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Author(s): David G. Cook and Mark R. Jennings

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MICROHABITAT USE OF THE CALIFORNIA RED-LEGGED FROG AND INTRODUCED BULLFROG IN A SEASONAL MARSH

DAVID G. COOK^{1,3,4} AND MARK R. JENNINGS²

¹Sonoma State University, Department of Biology, 1801 E. Cotati Avenue, Rohnert Park, CA 94928, USA

²Rana Resources, P.O. Box 2185, Davis, CA 95617, and Research Associate, Department of Herpetology, California Academy of Sciences, 875 Howard Street, San Francisco, CA 94103, USA

ABSTRACT: We quantified frog phenology and microhabitat use of the native California red-legged frog (*Rana draytonii*) and introduced bullfrog (*Rana catesbeiana*) in an 11-ha seasonal marsh, Sonoma County, California. Logistic regression showed that both species selected habitats nonrandomly from among the available habitats in the marsh. As adults, the two species overlapped in their habitat use, selecting dead spikerush in winter and spring, and aquatic buttercup in summer. Although the model emphasized overlap in frog habitats, there was more separation in habitat use between species during winter than other seasons when few bullfrogs were active (i.e., most bullfrogs hibernating). The egg-laying habitats and seasons differed dramatically between the two species. Red-legged frogs bred in winter almost exclusively in shallow dead spikerush and bullfrogs in spring and summer in deeper areas with dense cover, predominantly smartweed. Breeding periods of red-legged frogs and bullfrogs were separated by 10 wk, which coincided with peak adult abundances. We suggest that the separate reproductive seasons may reduce competition and predation by bullfrogs on red-legged frogs, allowing for coexistence. Furthermore, the marsh's late-season drying limits metamorphosis of bullfrog tadpoles, which usually require permanent water. The marsh's seasonal hydrologic pattern offers a model for habitat in which the native red-legged frog may persist despite negative interactions with the introduced bullfrog.

Key words: Anuran; Breeding; Endangered species; Introduced species; *Rana catesbeiana*; *Rana draytonii*; Seasonality

Loss of diversity or abundance of native species after the establishment of an exotic species has been well documented in the scientific literature (see review in Kats and Ferrer, 2003). However, anthropogenic changes to habitats, which may favor exotic species, may themselves have adverse effects on native species, confounding the ability to determine the separate effects of exotic species on native organisms (Adams, 1999). Because of their restricted habitat requirements, pond-breeding amphibians are particularly affected by exotic species and habitat modifications. Virtually all true frogs (Family Ranidae) and toads (Family Bufonidae) native to western North America have experienced range reductions and population declines in recent times (Davidson et al., 2002; Jennings and Hayes, 1988; Jennings and Hayes, 1994; Stebbins, 2003; Stebbins and Cohen, 1995). A 70 to 75% decline in the range of the California red-legged frog (*Rana draytonii*), primarily due to habitat loss and the in-

roduction of exotic species, including the bullfrog (*Rana catesbeiana*), has resulted in the listing of this species as threatened under the federal Endangered Species Act (Miller et al., 1996).

The bullfrog, a native of the midwestern and eastern United States, was first introduced into California in 1896 (Jennings and Hayes, 1985) and has long been implicated as a competitor of and predator on native western ranids (Kiesecker and Blaustein, 1997; Kupferberg, 1997; Licht, 1974; Moyle, 1973; Nussbaum et al., 1983). Hayes and Jennings (1986) discussed the long-held hypothesis that bullfrogs are the major cause of decline of Ranid frog populations. They pointed out that habitat modifications, such as changes in hydrology from seasonal to permanent water, removal of emergent vegetative cover, and elevation of water temperatures from increased solar radiation all favor the establishment of bullfrogs. Because of this, the separate effects of bullfrog presence and habitat modification are difficult to separate. They also suggested that widespread introduction of exotic fishes in California after 1870 may be at least as important as the

³ PRESENT ADDRESS: 3003 Magowan Drive, Santa Rosa, CA 95405.

⁴ CORRESPONDENCE: e-mail, dcook@scwa.ca.gov

introduction of the bullfrog in the decline of native frogs. They additionally indicated that the high frog densities and resource limits necessary for direct competition between bullfrogs and native frogs may rarely occur, and that it would be difficult to demonstrate that bullfrog predation is a significant factor in regional native frog declines. Their analysis leads to the prediction that bullfrogs and red-legged frogs should be able to coexist in complex marsh environments that are free of other environmental stressors such as exotic fishes.

More recent studies provide both support for and evidence against the hypothesis that introduced bullfrogs are responsible for the decline of native frogs. Laboratory studies indicate that bullfrogs by themselves can affect native frog tadpole development and survival (Kiesecker and Blaustein, 1997; Kupferberg, 1997) and have a stronger effect than exotic fish (Kiesecker and Blaustein, 1998; Lawler et al., 1999). In contrast, other studies indicate that exotic fish may have a stronger predatory effect than bullfrogs (Adams, 1999, 2000). The dominance of bullfrogs over natives may be attributed to the co-introduction of exotic fishes that coevolved with the bullfrog, facilitating its invasion (Adams et al., 2003). However, Rosen and Schwalbe (2002) indicated that the removal of some nonnative fishes may increase the bullfrog population. Also, negative effects of bullfrogs may be increased by habitat modifications (Kiesecker et al., 2001; Rosen and Schwalbe, 2002), although this pattern was not found in field studies by Adams et al., (2003). Clearly, a better understanding of interactions between introduced bullfrogs and native frogs is critical for conservation efforts.

