PREY SELECTION BY JUVENILE BULLFROGS IN A CONSTRUCTED VERNAL POOL COMPLEX

PETER S. BALFOUR, ECORP Consulting, Inc., 2260 Douglas Boulevard, Suite 160, Roseville, CA 95819, USA

STEVEN R. MOREY, U. S. Fish and Wildlife Service, 911 NE 11th Avenue (fourth floor), Portland, OR 97232

ABSTRACT: Bullfrogs (*Rana catesbeiana*) were introduced into California about 100 years ago and are common in permanent and semipermanent aquatic habitats, except those at high elevations and in some desert areas. In the Great Central Valley of California, urban and agricultural development has led to increased hydroperiods in areas that historically supported only ephemeral sources of water. This has increased breeding opportunities for bullfrogs and expanded their dispersal into grassland and vernal pool ecosystems. Because of their voracious feeding habits, the diet of bullfrogs has been well studied, and bullfrogs have been implicated in local declines of some native species. Little is known, however, about prey selection by bullfrogs in ephemeral ecosystems such as vernal pools. We studied aquatic prey availability and the diet of juvenile bullfrogs at a constructed vernal pool wetland mitigation site in Sacramento County, California from February to June, 1998. Early in the spring, bullfrogs were widely distributed on the study site, but as pools with shorter hydroperiods dried, they dispersed away from the site or moved to larger, deeper pools. In pools occupied by bullfrogs, aquatic macroinvertebrate samples were dominated by crustaceans and coleopterans early in the spring, and by hemipterans later in the spring and early summer. The majority of the juvenile bullfrogs' diets consisted of aquatic macroinvertebrates, but terrestrial coleopterans, hymenopterans, dipterans, odonates, and arachnids were also preyed upon. Aquatic prey selection was non-random, with crustaceans and beetles over-represented and hemipterans under-represented in the diet compared to their abundance in the pools.

Keywords: bullfrog, *Rana catesbeiana*, prey selection, vernal pools, aquatic beetles, clam shrimp, *Cyzicus californicus*.

1999 TRANSACTIONS OF THE WESTERN SECTION OF THE WILDLIFE SOCIETY 35:34-40

INTRODUCTION

Originally native to the eastern United States, bullfrogs (*Rana catesbeiana*) were introduced to California about 100 years ago, and are now widely distributed and often abundant in many habitats throughout the state (Bury and Luckenbach 1976, Jennings and Hayes 1985). Bullfrogs are notorious for their voracious feeding habits, and studies documenting their diet are numerous. Adult bullfrogs prey on a wide variety of aquatic and terrestrial organisms (Dickerson 1931, Korschegen and Baskett 1963, Bury and Whelan 1984, California Department of Fish and Game 1988) and have been implicated in declines of native amphibians and other vertebrates (Moyle 1973, Hammerson 1982, Hayes and Jennings 1986, Rosen and Schwalbe 1988, Schwalbe and Rosen 1988, United States Fish and Wildlife Service 1994a, 1996). Even though bullfrogs have gained notoriety for feeding on a wide variety of vertebrate species including alligators and bats (Bury and Whelan 1984 and references therein), rattlesnakes and turtles (Clarkson and DeVos 1986), and even a young mink (Beringer and Johnson 1995), their diet consists primarily of invertebrates (Frost 1935, Korschegen and Moyle 1955, Cohen and Howard 1958). Most bullfrog feeding studies have taken place in perennial wetland systems and little is known about the diet of bullfrogs in vernal pools (but see Hayes and Warner 1985, Morey and Guinn 1992).

Changes in the hydrology of grassland and vernal pool ecosystems in the Great Central Valley of California, as the result of various land uses including agricultural and urban development, have established more permanent sources of water and have increased the hydroperiod of many natural ephemeral drainages and pools. Fisher and Shaffer (1996) observed that vernal pool habitats are often altered by the construction of stock tanks and farm ponds, and concluded that habitat modifications have allowed alien species, including bullfrogs, to invade, contributing to the declines of native amphibians that they observed. This suggests that controlling the effects of bullfrogs and other alien species (e.g., centrarchid fishes, mosquitofish) should be a management priority for vernal pool preserves.

