SEASONAL SPATIAL PATTERNS OF TWO SYMPATRIC FROGS: CALIFORNIA RED-LEGGED FROG AND AMERICAN BULLFROG

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Abstract.—The introduced American Bullfrog (*Lithobates catesbeianus*) has been implicated in the decline of native amphibians. Bullfrogs have become widespread in California and are a threat to the native California Red-legged Frog (*Rana draytonii*). The two species are ecologically similar, and the bullfrog is a predator to the red-legged frog that may influence its habitat use patterns. We analyzed the spatial and temporal locations and body sizes of both frog species within a large, fishless seasonal marsh during 1996. Overall, California Red-legged frogs and American Bullfrogs showed similar spatial distributions; however, seasonal changes were observed. California Red-legged Frogs increased their mean distances between conspecifics in the marsh seasonally from winter through summer while frog numbers decreased. In contrast, bullfrogs showed the opposite pattern where mean distances between conspecifics decreased over time, but the abundance of bullfrogs increased from winter through summer. During each season the mean distances between red-legged frogs and bullfrogs was greater compared to distances to their respective conspecifics, except for spring when bullfrog conspecifics were slightly more distant than red-legged to bullfrog distances. American Bullfrogs were significantly larger than California Red-legged Frogs at our site. Our findings suggest that frog abundance, which is strongly influenced by breeding behavior, changing habitats, and possibly predation risk of red-legged frogs by bullfrogs are the dominant factors driving the spatial patterns observation at Ledson Marsh. Also, once winter breeding was completed, California Red-legged Frogs seemed to avoid predation by American Bullfrogs by spatial separation within the marsh or by leaving the marsh altogether.

Key Words.—amphibians; distribution; *Lithobates catesbeianus*; predator avoidance; *Rana draytonii*; size

INTRODUCTION

Unlike most birds and reptiles, ecologically similar species of amphibians have been found to overlap spatially more often than expected at random (Hofer et al. 2004). This spatial overlap is likely due to limited resources such as breeding ponds (following the resource tracking hypothesis), suggesting that resource effects override direct interspecific competition or predation (Hofer et al. 2004). However, ecologically similar species should spatially partition the use of these resources at a microhabitat scale if predation, in fact, influences amphibian assemblages (Sredl and Collins 1992).

The American Bullfrog (*Lithobates catesbeianus* [=*Rana catesbeiana*]) is native to eastern North America and are among the largest amphibians on the continent (Bury and Whelan 1984). Adult bullfrogs are a gape-limited, sit-and-wait predator that can take relatively large prey (Bury and Whelan 1984). Within their native range, bullfrogs play an important role in structuring amphibian assemblages through intraspecific predation and competition (Werner 1994; Hecnar and M'Closkey 1997).

In its introduced range, the American Bullfrog has been implicated in the decline and extirpation of many native ranid frogs (Licht 1974; Nussbaum et al. 1983; Hayes and Jennings 1986; Kiesecker and Blaustein 1997; Kupferberg 1997; Rosen and Schwalbe 2002) and is an invasive species in the western United States (Meshaka 2005). In California, American Bullfrogs were first in-

troduced in 1896 (Jennings and Hayes 1985) and now occur throughout the state except in desert and alpine areas. American Bullfrogs are known to prey on a variety of native aquatic and terrestrial vertebrate species in their introduced range (Bury and Whelan 1984; Wu et al. 2005; Govindarajulu et al. 2006), including the California Red-legged Frog (*Rana draytonii*) federally listed as threatened (Moyle 1973; Cook and Jennings 2001; Cook 2002). The California Red-legged Frog and American Bullfrog are ecologically similar. Both frog species are highly aquatic and mainly nocturnal (Lannoo 2005; Stebbins 2003; Storer 1925; pers. obs.). Maintaining endangered species populations where the invasive bullfrog is established is challenging, but is imperative for conservation efforts.

Seasonality of available habitat and animal activity play important roles in spatio-temporal frog assemblages (Kopp and Eterovick 2006) and may contribute to the persistence of red-legged frogs despite the predatory effects of the larger bullfrogs (Adams et al. 2011). Nonetheless, seasonal variation in activity of the California Red-legged Frog (e.g. breeding phenology) along with spatial distributions has not been assessed in the presence of American Bullfrogs. Complex interactions between pond breeding species are often difficult to discern, but microcosm experiments have elucidated some of these interactions (Luckinbill 1973; Morin 1986; Wilbur 1987; Kiesecker et al. 1998; Hero et al. 2001). However, few studies have examined this in a natural field setting. The

study of American Bullfrogs and prey interactions has been confounded by the presence of predatory fish and habitat alteration (Adams 1999; Kiesecker et al. 2001).