We conducted a study on the native red-legged frog and introduced bullfrog in a fish-free, structurally complex marsh not altered in ways that give obvious advantages to the bullfrog. Specifically, we determined (1) the phenology and seasonal abundance of both species, and (2) habitat use patterns in relation to habitat availability and to species-specific habitat preferences. Our goal was to determine if certain habitat or temporal factors would be conducive to coexistence, or whether the species overlap so much that compet-

itive or predatory relationships between them are likely.

MATERIALS AND METHODS

Study Site

Our study was conducted at Ledson Marsh, a seasonal wetland encompassing approximately 11 ha when full, located in Annadel State Park, Sonoma County, California. The marsh is situated on a hilly plateau surrounded by native grassland, oak (*Quercus* spp.) woodland, and Douglas-fir (*Pseudotsuga menziesii*) forest at an elevation of 476 m. It was created in 1930 by a small earthen and rock dam in the shallow outlet of what was probably a large vernal pool and surrounding wet meadow (Cook, 1997). The bottom of this eutrophic marsh was covered with detritus and marsh plants. Maximum water depth was approximately 150 cm.

Field Surveys

Because the habitat features of the marsh varied markedly throughout the year, we sampled frog populations and habitat periodically to capture such change from June 1995 to March 1997. We recorded frogs, egg masses, and habitat conditions in the marsh at 1–4 wk intervals. Fieldwork ended each fall when the marsh was entirely dry and resumed with the first heavy winter rains (Fig. 1). We conducted nocturnal frog surveys by wading through the marsh or by poling an inflatable boat. Frogs were captured by hand and identified to species, sexed, measured for snout–vent length and released at the point of capture. Each survey covered the entire marsh except for the impenetrable stands of California bulrush (*Scirpus californicus*). We sampled the edges of the bulrush stands. Our preliminary visual searches in these stands found no frogs. Although frogs may use the centers of bulrush stands for escape and hibernation, our experience at the marsh indicates that active frogs of both species use the edges of these stands, not interior regions. We conducted daytime surveys for egg masses for both frog species. Each egg mass was flagged and numbered to avoid duplicate counting.