Eliminating bullfrogs from vernal pool areas is going to be difficult because juveniles can disperse across grasslands from nearby permanent waters occupied by adults. Developing efficient management strategies for bullfrogs at vernal pool mitigation sites or preserves is hindered at present because even the basic natural history of bullfrogs, including their dietary habits, while occupying vernal pools, is not well understood. In this paper we report the results of a study in which we evaluate prey selection by juvenile bullfrogs in a constructed vernal pool complex.

STUDY AREA

Our study site was a 162-hectare constructed vernal pool wetland mitigation site in southern Sacramento County, California. The site is adjacent to natural vernal pool landscapes and historically supported a natural vernal pool complex until it was converted for agricultural uses. There are now approximately 15 hectares of constructed vernal pools and other seasonal wetlands on the site. Juvenile bullfrogs are present when the pools are filled. They probably disperse to the site from a nearby creek, portions of which are artificially semi-perennial due to urban and agricultural runoff and support breeding populations of bullfrogs.

METHODS

Field Sampling. The study site was visited on 6 occasions between February 27 and June 24, 1998. Pools (about 12 pools per visit) were inspected for the presence of bullfrogs which, when observed, were counted. A haphazard subsample of frogs from each occupied pool was collected using minnow nets (3/8 inch mesh) and gigs. The frogs we collected (n = 22) were killed, weighed to the nearest 1 g with a hand held Pesola scale, and measured (snout-vent length to the nearest 1 mm). While we are not certain, the method of collection (net versus gig) may have had small effects on mass and length estimates, including increased variance around the mean. Each collected frog was dissected, labeled, and preserved in ethanol. The digestive tracts were labeled and preserved after being perfused with ethanol. Voucher specimens are maintained by PSB.

From each pool where bullfrogs were collected, aquatic macroinvertebrates were sampled using a D-frame aquatic dipnet (8x9 mesh/cm). A sample consisted of three sweeps, one 3-meter pass made along the edge of the pool, along the deepest portion of the pool, and one sweep between these areas. One sample was taken at each pool, ensuring that a consistent volume of water passed through the net in each pool. The face of the net was oscillated vertically to capture organisms present within the water column and benthic areas. Samples were placed in a white porcelain tray, and all organisms 1-cm or greater in length were identified to the level of Order and counted. The 1-cm length threshold was selected after a pilot study in 1997 at the same site revealed that most food items taken by juvenile bullfrogs are over 1-cm in length.

Lab Methods. The preserved contents of the stomachs were identified at least to the level of Order using a dissecting microscope (10x30x), and individual prey items were counted. All prey were categorized as either aquatic or terrestrial. Adult aerial forms of some aquatic taxa (e.g., Odonata) were included in the terrestrial category. Inferences about diet based on stomach contents can be biased due to differential passage time of some types of prey items (e.g., soft bodied prey versus prey with heavily chitinized exoskeletons). We elected, however, to analyze stomach contents anyway, because it is a standard method and is consistent with studies with which we compare our work.

