



Population declines lead to replicate patterns of internal range structure at the tips of the distribution of the California red-legged frog (*Rana draytonii*)



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ABSTRACT

Demographic declines and increased isolation of peripheral populations of the threatened California red-legged frog (*Rana draytonii*) have led to the formation of internal range boundaries at opposite ends of the species' distribution. While the population genetics of the southern internal boundary has been studied in some detail, similar information is lacking for the northern part of the range. In this study, we used micro-satellite and mtDNA data to examine the genetic structuring and diversity of some of the last remaining *R. draytonii* populations in the northern Sierra Nevada, which collectively form the northern external range boundary. We compared these data to coastal populations in the San Francisco Bay Area, where the species is notably more abundant and still exists throughout much of its historic range. We show that 'external' Sierra Nevada populations have lower genetic diversity and are more differentiated from one another than their 'internal' Bay Area counterparts. This same pattern was mirrored across the distribution in California, where Sierra Nevada and Bay Area populations had lower allelic variability compared to those previously studied in coastal southern California. This genetic signature of northward range expansion was mirrored in the phylogeography of mtDNA haplotypes; northern Sierra Nevada haplotypes showed greater similarity to haplotypes from the south Coast Ranges than to the more geographically proximate populations in the Bay Area. These data cast new light on the geographic origins of Sierra Nevada *R. draytonii* populations and highlight the importance of distinguishing the genetic effects of contemporary demographic declines from underlying signatures of historic range expansion when addressing the most immediate threats to population persistence. Because there is no evidence of contemporary gene flow between any of the Sierra Nevada *R. draytonii* populations, we suggest that management activities should focus on maintaining and creating additional ponds to support breeding within typical dispersal distances of occupied habitat.

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1. Introduction

Spatial variation in abundance within a species range can lead to internal range structure, with the number, size and location of gaps and fragments tending to increase towards the range edge. This 'globular' nature of a species' internal range can be the result of several processes, including long-range dispersal of a few individuals across one or more biogeographic barriers leading to new isolated populations, the formation of barriers within a continuous distribution to create satellite populations, spatiotemporal variation in the environment, or rapid contraction of a formerly

widespread species leaving small isolates in the wake of the contraction (Brown et al., 1996). Internal disjunctions that develop as a result of the latter processes can be a cause for conservation concern, particularly for threatened and endangered taxa, because they have the potential to eliminate important dispersal and genetic resupply routes. The problem may be especially acute if internal structure forms towards the tips of the species range, where edge populations are often already challenged by greater isolation and lower abundance (Sexton et al., 2009).

The threatened California red-legged frog *Rana draytonii* is one such species for which the internal range structure has changed considerably in recent times, and it is widely accepted among herpetologists that the species is in decline (Davidson et al., 2001; Fellers, 2005; Fisher and Shaffer, 1996; Jennings and Hayes, 1985,

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1994; Moyle, 1973; Richmond et al., 2013). Some of the most extreme examples of local extirpation causing shifts in range structure have occurred in southern California – since the 1960s, the species has disappeared from virtually all historical localities spanning from the US–Mexico border northward through the Transverse Ranges, with the exception of a single coastal population that persists in the Santa Monica Mountains to the west/northwest of the Los Angeles Basin. This rapid extirpation has led to the formation of an internal range boundary and a ~500 km distributional gap between the southern-most *R. draytonii* populations in California and six remnant populations in the Sierra San Pedro Martir of Baja California (Fig. 1), where the species also appears to be extirpated from much of its historical range (A. Peralta Garcia, unpub. data).

Extensive local extirpation has also occurred at the southern end of California's Great Central Valley (i.e. Tulare Basin), where *R. draytonii* was commercially harvested as a food resource during the Gold Rush era of the late 1800s and early 1900s (Jennings and Hayes, 1985). Subsequent loss of suitable habitat due to water diversion, agriculture, and extensive urbanization throughout the 1900s has led to the complete disappearance of *R. draytonii* from the southern Valley floor and possibly the southern Sierra Nevada. At the northern end of the Great Central Valley, the species' range has deteriorated in a manner that resembles the patterns in southern California and northern Baja California, but the timing of population declines in this part of the range and the area encompassed by the historical distribution are less clear. Currently, Sierra Nevada populations are no longer connected to coastal populations around the north end or across the Central Valley floor, leaving a detached cluster of small, isolated populations in the Sierra Nevada

foothills that geographically resemble the remnant group in the Sierra San Pedro Martir (Fig. 1).