In 1996, we established 34 permanent points to determine the seasonal conditions

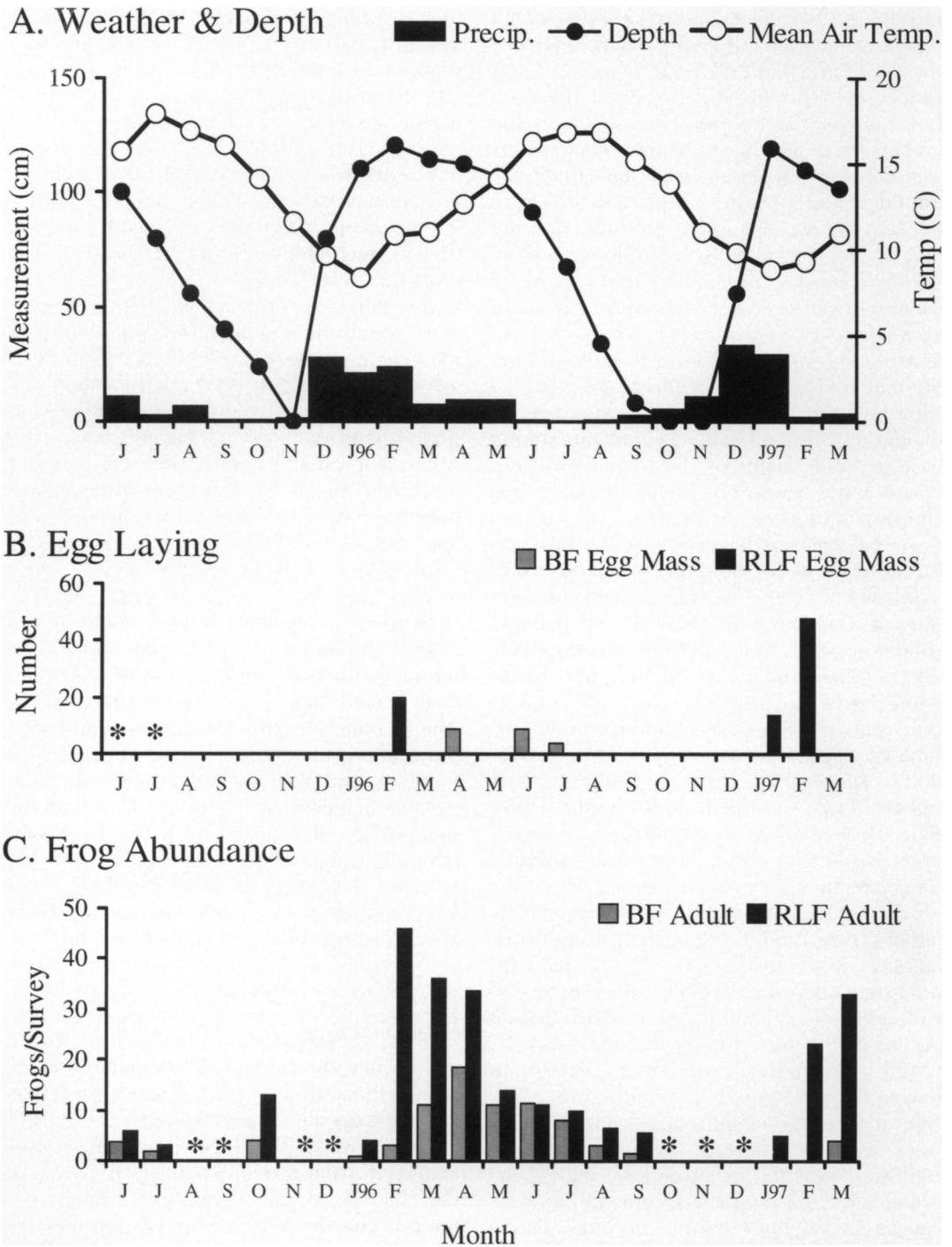


FIG. 1.—Seasonal abundance and phenology of red-legged frogs and bullfrogs at Ledson Marsh, 1995–1997. Descriptions of panels are as follows: A. average monthly weather conditions and average maximum depths of the marsh, B. egg masses deposited by frog species, and C. frog abundances based on frog observations. Asterisk (*) indicates no surveys conducted due to dry conditions and/or low frog activity. No egg mass surveys were conducted during June and July 1995.

present at the marsh using a randomized design for sampling ponds similar to Shaffer et al., (1994). We located points along randomly located transects. First, we established a baseline transect along one shoreline of the triangle-shaped marsh. We then divided this baseline into 40-m sections and randomly extended a sampling transect across the entire marsh perpendicular to the baseline. To avoid bias in sample locations, two random distances between 1 m and 40 m were used as x and y coordinates to select the first point location in each transect. We then placed points at 40-m intervals along each random transect across the marsh. The 40-m interval procedure was used instead of depth zones described in Shaffer et al., (1994) due to the hummocky bottom of the marsh. Point locations were permanently marked with numbered stakes and data were taken monthly.

We collected data on microhabitat variables for each site where egg masses were observed, frogs were captured or observed, and at the permanent points. Data represented the conditions at or just below the water surface. The study feature (i.e., marsh permanent point, frog, egg mass) was the center of a 1-m-radius sample plot. Variables included a visual estimate of percent cover of vegetation by species, percent cover of other habitat features (e.g., open water), and water depth. Plots with no water, regardless of actual vegetative cover, were recorded as "dry" microhabitat.

We deployed HOBO® temperature data loggers to record temperatures at frog breeding sites. We collected data during the 1996 bullfrog spring and summer breeding period and the 1997 red-legged frog winter breeding period. The devices recorded temperatures at hourly intervals and were suspended 15 cm below the water surface in sites with solar exposure. Daily temperature averages were used for data analysis. We obtained precipitation and air temperature data from a permanent California Department of Water Resources weather station located 12 km away.

Statistical Analyses

For statistical analysis we grouped 1996 data into three seasons: (1) winter red-legged

frog breeding: 17 January to 25 March; (2) spring early bullfrog breeding: 26 March to 9 June; and (3) summer late bullfrog breeding: 10 June to 14 August. During fall of 1996, the marsh was either dry or contained very low water levels from early rains and contained too few active frogs to permit statistical analysis. Within each season, we averaged values for the marsh permanent points, and included data on each egg mass and all observed frog locations.

We compared habitat use of frog species and habitats present in the marsh, based on permanent points. Using JMP IN™ statistical software (version 5.0; SAS Institute Inc.), we performed ordinal logistic regression for each season with a pair of plot types as the dependent variable and habitat values measured on plots as a set of independent variables. We excluded "dry" habitat and open water from the model because frogs were never observed in dry areas of the marsh, and open water is essentially the absence of vegetative cover. Within the ordinal dependent variable, we coded one set of plots (for example "red-legged frog plots") as "1" and the other set (for example "marsh plots") as "0." The model assumes no distribution for values in the independent variables and evaluates the effect of each variable independent of others. We tested for significance of effects using the likelihood ratio Chi-square test with a significance level of $P \leq 0.05$. To compare breeding water temperatures between species we used the nonparametric Wilcoxon signed-rank test.

RESULTS

Seasonal Frog Abundance and Phenology

Seasonal climatic conditions largely separated high activity periods of red-legged frogs and bullfrogs although there was considerable overlap (Fig. 1). Red-legged frogs were most abundant from February to April following the coldest month of January. This time period coincides with the winter rainy season when the marsh is full. The highest abundance of red-legged frogs was during February 1996 at 46.0 frogs/survey when the average monthly air temperature was 10.8 C. During 1997, March had the highest red-legged frog

abundance at 33.0 frogs/survey and similar temperature of 10.9 C. Bullfrogs were primarily active from April through July 1996 when little or no rain occurred. July was the hottest month of the year at 16.8 C. Bullfrog abundance was highest in April at 18.5 frogs/survey at a temperature of 12.6 C. Relatively high abundances of both red-legged frogs and bullfrogs overlapped during March and April, 1996.