Statistical Analyses. We described the snout-vent length and mass of the bullfrogs with descriptive statistics (mean, standard error) and the unit of analysis was the individual. We observed a shift in the aquatic macroinvertebrate community as the season progressed, so we analyzed the pooled early season samples (27 February, 18 March, and 22 April) and the pooled late season samples (18 May, 03 June, and 24 June) separately to more accurately characterize the aquatic prey available to bullfrogs. Stomach contents from bullfrogs taken at the same vernal pool on the same date were pooled, but otherwise stomach contents and the macroinvertebrate samples were analyzed identically (i.e., pooled early and late season samples). We evaluated aquatic prey selectivity in the early and late season collections with separate Chi-square goodness of fit tests (Zar 1984). One source of bias inherent in our sampling design is that some pools were sampled only once while others were sampled more than once. This happened because we decided in advance to sample the aquatic macroinvertebrates in each pool from which we collected frogs. Frogs were repeatedly encountered in some pools but not in others. Thus, of the 9 different pools sampled over the course of the study, 5 were sampled once, 3 were sampled twice, and 1 pool was sampled three times. We found that removing the repeated samples did not qualitatively change the results, so we present the analysis of the full sample.

RESULTS

Use of the site by bullfrogs. We made 6 visits to the study site and searched for frogs in about 12 pools per visit, observing an average of 30 juvenile bullfrogs (range= 21 - 44) per visit. Early in the season (February - April) frogs were widely distributed on the site, occupying over half (59%) of the pools. Later in the season (May-June) the frogs moved away from the smaller, shallower pools in favor of the largest, deepest pools on the site. On June 24, for example, 10 pools still held water, but the 30 frogs we observed on that date were restricted to only 2 pools. All bullfrogs collected were dissected to confirm their reproductive status and were all found to have small, undeveloped gonads.

Aquatic macroinvertebrates. Over the course of the study there was a shift in the composition of the early and late season macroinvertebrate assemblages. Early in the season, crustaceans and beetles made up almost 80% of the sample (Figure 1). The most common crustacean was the California clam shrimp, *Cyzicus californicus* (Spinicaudata). Vernal pool tadpole shrimp, *Lepidurus packardi* (Notostraca), were collected only once, although exoskeletons of this species were observed in several of the pools we sampled. The most abundant aquatic beetles early in the season were adult and larval Dytiscidae. Among several changes in the macroinvertebrate assemblage from early to late in the spring, the most notable was the increase in the proportion of the sample made up of the Hemiptera (Figure 1), primarily water boatmen (Corixidae). In the late season sample, the Hydrophilidae replaced the Dytiscidae as the most abundant aquatic beetles, the proportion of California clam shrimp decreased from 41% to only 2%, and the proportion of Odonata (mostly damselfly nymphs), Diptera (Chironomidae), and mayfly nymphs (Baetidae) increased markedly (Figure 1). In addition to distinct changes in relative abundance and composition, we also observed changes in overall abundance of the macroinvertebrate assemblage. Over the course of the study we observed over a 20-fold increase in the number of macroinvertebrates in our standardized aquatic

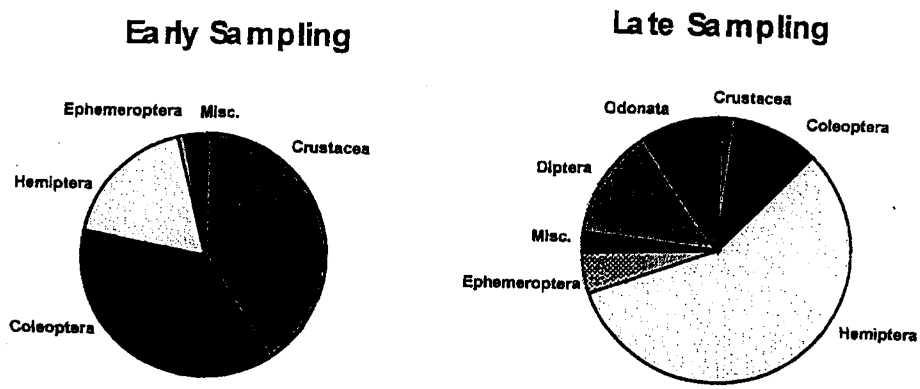

Figure 1. Proportions of aquatic macroinvertebrates present within vernal pools, based on sampling conducted in a constructed vernal pool complex in Sacramento County, California, in 1998. Early sampling was conducted between February and April, 1998; late sampling was conducted between May and June, 1998.

