin 83:375-388.

Moyle, P. B. 1973. Effects of introduced bullfrogs, *Rana catesbiana*, on the native frogs of the San Joaquin Valley, California. Copeia 1973:18-22.

Northen, P.T. 1993. Report on the status of the California red-legged frog in Ledson Marsh, Annadel State Park, Sonoma County, California. Technical Report submitted to the California Dept. of Parks and Recreation, Sonoma, CA.

Nussbaum, R. A., E.D. Jr. Brodie, and R.M. Storm. 1983. Amphibians and reptiles of the Pacific Northwest: University Press of Idaho. 332 p.

Olson, D. H. 1991. Ecological susceptibility of amphibians to populations declines. In proceedings from the Symposium on biodiversity on northwestern California. Oct. 28-30; Santa Rosa, CA. p 55-62.

Stebbins, R. C. 1985. A field Guide to Western Reptiles and Amphibians. Second ed., revised. Boston: Houghton Mifflin Company. 336 p.

Storer, T. I. 1925. A synopsis of the amphibia of California. University of Publications in Zoology 27:1-342.

Storm, R. M. 1960. Notes on the breeding biology of the red-legged frog (*Rana aurora aurora*). Herpetologica 16:251-259.

Toft, C. A. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985:1-21.

Twedt, B. 1993. A comparative ecology of *Rana aurora aurora* Baird and Girard and *Rana catesbeiana* Shaw at Freshwater Lagoon, Humboldt County, CA. M.A. Thesis. Arcata: Humboldt State University. 59 pp.

Werner, E., and M. McPeak. 1994. Direct and indirect effects of predators on two anuran species along an envornmental gradient. Ecology 7:1368-1375.