The observed numbers of both frog species declined continuously from spring through fall 1996 as the marsh dried out (Fig. 1). This decline indicates that the frogs did not merely congregate in the remaining wetted area as seasons changed, but that some of them moved to different areas. Many could have taken cover in moist portions of the marsh with thick bulrush stands or moved away into the surrounding uplands (M. Foster, personal communication).

Although there was substantial overlap in the activity patterns of red-legged frogs and bullfrogs, their breeding periods were separated by about 10 wk, and their breeding durations differed. Breeding periods of both species coincided with their respective peak adult activity (Fig. 1). Red-legged frog egg masses were deposited in relatively short periods of 2 wk starting around 1 February 1996 when 20 egg masses were deposited and beginning around 17 January 1997 with 62 egg masses. The prolonged breeding period of bullfrogs occurred for about 13 wk from 27 April through 24 July 1996, when 22 egg masses were deposited. Daily water temperatures at breeding sites were significantly warmer during the spring-summer bullfrog breeding period than the winter red-legged frog breeding period (Wilcoxon signed-rank test, $\bar{x}_{RLF} = 10.3$ C, $n = 15$; $\bar{x}_{BF} = 18.3$ C, $n = 71$; $P < 0.001$). Water temperatures varied as much as 5.0 C during red-legged frog breeding (range: 7.7 C to 13.7 C) and 11.2 C during bullfrog breeding (range: 14.4 C to 25.6 C).

Patterns of Microhabitat Use

A description of seasonal changes in the marsh helps in understanding the attributes of Ledson Marsh that might affect bullfrog and red-legged frog interactions. Seasonal changes in habitat at the marsh are illustrated in

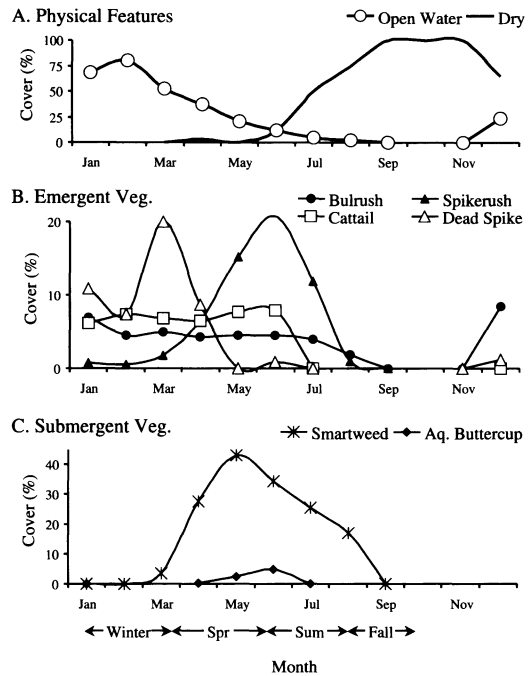


FIG. 2.—Dominant habitat types at Ledson Marsh during 1996. Values represent habitats present in the marsh from permanent points. Seasons are related to frog breeding periods as defined in the Methods section.

Fig. 2. The Mediterranean climate of the region imposes a drought from June through October during which time the marsh dries gradually (Fig. 1A). Rains in late November through January fill the marsh to its maximum depth, but cold temperatures prevail and limit the growth of vegetation. From mid-January through February, much of the deeper marsh area is open water while in shallow areas dead stalks of spikerush (*Eleocharis macrostachya*) and broad-leaved cattail (*Typha latifolia*) are abundant. Large, thick stands of bulrush occur in some deeper water areas and remain green year round. From March through September, the water surface becomes covered with spikerush in shallow margins and floating stems and leaves of such plants as smartweed (*Polygonum hydropiperoides*) and aquatic buttercup (*Ranunculus lobbii*) in deeper areas. Mats of filamentous algae also occur. From September through early November, the marsh typically dries completely (i.e., no surface water and soils are cracked from dehydration), and many marsh plants die

back. During fall, most of the remaining water was located in small, shallow depressions in the marsh. Frog activity during this season was very low, no breeding occurred, and both frog species (in low numbers) were observed in the remaining wet habitats.

Seasonal patterns of frog habitat use and habitats present in the marsh are shown in Fig. 3. The logistic regression model indicated significant differences between habitats utilized by frog species and marsh habitats, indicating a significant preference for certain habitats (Table 1). Both frog species selectively used dead spikerush areas in winter and spring, even though this plant cover in the marsh decreased by two-thirds from winter to spring. During summer, both frog species preferred aquatic buttercup, and this plant cover was rare in the marsh. We found each frog species at similar water depths throughout the year, although the marsh depth changed seasonally (Fig. 4). The average depth of the marsh in winter was 62.9 cm and receded to 23.7 cm in summer. Red-legged frog depths ranged from 36.9 cm to 41.3 cm and bullfrogs ranged from 37.7 cm to 54.8 cm.