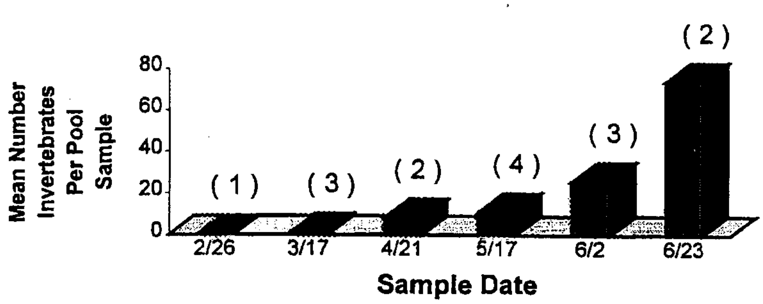

Figure 2. Changes in relative invertebrate abundance over time, based on sampling conducted in a constructed vernal pool complex in Sacramento County, California, in 1998. Number of pools sampled on each date are shown in parentheses on each bar.

samples (Figure 2). Most of this change was the result of increases in the abundance of water boatmen, chironomids, damselfly nymphs and mayfly nymphs as spring progressed.

Diet and prey selection by bullfrogs. It appears that the majority of bullfrogs on the site were feeding throughout the study because, of the 22 frogs collected, only a single individual (collected 24 June) had an empty stomach. Over the course of the spring, we observed a greater than four-fold increase in mass among the frogs we collected (Figure 3). The majority of the prey items in the stomachs of the juvenile bullfrogs we examined were aquatic (62% of the early sample; 80% of the late season sample) (Figure 4). The proportion of terrestrial and aerial food items in the stomachs was greatest early in the season when the abundance of aquatic prey was lowest. Terrestrial and aerial prey taken early in the early in the season included various Coleoptera (e.g., Chrysomelidae, Coccinellidae, Carabidae), Diptera (e.g., Tipulidae, Muscidae), and Hymenoptera (Apidae). Later in the season, terrestrial and aerial prey included Coleoptera, Diptera, Odonata (including adult damselflies [Lestidae] and dragonflies [Libellulidae]), and spiders (Arachnida).

Aquatic taxa identified in both early and late season stomach samples consisted almost entirely of adult and larval Coleoptera and clam shrimp (Figure 5). California clam shrimp, hydrophilid beetles (*Tropisternus* sp., *Berosus* sp.), and dytiscid beetles (*Agabus* sp., *Rhantus* sp., *Colymbetes* sp.) comprised the majority of the early season aquatic stomach contents. The late season aquatic stomach contents were similar to the early season stomach contents (d.f. = 3, $X^2 = 3.71$, $P > 0.25$), except for the addition of Hemiptera (Corixidae and Notonectidae) and odonate nymphs (Lestidae and Libellulidae) which made up a small proportion of the overall sample (Figure 5).

Nine of the 22 frog stomachs contained small numbers of tiny (<1 cm in length) dytiscid beetles (*Hydroporus* sp.), unidentified adult flies (Diptera) and a single aphid (Homoptera: Aphidae). We do not know if these items were preyed upon or if they were taken incidentally along with larger prey. Other items in the stomachs included plant parts (leaves, seeds and stems), rocks, and feathers.

