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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 observed at Lodon 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

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photo by H. Clark