The logistic regression model tended to emphasize the similarities of habitat use when comparing red-legged frogs and bullfrogs, but significant differences of a few variables did occur (Table 1). There was more separation in habitat use between frog species during winter than other seasons; however, active bullfrogs were few in number (Fig. 3A). During spring, there were no significant differences in vegetative cover utilized by the two frog species, but bullfrogs preferred deeper water and red-legged frogs shallower water, suggesting that, when vegetative cover is abundant, depth is a better group predictor than vegetation type as to where each species is most likely to be found. During summer, spikerush was the only variable found to be significantly different between frog species, although the spikerush variable was small in absolute value with <5% average cover for both frog species (Fig. 3C).

Habitat differences of frog species were more apparent for egg masses than for adults. Red-legged frog egg masses occurred almost exclusively in dead spikerush, which occurs in shallow water (Table 1; Fig. 3). The logistic

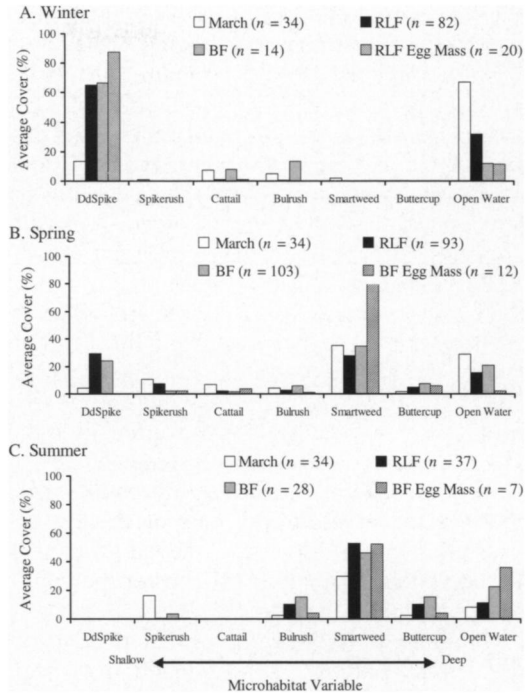


FIG. 3.—Microhabitat cover variables during three seasons in 1996, Ledson Marsh. Microhabitat data are from 1-m-radius plots centered on observations of frogs, egg masses, and marsh permanent points. The arrow indicates the typical relation of plant species and hydrologic gradient. Sample sizes (n) are shown in parentheses. “Dry” variable that indicates dry portions of the marsh is not shown. Microhabitat data for three bullfrog egg masses was not recorded.

regression was undefined for water depth in the multivariate model due to the dominance of dead spikerush. However, winter water depth at the marsh was nearly twice as deep as at red-legged frog egg masses (Fig. 4). Bullfrog egg masses were found in deep areas with dense cover, predominantly smartweed (Table 1; Figs. 3, 4).

DISCUSSION

In his review of resource partitioning in animals, Schoener (1974) cited many examples in which coexistence occurs, presumably due ultimately to evolutionary co-adaptation of closely related species to one another. Toft (1985) pointed out that Schoener and other earlier authors had focused exclusively on competition as a causal factor in resource partitioning, but other factors, particularly

TABLE 1.—Summary of logistic regression examining the microhabitat effects of red-legged frog, bullfrog, and habitat present at Ledson Marsh for three seasons. Covariates with significant values ($P \leq 0.05$), shown in bold type, during at least one season are included in the table. For winter RLF egg mass, depth was undefined due to the strong effect of dead spikerush. The likelihood ratio Chi-square statistic (χ^2), probability of significance (P), and sign relationship (“–” or “+”) are shown in columns for each season. A positive sign indicates that larger values of covariates are associated with the part of the dependent variable coded as “1” and a negative sign that larger values of covariates are associated with the part of the dependent variable coded as “0”. Values of n are shown in Fig. 3.

Dependent variable	Covariate	Winter			Spring			Summer		
		Sign	χ^2	P	Sign	χ^2	P	Sign	χ^2	P
RLF (1) and Marsh (0)	Bulrush	–	1.29	0.26	+	0.78	0.38	+	9.25	<0.01
	Buttercup				+	3.68	0.06	+	8.02	<0.01
	Dd. Spikerush	+	7.78	0.01	+	10.02	<0.01			
	Depth	–	4.54	0.03	–	11.55	<0.01	–	0.08	0.78
BF (1) and Marsh (0)	Bulrush	+	16.56	<0.01	+	1.49	0.22	+	2.14	0.14
	Buttercup				+	7.20	0.01	+	9.20	<0.01
	Cattail	+	7.03	0.01	–	0.50	0.48			
	Spikerush				–	8.35	<0.01	–	1.10	0.29
RLF Eggs (1) and Marsh (0)	Dd. Spikerush	+	69.09	<0.01						
	Depth	–	–	–						
BF Eggs (1) and Marsh (0)	Buttercup				+	4.17	0.04	–	0.75	0.39
	Smartweed				+	15.94	<0.01	–	2.13	0.14
	Depth				–	0.45	0.50	+	9.91	<0.01
RLF (1) and BF (0)	Bulrush	–	22.39	<0.01	–	0.13	0.72	+	0.19	0.67
	Cattail	–	15.43	<0.01	+	0.01	0.92			
	Spikerush				+	1.14	0.29	–	3.87	0.05
	Dd. Spikerush	–	8.18	<0.01	–	1.75	0.19			
	Depth	+	0.11	0.74	–	20.88	<0.01	–	1.61	0.20

predation and the independent adaptation of species to physiological constraints, also play a role. Both Toft and Schoener view resource partitioning as an evolutionary phenomenon.