We did not sample the terrestrial or aerial prey available to bullfrogs at the study site, but aquatic sampling did provide an approximation of aquatic prey availability. The proportions of aquatic macroinvertebrates present in the pools occupied by bullfrogs (Figure 1) were substantially different than the proportions of aquatic prey taken by bullfrogs (Figure 5) during early

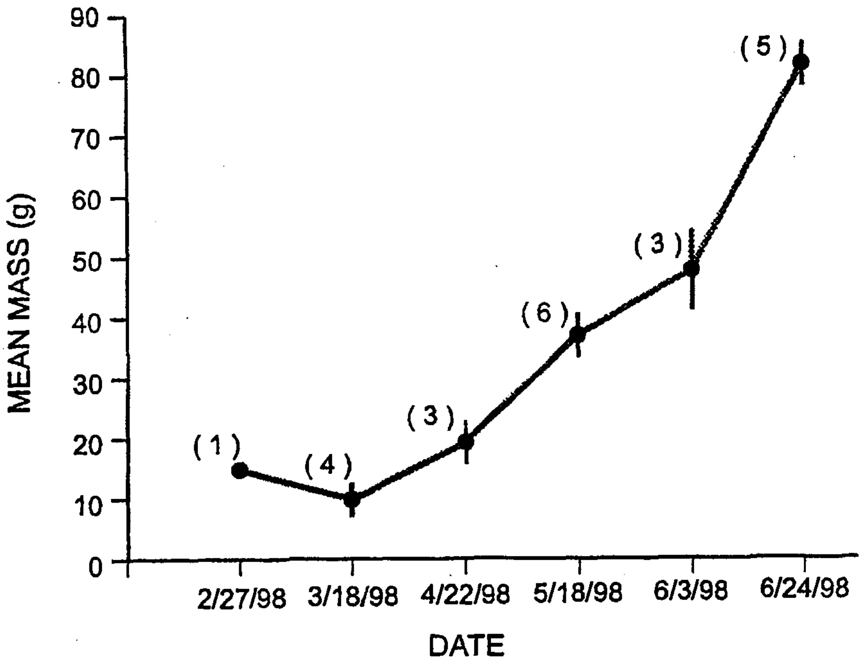

Figure 3. Changes in mass of juvenile bullfrogs over time, based on sampling conducted in a constructed vernal pool complex in Sacramento County, California, in 1998. Numbers of frogs sampled shown in parentheses. Error bars=1 SE. Early sampling was conducted between February and April, 1998; late sampling was conducted between May and June, 1998.

and late season samples (early season, d.f. = 4, X^2 = 2.65, $P > 0.001$; late season, d.f. = 5, X^2 = 3,628, $P < 0.001$). Overall, early and late in the season, crustaceans and beetles were over-represented and hemipterans were under-represented in the stomach contents compared to their availability in the pools. Late in the season, odonate nymphs, mayfly nymphs, and chironomid larvae were also under-represented in the stomach contents compared to their availability in the pools occupied by bullfrogs.

DISCUSSION

All of the frogs observed on the study site were juveniles. All of those collected had undeveloped gonads and ranged from 39 to 83 mm, snout-vent length. This conforms with the observation by Morey and Guinn (1992) that bullfrogs under 80 mm snout-vent length are almost certainly juveniles. The frogs we observed probably transformed during the previous summer or fall after living as larvae in a semi-perennial creek which passes within 0.35 km of the study site.

In a previous study, Morey and Guinn (1992) examined the stomach contents of bullfrogs collected on rainy nights on roads passing through a vernal pool landscape in the San Joaquin Valley, and found about 60% of the stomachs were empty. Those that did contain food contained an average of only about 3 prey items per frog, and the prey were almost exclusively terrestrial in origin. They concluded that the main behavioral activity on rainy nights was dispersal, not feeding. By contrast, only one of the 22 stomachs (5%) we analyzed were empty, and the average number of prey items per stomach was 10 (range= 3 - 31). The full stomachs, containing mainly vernal pool invertebrates, and the pronounced increase in mass over the course of the study (which appeared to follow a growth curve), make it tempting to