The dissociation of peripherally isolated groups of populations at the northern and southern tips of the *R. draytonii* distribution have eliminated opportunities for dispersal and gene exchange with a larger and more robust 'core' formed by interior populations in the south Coast Ranges of California (U.S. Fish and Wildlife Service, 1996; Fellers, 2005; Jennings and Hayes, 1994). This core extends from the Russian River in Sonoma County to the Santa Ynez Mountains in Santa Barbara County. Although habitat loss has reduced the number of populations within the core distribution, many large populations still persist throughout much of this part of the range (Fellers, 2005; M. Westphal pers. comm.). This higher abundance and presumably greater connectivity among central coast populations likely places them at an evolutionary advantage with respect to marginal populations at the tips of the species distribution, where small population sizes and greater isolation among marginal groups may leave them more susceptible to loss of genetic diversity through drift (Eckert et al., 2008; Kirkpatrick and Barton, 1997; Sexton et al., 2009). Stochastic environmental and demographic events may also have more pronounced effects on marginal populations because they cannot be recolonized naturally due to their degree of isolation. These factors ultimately translate to a higher risk of extinction.

While the genetic effects of demographic declines have been studied to some extent at the southern internal range boundary in California (Richmond et al., 2013), very little genetic data exists from northern *R. draytonii* populations for comparative analysis (but see Pauly et al., 2008; Shaffer et al., 2004). Current data suggest that the species occurs at only seven of its 26 historically

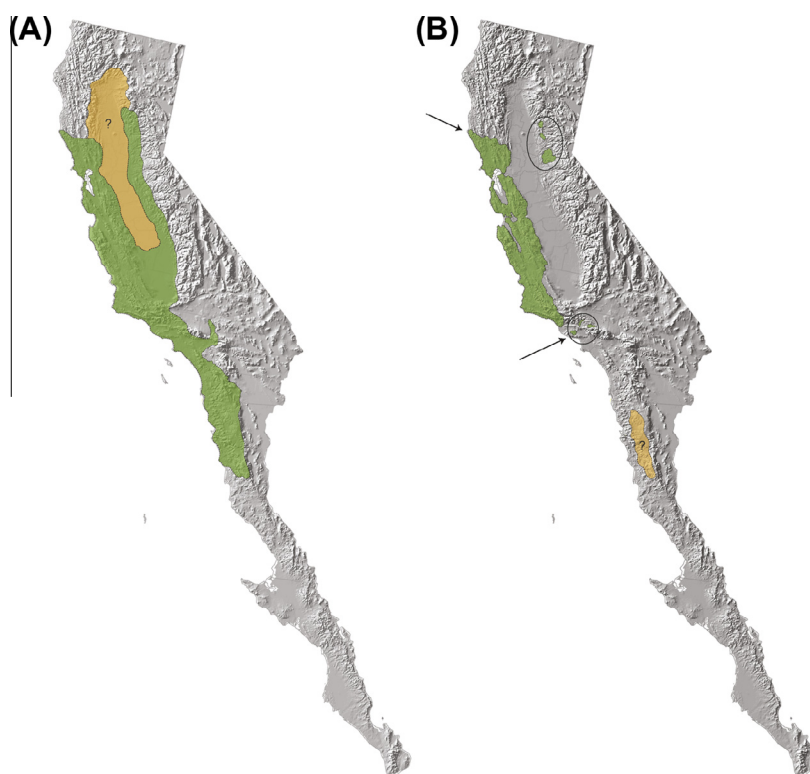


Fig. 1. Approximate distribution of the historical (A) and contemporary range (B) of *Rana draytonii*. Orange polygons indicate uncertainty about the distribution. Dark ovals highlight marginal populations in the northern Sierra Nevada and southern California; arrows denote internal range boundaries. Little is known about the extent of the historical distribution of *R. draytonii* on the Central Valley floor, particularly for the mid to northern end (i.e. delta region, the Sacramento Valley and the San Joaquin Valley); however, Jennings and Hayes (1985) cite historical notes claiming that commercial amounts of *R. draytonii* were harvested from the southern end of the Central Valley (Tulare Basin) prior to bullfrog introductions. This end of the Valley contained the largest freshwater lake west of the Mississippi River and an extensive mosaic of marshes and sloughs as recently as the late 1800s.

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