For exotic and native species pairs, such as bullfrogs and red-legged frogs, significant evolutionary adaptations have not had time to occur (but see the discussion by Kiesecker and Blaustein, 1997). Instead, niche partitioning should be viewed as the product of independent adaptations to past conditions. Coexistence then would be fortuitous, and doubly so when it occurs under circumstances influenced by human-modified habitats such as at Ledson Marsh over the past 70+ years.

In our study, we noted both frog species utilizing similar habitats during the winter; however, overlap was effectively minimal because adult red-legged frog observations were highest in February and March when bullfrogs were just emerging from hibernation and therefore found in low numbers. During the spring and summer (the peak of bullfrog

breeding activity), our logistic regression showed a significant interspecific difference in water depth use and an overlap in vegetative cover habitat use. Overlap in microhabitat use was especially broad in summer, a time when both species are actively foraging for prey.

Hayes and Jennings (1988) reviewed habitat characteristics of red-legged frog populations in the Central Valley of California and indicated that bulrushes (*Scirpus* spp.) were an important habitat correlate. In our study, a contrary pattern was observed (Table 1), but only during the winter and spring. However, bulrushes may be an indicator of other important conditions that are within tolerable limits for the red-legged frog. For example, conditions that allow for the survival of bulrushes may be a good indicator of the duration of ponded water required for tadpole metamorphosis (i.e., water present into summer). Aquatic habitat with “water at least 0.7 m deep” has been identified as an

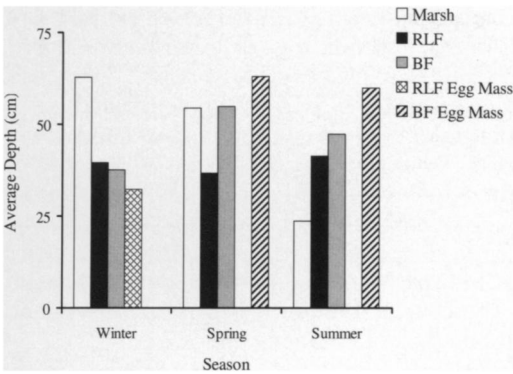


FIG. 4.—Water depths for frog species and the marsh during three seasons in 1996, Ledson Marsh. Microhabitat data are from 1-m-radius plots centered on observations of frogs, egg masses, and marsh permanent points. Values of n for groups are provided in Fig. 3.

important habitat characteristic of the red-legged frog (Hayes and Jennings, 1988). During winter and spring of 1996, bulrush in our study was associated with average water depths of 76.5 and 69.1 cm, respectively. Our study suggests that a 70 cm water depth is a habitat correlate for California bulrush and not necessarily red-legged frogs, as the latter prefers depths of about 40 cm in Ledson Marsh.

Both adult red-legged frogs and bullfrogs are gape-limited predators observed to prey on a variety of species, including other anurans (Bury and Whelan, 1984; Hayes and Tennent, 1985; Govindarajulu et al., 2006; Wu et al., 2005), and bullfrogs are known to structure amphibian assemblages (Hecnar and M'Closkey, 1997). Bullfrogs have also been documented consuming red-legged frogs at the tadpole, metamorph, and adult life stages (Cook, 2002; Cook and Jennings, 2001; D. G. Cook, unpublished data). The pattern of adult activity periods of both frog species at Ledson Marsh coupled with microhabitat overlap suggests that predation pressure on red-legged frogs by bullfrogs is probably highest during summer. The effect of bullfrog predation on the red-legged frog depends on the sizes of the individuals involved in the interaction. The much larger body size of the bullfrog suggests it could have a significant impact, especially if it were to become numerically superior (Pearl et al., 2004).

Whether or not such bullfrog predation will contribute to local extinction of the red-legged frog likely depends, in part, on the numerical abundance achieved by the bullfrog.

The manner in which red-legged frogs deposit eggs at Ledson Marsh differs substantially from that described by Hayes and Miyamoto (1984), and this difference may have functional significance. Frogs that they observed in San Luis Obispo and Santa Barbara counties, California, laid egg masses at the surface of the water attached to emergent vegetation. We found the vast majority of masses to be unattached or to be loosely attached to dead spikerush, which lies as a floating mass of dead stems at the water surface. Masses laid in this fashion will still remain at the water surface if the water level recedes, as it may often do between storms in winter. Masses attached to rigid upright supports, by contrast, will be exposed and embryos subject to desiccation. We observed desiccation for one egg mass in 1996 attached to a dead cattail stock. It is possible that frogs choose more rigid attachment sites in lotic environments, where loss of eggs due to flood currents is possible, but that they prefer floating attachments in lentic habitats.

Rates of embryonic development for 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 M. R. Jennings and M. P. Hayes (unpublished data) indicated that for eggs it is at least 23 C. The northern red-legged frog (*Rana aurora*) occurs at higher latitudes with cooler climate than *R. draytonii* and has a critical thermal maximum of 21 C (Licht, 1971). In contrast, bullfrog embryos have the highest critical thermal maximum of any North American frog at 32 C and the lower temperature limit for normal embryonic development is 15 C (Moore, 1942).