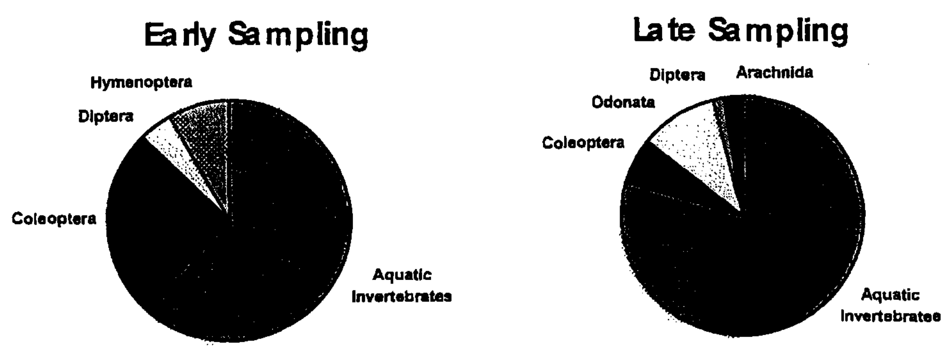

Figure 4. Stomach content proportions of juvenile bullfrogs, based on sampling conducted in a constructed vernal pool complex in Sacramento County, California, in 1998. Early sampling was conducted between February and April, 1998; late sampling was conducted between May and June, 1998.

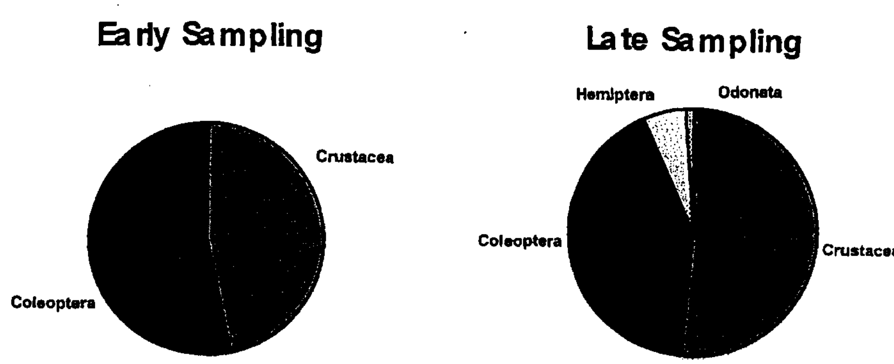

Figure 5. Proportions of aquatic prey of juvenile bullfrogs, based on sampling conducted in a constructed vernal pool complex in Sacramento County, California, in 1998. Early sampling was conducted between February and April, 1998; late sampling was conducted between May and June, 1998.

speculate that the juvenile bullfrogs we studied were resident on the study site over the course of the study, but other interpretations are possible.

We find it interesting that even though the composition and relative abundance of the aquatic macroinvertebrate assemblage in the pools changed dramatically as the season progressed, the aquatic prey taken by bullfrogs changed very little. Early in the season clam shrimp and larval and adult beetles comprised about 80% of the available aquatic prey. Not surprisingly, over this period bullfrogs ate mostly clam shrimp and beetles; they excluded hemipterans which made up 18% of the available aquatic prey. Later in the season, clam shrimp abundance declined and made up only 2% of the aquatic macroinvertebrate assemblage. Beetles remained abundant, but because of a large increase in abundance of hemipterans, they made up only 11% of the late season assemblage. During this period bullfrogs continued to prey primarily on clam shrimp and beetles while feeding only sparingly on hemipterans, which formed the preponderance of the available aquatic prey.

Our descriptive approach provided no clues about why crustaceans and beetles were over-represented and hemipterans and some other groups were under-represented in the bullfrog diet when compared to their availability. We assume that several factors probably influenced prey selection including prey size, crypsis, and behavior. We did not measure the prey items found in the stomach contents, but the taxa most abundant in the stomach contents tended to be relatively large and active. Ephemeroptera and odonate nymphs may be inconspicuous to bullfrogs because they are relatively sedentary and cryptically colored. Larval midges (Chironomidae) may be inconspicuous to bullfrogs because they are largely benthic and relatively small. Hemipterans, while present in the late season stomach contents, were also a much under-represented prey group. Corixids and notonectids both retreat quickly in response to water disturbances and it is possible that their rapid and frenetic swimming behavior makes them difficult to capture. Whatever the reason, the avoidance of hemipterans as prey by bullfrogs has been observed before (Korschgen and Moyle 1955).