Our study was undertaken at a large, fishless marsh with stable wetland habitats. We analyzed body size and the spatial and temporal patterns of American Bullfrogs and California Red-legged Frogs to determine spatial partitioning and how it may be attributable to physical and biological factors, such as predation risk. Based on the size and immobile feeding behavior of American Bullfrogs, we predict that predation risk is related to relative abundances of both frog species and the proximity of individual frogs.

METHODS

Study area.—Ledson Marsh is a seasonal wetland encompassing approximately 11 ha when fully hydrated, located in Annadel State Park, Sonoma County, California. It lies at an elevation of 476 m on a hilly plateau surrounded by native grassland, oak woodland (*Quercus* spp.), and Douglas-fir (*Pseudotsuga menziesii*) forest. Ledson Marsh was created in 1930 by the construction of a small earthen dam and has had established marsh vegetation for over half a century. Dominant plants include California Bulrush (*Scirpus californicus*), Broad-leaved Cattail (*Typha latifolia*), Spikerush (*Eleocharis macrostachya*), and Smartweed (*Polygonum hydropiperoides*). During winter the marsh fills to a maximum depth of approximately 1.5 m. Water levels slowly recede during spring and summer and the marsh is typically completely dry in early fall, a pattern likely prevalent under natural conditions prior to widespread manipulation of California's hydrology during the past century. Red-legged frog breeding occurs during winter whereas the bullfrog breeding period is longer, occurring in spring and summer.

Data collection.—We collected field data in 1996 from winter until the marsh dried in the fall (17 January to 23 September). Surveys were performed at one to four week intervals depending on frog activity. We conducted nocturnal frog surveys with headlamps by walking through the marsh or by poling an inflatable boat. We identified frogs to species in the water and we estimated their sizes. When possible, we hand-captured frogs and we recorded snout-vent length (SVL). We grouped all frogs either observed in situ or captured into three size categories based on SVL: small (50–100 mm), medium (101–150 mm), and large (> 150 mm [American Bullfrog only]). We classified season based on observed frog activity patterns: winter (17 January to 10 March), spring (11 March to 9 June), summer (10 June to 14 August), and fall (15 August to 23 September). We recorded frog and egg mass locations with a Trimble Navigation Explorer GPS. We rectified coordinates using a base station resulting in GPS accuracy ≤ 2 m.

Data analysis.—To compare frog size data, we used a Pearson's chi-square test using the aforementioned size categories for both species. We used the frog location data to create point layers in ArcGIS Desktop 9 (version 9.3.1; ESRI 2009) then used Hawth's Analysis Tools (Beyer 2004) to calculate distance metrics from those point layers. We measured Euclidian distances between each individual frog and the nearest red-legged frog and bullfrog for each survey visit. To detect differences in Euclidian distances within groups by season and in inter- and intra-specific mean distances over all seasons combined, we used full factorial generalized linear mixed models with unbounded variance components in JMP (SAS 2008). We used survey visit, season, species pair, and their interactions as fixed effects and randomized individuals nested in survey visit. Hence, we treated each survey visit as an independent survey and we accounted for repeated measures of any individual in the model. We chose the more conservative method of a repeated-measures technique here because we could not rule out the possibility of re-recording the same individuals each survey visit. To detect significant differences across effect levels, we used post-hoc Tukey-Kramer pairwise comparisons or Student's *t*-tests (for single comparisons) where appropriate. For all tests, $\alpha = 0.05$.

RESULTS

Frog sizes.—During 22 sampling nights at Ledson Marsh, we estimated the sizes of 202 California Red-legged Frogs and 113 American Bullfrogs (Table 1). American Bullfrogs were significantly larger than California Red-legged Frogs across all study seasons ($\chi^2 = 136.05$, df = 131, $P < 0.001$). American Bullfrogs were predominantly of adult size, with 54% > 150 mm SVL. In comparison, California Red-legged Frogs were composed entirely of small and medium-sized frogs. The largest frog we recorded at Ledson Marsh was an American Bullfrog at 210 mm SVL, whereas the largest California Red-legged Frog we found was little more than half this size at 135 mm SVL. In comparison, the maximum reported size of an American Bullfrog size is about 200 mm SVL (Bury and Whelan 1984) and 138 mm SVL for the California Red-legged Frog (Hayes and Miyamoto 1984).