The thermal limitations of red-legged frogs and bullfrogs reflect and reinforce a separation of breeding periods. Red-legged frogs breed in the winter when temperatures are cool, whereas bullfrog breeding is restricted to warmer periods during spring and summer. In this part of its range, red-legged frog

breeding typically occurs during January and February. We observed bullfrog oviposition from late April through July when surface water temperatures ranged from 14.4 C to 25.6 C, suggesting that bullfrogs began breeding only when water temperatures reached their minimum thermal limit of 15 C for a sustained period of time in the spring. Thermal limits are similar for bullfrogs in their native (Moore, 1942) and introduced ranges (Govindarajulu et al., 2006), suggesting that geographic variation in thermal limits is not present in the species.

Competitive effects of tadpoles between red-legged frogs and bullfrogs, although potentially potent (Kiesecker and Blaustein, 1997; Kupferberg, 1997), are likely minimal in Ledson Marsh's eutrophic seasonal system. The thermal intolerance of eggs separates the breeding periods of both frog species by at least 2.5 mo and red-legged frog tadpoles began metamorphosis in mid-July (D. G. Cook, unpublished data) when bullfrogs were still breeding. Observations of bullfrog tadpoles in the marsh indicate that unless eggs are laid early in April and there is an exceptionally long growing season, no or very few metamorphs will occur until after a second season of larval growth (Cook, 1997). This prolonged growing period is generally unlikely because Ledson Marsh normally dries by either the late summer or early fall. Thus, although Kiesecker and Blaustein (1997) and Kiesecker et al., (2001) found significant competitive, and possibly predatory impacts of large, overwintering bullfrog tadpoles on young *R. aurora* tadpoles, this circumstance is prevented at Ledson Marsh by the seasonal drying of the aquatic habitat. The extent to which the seasonal drying of Ledson Marsh prevents maximal reproductive success and controls the population density in bullfrogs at this location remains to be evaluated. However, bullfrogs have been present in this localized part of Sonoma County since the 1920's (Storer, 1922) and presumably colonized Ledson Marsh soon after it was created during 1930.

The maximum density of tadpoles of red-legged frogs and bullfrogs at Ledson Marsh, based on estimates of the number of eggs laid for each species (Cook, 1997), would be on

the order of 2/m² for the red-legged frog and 4/m² for the bullfrog. In experimental environments, Werner and Anholt (1996) and Kiesecker et al., (2001) demonstrated competition between bullfrog tadpoles and green frog (*Rana clamatans*) tadpoles at densities of 22 tadpoles/m² and between bullfrog tadpoles and *R. aurora* at 9 tadpoles/m², respectively. With even modest early mortality of tadpoles at Ledson Marsh, competitive densities would not occur at Ledson Marsh as demonstrated by these experimental studies.

In summary, we suggest that Ledson Marsh's aquatic seasonality apparently restricts the competitive advantage of bullfrog reproduction, and thus restricts the overall bullfrog population size and the predatory impact of bullfrogs found in this ecosystem. This seasonal hydrologic pattern and associated frog fauna has probably been present for at least 70 yr and offers a model for habitat management in which the native red-legged frog may persist despite negative interactions with the introduced bullfrog. If so, management and habitat preservation programs favoring the regional natural hydrologic regime may offer a successful venue for native ranid frog conservation.

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LITERATURE CITED

- ADAMS, M. J. 1999. Correlated factors in amphibian decline: Exotic species and habitat change in western Washington. *Journal of Wildlife Management* 63: 1162–1171.
- ADAMS, M. J. 2000. Pond permanence and the effects of exotic vertebrates on anurans. *Ecological Applications* 10:559–568.
- ADAMS, M. J., C. A. PEARL, AND R. B. BURY. 2003. Indirect facilitation of an anuran invasion by non-native fishes. *Ecological Letters* 6:343–351.
- 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.
- COOK, D. G. 1997. Microhabitat Use and Reproductive Success of the California Red-legged Frog (*Rana*