The study site was a constructed vernal pool wetland mitigation site, so our comparisons with natural vernal pool landscapes are tentative. We believe, however, that the behavior of bullfrogs that we observed, and our general conclusions, are applicable to both naturally-occurring vernal pools and constructed ephemeral wetlands. The U. S. Fish and Wildlife Service (1994) has expressed concerns about potential effects of bullfrogs on listed vernal pool crustaceans. This concern may be justified given that bullfrogs are known to be voracious predators (Frost 1935, Clarkson and DeVos 1986), and because juvenile bullfrogs are likely to temporarily occupy vernal pool complexes wherever perennial water exists nearby. We commonly encounter small bullfrogs in unaltered vernal pools, and as Fisher and Shaffer (1996) pointed out, many natural vernal pool landscapes tend to be altered in places, allowing bullfrogs and other alien species to invade. Opportunities for bullfrog dispersal increase wherever urban runoff and irrigated agriculture create permanent water sources. Considering that habitat conversions of this type have already occurred at a high level (USFWS 1994, Holland 1998), and that alteration and fragmentation of vernal pool landscapes is expected to continue, it seems realistic to conclude that juvenile bullfrogs are likely to be, at least while pools are filled, an increasingly common component of many vernal pool communities.

Our study provides circumstantial evidence that juvenile bullfrogs can spend several weeks in vernal pool complexes, or as long as some pools remain filled. We have shown that while occupying vernal pools, juvenile bullfrogs will feed primarily on aquatic prey that live in the pools, and that they will selectively prey on large crustaceans and beetles, even when other invertebrate prey is much more abundant. These results do not, however, suggest any particular effects on prey populations. Demonstrating effects of bullfrogs on prey populations or on vernal pool community structure would require an experimental approach. In the future, as vernal pool landscapes are altered or converted to other uses, vernal pool preserves and mitigation banks will make up a larger proportion of the remaining vernal pool landscape, and their success at achieving conservation goals will depend on efficient and cost effective management. Establishing management priorities among competing management needs, and developing effective strategies for bullfrogs in vernal pool preserves will be easier once we understand whether bullfrogs are simply an aesthetic nuisance, or a serious threat to native vernal pool species. Determining this will require field manipulations and analyses of natural experiments that could shed light on whether or not bullfrogs are likely to influence vernal pool community dynamics.

ACKNOWLEDGMENTS

We gratefully acknowledge Michael Westphal's encouragement and assistance in the field and laboratory aspects of this study, including the pilot study, 1997. We also thank Brad Shaffer for reviewing an earlier draft of this paper and offering suggestions that improved the finished product.

LITERATURE CITED

Beringer, J. And T. R. Johnson. 1995. Natural history notes: Rana catesbeiana (Bullfrog). Diet. Herpetol. Rev. 26(2):98.

Bury, R. B. and R. A. Luckenbach. 1976. Introduced amphibians and reptiles in California. Biol. Conserv. 1:1-14.

Bury, R. B. and J. A. Whelan. 1984. Ecology and management of the bullfrog. U. S. Dept. of Interior, Fish and Wildlife Serv., Resour. Publ. (155):1-23.

California Department of Fish and Game. 1988. California's Wildlife. Vol. I, Amphibians and Reptiles. Zeiner, D. C., W. F. Laudenslayer, Jr., K. E. Mayr, and M. White, eds. California Department of Fish and Game, Sacramento, 272 p.

Clarkson, R. W. and J. C. deVos. 1986. The bullfrog, Rana catesbeiana Shaw, in the lower Colorado River, Arizona-California. J. Herpetol. 20(1):42-49.