Seasonal frog patterns and habitat.—Overall, both California Red-legged Frogs and American Bullfrogs showed similar spatial distributions under changing seasonal habitats at Ledson Marsh (Fig. 1). The exception was during winter when the marsh was inundated and California Red-legged Frogs were aggregated mainly in two breeding areas along the southern edge of the marsh where most eggs were deposited (Fig. 1-A). Although fewer in number, American Bullfrogs were located peripherally around the marsh. Very few frogs of either species were in the deep, open water at the interior of the
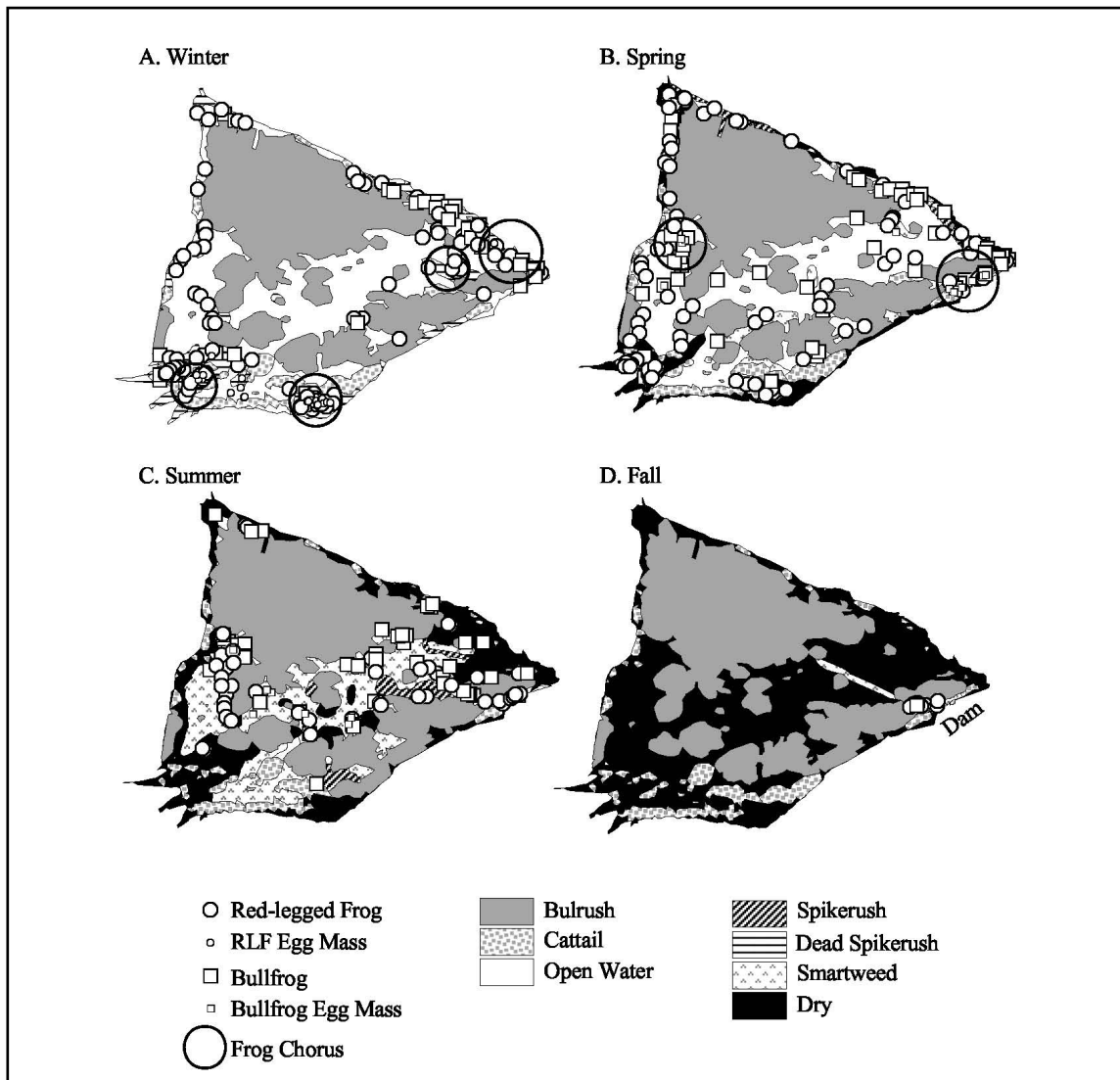
Figure 1. Seasonal distribution of California Red-legged Frogs (*Rana draytonii*) and American Bullfrogs (*Lithobates catesbeianus*), egg masses, breeding chorus', and habitats at Ledson Marsh in Sonoma County, California, in 1996. During fall season most cattail and bulrush contained wet soils and limited standing water. North is up and the maximum width of the marsh is 515 m.

marsh. American Bullfrogs began to breed in the spring when the water level began to decrease. At this time both frog species were distributed along the perimeter of the marsh and some occupied the interior (Fig. 1-B). During summer, the shoreline had substantially receded and both frog species used the marsh interior (Fig. 1-C). During fall most of the marsh was dry and the few active frogs of either species were clustered in a small wetted area near the dam (Fig. 1-D).