- aurora draytonii*) and Bullfrog (*Rana catesbeiana*) in an Ephemeral Marsh. Master's Thesis, Sonoma State University, Rohnert Park, California, U.S.A.
- COOK, D. G. 2002. *Rana aurora draytonii* (California red-legged frog). Predation. *Herpetological Review* 33:303.
- COOK, D. G., AND M. R. JENNINGS. 2001. *Rana aurora draytonii* (California red-legged frog). Predation. *Herpetological Review* 32:182–183.
- DAVIDSON, C., H. B. SHAFFER, AND M. R. JENNINGS. 2002. Spatial tests of the pesticide drift, habitat destruction, UV-B, and climate-change, hypotheses for California amphibian declines. *Conservation Biology* 16: 1588–1601.
- GOVINDARAJULU, P., W. S. PRICE, AND B. R. ANHOLT. 2006. Introduced bullfrogs (*Rana catesbeiana*) in western Canada: Has their ecology diverged? *Journal of Herpetology* 40:249–260.
- HAYES, M. P., AND M. R. JENNINGS. 1986. Decline of ranid frog species in western North America: Are bullfrogs (*Rana catesbeiana*) responsible? *Journal of Herpetology* 20:490–509.
- 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 boylei*): Implications for management. Pp. 144–158. In R. Szaro (Ed.), *Proceedings of the Symposium, Management of Amphibians, Reptiles, and Small Mammals in North America*. U.S.D.A. Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report (RM-166).
- 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 M. R. TENNENT. 1985. Diet and feeding behavior of the California red-legged frog, *Rana aurora draytonii* (Ranidae). *The Southwestern Naturalist* 30:601–605.
- HECNAR, S. J., AND R. T. M'CLOSKEY. 1997. Changes in the composition of a ranid frog community following bullfrog extinction. *The American Midland Naturalist* 137:145–150.
- JENNINGS, M. R., AND M. P. HAYES. 1985. Pre-1900 overharvest of California red-legged frog (*Rana aurora draytonii*): The inducement for bullfrog (*Rana catesbeiana*) introduction. *Herpetologica* 41:94–103.
- JENNINGS, M. R., AND M. P. HAYES. 1988. Natural history and decline of native Ranids in California. Pp. 61–72. In H. F. De Lisle, P. B. Brown, B. Kaufman, and B. M. McCurty (Eds.), *Conference on California Herpetology*. Southwestern Herpetologists Society, Special Publication (4). Van Nuys, California, U.S.A.
- JENNINGS, M. R., AND M. P. HAYES. 1994. Amphibian and Reptile Species of Special Concern in California. California Department of Fish and Game, Inland Fisheries Division, Rancho Cordova, California, U.S.A.
- KATS, L. B., AND R. P. FERRER. 2003. Alien predators and amphibian declines: Review of two decades of science and the transition to conservation. *Diversity and Distributions* 9:99–110.
- KIESECKER, J. M., AND A. R. BLAUSTEIN. 1997. Population differences in responses of red-legged frogs (*Rana aurora*) to introduced bullfrogs. *Ecology* 78:1752–1760.
- KIESECKER, J. M., AND A. R. BLAUSTEIN. 1998. Effects of introduced bullfrogs and smallmouth bass on micro-habitat use, growth, and survival of native red-legged frogs (*Rana aurora*). *Conservation Biology* 12:776–787.
- KIESECKER, J. M., A. R. BLAUSTEIN, AND C. L. CHERI. 2001. Potential mechanisms underlying the displacement of naïve red-legged frogs by introduced bullfrogs. *Ecology* 82:1964–1970.
- KUPFERBERG, S. J. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California river: The role of larval competition. *Ecology* 78:1736–1751.
- LAWLER, S. P., D. DRITZ, T. STRANGE, AND M. HOLYOAK. 1999. Effects of introduced mosquitofish and bullfrogs on the threatened California red-legged frog. *Conservation Biology* 13:613–622.
- LICHT, L. E. 1971. Breeding habits and embryonic thermal requirements of the frogs, *Rana aurora aurora* and *Rana pretiosa pretiosa* sympatric the Pacific Northwest. *Ecology* 52:116–124.
- 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.
- 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* 61:25,813–25,833.
- MOORE, J. A. 1942. Embryonic temperature tolerance and rate of development in *Rana catesbeiana*. *Biological Bulletin* 83:375–388.
- MOYLE, P. B. 1973. Effects of introduced bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. *Copeia* 1973:18–22.
- NUSSBAUM, R. A., E. D. BRODIE, JR., AND R. M. STORM. 1983. Amphibians and Reptiles of the Pacific Northwest. University Press of Idaho, Moscow, Idaho, U.S.A.
- PEARL, C. A., M. J. ADAMS, R. B. BURY, AND B. MCCREARY. 2004. Asymmetrical effects of introduced bullfrogs (*Rana catesbeiana*) on native ranid frogs in Oregon. *Copeia* 2004:11–20.
- ROSEN, P. C., AND C. R. SCHWALBE. 2002. Widespread effects of introduced species on reptiles and amphibians in the Sonoran Desert region. Pp. 220–240. In B. Tellman (Ed.), *Invasive Exotic Species in the Sonoran Region*. University of Arizona Press, Tucson, Arizona, U.S.A.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- SHAFFER, H. B., R. A. ALFORD, B. D. WOODWARD, S. J. RICHARDS, R. G. ALTIG, AND C. GASCON. 1994. Quantitative sampling of amphibian larvae. Standard techniques for inventory and monitoring. Pp. 130–141. In W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (Eds.), *Measuring and Monitoring Biological Diversity, Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C., U.S.A.
- STEBBINS, R. C. 2003. *A Field Guide to Western Reptiles and Amphibians*. Third edition. Houghton Mifflin Company, Boston, Massachusetts, U.S.A.
- STEBBINS, R. C., AND N. W. COHEN. 1995. *A Natural History of Amphibians*. Princeton University Press, Princeton, New Jersey, U.S.A.

- STORER, T. I. 1922. The eastern bullfrog in California. *California Fish and Game* 8:219–224.
- TOFT, C. A. 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985:1–21.
- WERNER, E. E., AND B. R. ANHOLT. 1996. Predator-induced behavioral indirect effects: Consequences to competitive interactions in anuran larvae. *Ecology* 77:157–169.
- WU, Z., Y. LI, Y. WANG, AND M. J. ADAMS. 2005. Diet in introduced bullfrogs (*Rana catesbeiana*): Predation on and diet overlap with native frogs on Daishan Island, China. *Journal of Herpetology* 39:668–674.

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