Cohen M. W. and W. E. Howard. 1958. Bullfrog food and growth at the San Joaquin Experimental Range, California. Copeia 1958(2):223-225.

Dickerson, M. C. 1931. The frog book. Doubleday, Page and Company, Inc., Garden City, N.Y. 253 p.

Hammerson, G. A. 1982. Amphibians and Reptiles in Colorado. Colorado Div. Wildl. Publ. DOW-M-I-2782. vii + 131 p.

Hayes, M. P. and M. R. Jennings. 1986. Decline of ranid frog species in western North America: are bullfrogs (*Rana catesbeiana*) responsible? J. Herpetol. 20(4):490-509.

Hayes, M. P. And J. Warner. 1985. *Rana catesbeiana* (bullfrog). Food. Herpetol. Rev. 16:109.

Holland, R. F. 1998. No net loss? Changes in Great Valley vernal pool distribution from 1989 to 1997.California Department of Fish and Game, Natural Heritage Division, June 1998.

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

Frost, S. W. 1935. 1935. The food of *Rana catesbeiana* Shaw. Copeia 1935(1):15-18.

Jennings, M. R. and M. P. Hayes. 1985. Pre-1900 Overharvest of California red-legged frogs (*Rana aurora draytonii*): the inducement for bullfrog *(Rana catesbeiana)* introduction. Herpetologica 41(1):94-103.

Korschegen, L. J. and T. S. Baskett. 1963. Foods of impoundment and stream-dwelling bullfrogs in Missouri. Herpetologica 19(2):89-99.

Korschegen, L. J. and D. L. Moyle. 1955. Food habits of the bullfrogs in central Missouri farm ponds. Herpetologica 19(2):89-99.

Morey, S. R. and D. A. Guinn. 1992. Activity patterns, food habits, and changing abundance in a community of vernal pool amphibians. *In* Williams, D. F., S. Byrne, and T. A. Rado, eds. Endangered and sensitive species of the San Joaquin Valley, California. California Energy Commission. *xv* + 388 p.

Moyle, P. B. 1973. Effects of introduced bullfrogs, *Rana catesbeiana*, on native frogs of the San Joaquin Valley, California. Copeia 1973(1):18-22.

Rosen, P. C. and C. R. Schwalbe. 1988. Status of the Mexican and narrow-headed garter snakes (*Thamnophis eques* and *Thamnophis rufipunctatus*) in Arizona. Arizona Game and Fish Dept., Unpubl. Rep. Submitted to U. S. Fish and Wildlife Service, Albuquerque, New Mexico. 69 p.

Schwalbe, C. R. And P. C. Rosen. 1988. Preliminary report on effect of bullfrogs on wetland herpetofaunas in southeastern Arizona, p. 166-173. *In* R. C. Szaro, K. E. Severson, and D. R. Patton (ed.), Management of amphibians, reptiles, and small mammals in North America. USDA Forest Service, Rocky Mountain Forest Range Exp. Sta., Gen, Tech. Rept. RM-166, Fort Collins, Colorado. 458 p.

United States Fish and Wildlife Service. 1994a. Endangered and threatened wildlife and plants; determination of endangered status for the arroyo southwestern toad. Federal Register 59 (241):64859-64866.

United States Fish and Wildlife Service. 1994b. Endangered and threatened wildlife and plants; determination of endangered status for the Conservancy fairy shrimp, longhorn fairy shrimp, and vernal pool tadpole shrimp; and threatened status for the vernal pool fairy shrimp. Federal Register 59 (180):48136-48153.

United States Fish and Wildlife Service. 1996. Endangered and threatened wildlife and plants; determination of endangered status for the California red-legged frog. Federal Register 61(101):25813-25833.

Zar, J. H. 1984. Biostatistical Analysis. Prentice Hall, Englewood Cliffs, New Jersey. *xiv* + 718 p.