Spatial distribution and distances between individual frogs.—Overall, the distances between frog conspecifics were similar to the abundance of frogs observed at the marsh, except during fall (Tables 2 and 3). California Red-legged Frogs increased their mean distances between conspecifics in the marsh seasonally from winter through summer while frog numbers decreased. Also, the

wetted surface area of the marsh decreased during this period. Only during fall, when the marsh was nearly dry and red-legged frog abundance was low, did distances between California Red-legged Frogs decrease from the previous season. In contrast, American Bullfrogs showed the opposite pattern where mean distances between conspecifics decreased from winter through fall; however, the abundance of bullfrogs increased from winter through summer.

The annual mean distances of American Bullfrogs to conspecifics ($\overline{x}_{B:B}$ = 59.8 m) was significantly less compared to red-legged frog to bullfrog distances ($\overline{x}_{R:B}$ = 86.8 m; $F_{1,90}$ = 4.16, P = 0.044). Also, the California Red-legged Frog to conspecific distances ($\overline{x}_{R:R}$ = 26.9 m) compared to red-legged frog to bullfrog distances ($\overline{x}_{R:B}$ = 86.8 m) for all seasons was significantly different ($F_{1,168}$ = 46.23, P < 0.001). This indicates that overall there was

Table 1. Sample size (*n*) and sizes of California Red-legged Frogs (*Rana draytonii*) and American Bullfrogs (*Lithobates catesbeianus*) at Ledson Marsh in Sonoma County, California, in 1996. Size categories are from captured and observed frogs recorded during evening surveys from all seasons. The sizes of 22 Caifornia Red-legged Frogs and six American Bullfrogs were not recorded during field surveys.

Species	*n*	Size Category (SVL)		
		Small (50–100 mm)	Medium (101–150 mm)	Large (>150 mm)
California Red-legged Frog	202	36.1%	63.9%	0%
American Bullfrog	113	20.3%	25.7%	54.0%

Table 2. Season and number of surveys, number found, and abundances (frogs per survey) of California Red-legged Frogs (RLF; *Rana draytonii*) and American Bullfrogs (BF; *Lithobates catesbeianus*) at Ledson Marsh in Sonoma County, California, in 1996. Frogs were observed during evening spotlight surveys.

Season	Surveys	Number Found		Abundance	
		RLF	BF	RLF	BF
Winter	5	78	13	15.6	2.6
Spring	9	91	60	10.1	6.7
Summer	5	38	41	7.6	8.2
Fall	3	17	5	5.7	1.7
All	22	224	119	10.2	5.4

Table 3. Mean, standard deviation (s), minimum (Min), and maximum (Max) of relative distances between California Red-legged Frogs (*Rana draytonii*) and American Bullfrogs (*Lithobates catesbeianus*) at Ledson Marsh in Sonoma County, California, in 1996. Frog groupings for red-legged frog (R) and bullfrog (B) are listed by season. Frog groups within a season that share the same letter are not significantly different ($P > 0.05$).

	Mean (m)	s	Min	Max
Winter				
R:R	16.3a	25.5	2.47	155.0
R:B	176.9b	162.4	3.77	441.0
B:B	93.8b	138.4	6.67	329.0
Spring				
R:R	33.9a	41.7	1.6	258.0
R:B	58.3b	56.0	2.0	258.0
B:B	61.9b	111.0	5.6	453.0
Summer				
R:R	35.6a	31.2	2.2	110.0
R:B	57.9a	60.2	1.9	283.0
B:B	51.8a	57.0	2.9	248.0
Fall				
R:R	18.2a	39.5	2.4	170.0
R:B	30.1ab	44.1	2.9	208.0
B:B	8.4b	6.5	2.7	14.0

more spatial separation between California Red-legged Frogs and American Bullfrogs than to conspecifics of either species at the marsh.

The distance patterns between California Red-legged Frogs and American Bullfrogs differed during the four seasons studied (Table 3). During each season the mean distances between red-legged frogs and bullfrogs was greater compared to distances to their respective conspecifics, except for spring when American Bullfrog conspecifics were slightly more distant then red-legged to bullfrog distances. When comparing distances between frog groups (R:R, R:B, and B:B) within each season, significant differences were found between American Bullfrog conspecifics (B:B) and red-legged frogs conspecifics (R:R) during the winter, spring, and fall. Additionally, the distances between red-legged frogs and bullfrogs (R:B) were more distant than between red-legged frog conspecifics (R:R) during all seasons, but was significant only in winter and spring (Table 3).

DISSCUSSION

There are several physical and biological factors that could be influencing spatial patterns of California Red-legged Frogs and American Bullfrogs at Ledson Marsh. Possible factors include competition, habitat and resource use, breeding and foraging behavior, and predation. Ecologically similar species, such as the California Red-legged Frog and American Bullfrog, should show spatial separation if one or more of these factors are present (Toft 1985; Cook and Jennings 2007). Also, the confounding indirect effects from predatory fish introductions or habitat alterations (Kiesecker and Blaustein 1997) are absent from Ledson Marsh, and therefore can be eliminated from further consideration.

Although competition for food resources may influence the distribution of California Red-legged Frogs and American Bullfrogs, it is unlikely that the high frog densities and resource limits necessary for competition to occur (Hayes and Jennings 1986) would be present at Ledson Marsh because of the productive, eutrophic marsh with an abundance of aquatic and semi-aquatic prey (pers. obs.; also see Cook and Jennings 2007).

Cook and Jennings (2007) compared habitat uses of California Red-legged Frogs and American Bullfrogs at Ledson Marsh during 1996. Their study emphasized the similarities of habitat use between frog species, but there was more separation in habitat use during winter than other seasons. We found a congruent spatial pattern where both frog species were most spatially separated during winter. However, this spatial separation between frog species continued into spring and fall even though their use of habitat overlapped (Cook and Jennings 2007). This suggests that habitat use cannot explain the spatial patterns between frog species at Ledson Marsh.

A possible explanation for the observed spatial patterns could be breeding behavior of frogs that affects their abundance and, in turn, the distances between frogs. Both California Red-legged Frogs and American Bullfrogs had their highest abundance and shortest conspecific distances during their respective breeding periods. The exception was during fall when the marsh was nearly dry and neither frog was breeding. Frogs clustered seasonally at breeding sites and formed a ring of frogs around the margins of the marsh that shrank with the receding shoreline. This suggests that frogs were not randomly distributed and frog abundances alone cannot entirely explain spatial patterns at Ledson Marsh.

Both American Bullfrogs and California Red-legged Frogs are opportunistic, gape-limited predators with similar diets (Lannoo 2005). Although breeding aggregates of California Red-legged Frogs can explain winter spatial patterns, the similar foraging behavior and habitat overlap of both frog species coupled with the contrasting spatial separation during spring and fall cannot entirely explain the observed spatial pattern of these frogs at Ledson Marsh during all seasons. Kiesecker et al. (2001) showed that native frogs have the ability to chemically detect American Bullfrogs and alter their habitat use and foraging behavior to avoid predators. Our spatial analysis suggests that California Red-legged Frogs may possess such ability and respond similarly. We found potential predation is lowest during the winter season when American Bullfrogs have the broadest spatial distribution and low abundances. However, when American Bullfrogs increased in numbers during the spring season, California Red-legged Frogs appeared to avoid American Bullfrogs by congregating with conspecifics, even though both frog species used similar microhabitats (Cook and Jennings 2007) and California Red-legged Frog breeding aggregations had dispersed.

Although predation may be reciprocal between frog species through ontogeny, size disparity suggests higher predation on California Red-legged Frogs by American Bullfrogs. Due to the seasonally fluctuating water levels at Ledson Marsh, American Bullfrog reproduction is minimal and most individuals apparently are adult immigrants (Cook and Jennings 2007; pers. obs.). Based on the size structure of frogs at Ledson Marsh, it is reasonable to conclude that California Red-legged Frogs of all sizes are vulnerable to predation by the predominantly large-sized American Bullfrog.

We conclude that frog abundance, which is strongly influenced by breeding behavior, changing habitats, and possibly predation risk of California Red-legged Frogs by American Bullfrogs are the dominant factors driving the spatial patterns observation at Ledson Marsh. Despite the lack of replication that would be seen in a long-term study over many years, the decrease we found in interspecific distances and corresponding decrease in California Red-legged Frogs abundances at the marsh suggests

that once winter breeding is completed, red-legged frogs avoid predation from American Bullfrogs by distancing themselves spatially or by leaving the marsh altogether. Also, post-breeding California Red-legged Frogs that remain at the marsh have a relatively high exposure to American Bullfrog predation.

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