



Assessing selective introgression of nonnative red fox genes into the genomic background of the native Sacramento Valley red fox

Sophie Preckler-Quisquater^{1, 2}, Stacy Anderson², Mike Buchalski², and Ben Sacks^{1,3}

(1) Mammalian Ecology and Conservation Unit, Veterinary Genetics Laboratory, School of Veterinary Medicine, University of California, Davis, Davis, CA; (2) California Department of Fish and Wildlife, Rancho Cordova, CA; (3) Department of Population Health and Reproduction, School of Veterinary Medicine, University of California, Davis, Davis, CA.

Introduction

The Sacramento Valley red fox (SVRF, *Vulpes vulpes patwin*) is endemic to the northern Central Valley of California, and is considered a State Species of Greatest Conservation Need due to the apparent decline in abundance from historic levels, the recognition of its low genetic effective population size ($n = 50$), and its restricted and sparse distribution. Along with habitat loss, hybridization with nonnative red foxes of captive-bred origin has been identified as one of the most significant threats to the persistence of the SVRF¹. Through genetic monitoring (2007–2015) and the use of microsatellite markers, we observed low level (neutral) gene flow across a stable zone of hybridization^{1,2}. However, if particular genes are positively selected for across the two populations, they could be transferred at far greater rates than were observed for neutral genes and may become fixed. Possible genes under selection include those associated with the nonnative population's long history in captivity (e.g. tameness). Selective introgression of nonnative genes could reduce the long-term fitness of the SVRF and affect its role in the greater ecological community³. Thus, we propose using a genome-wide approach to elucidate potential candidate genes under selection in this system.

Predicted Genes Under Selection



Based upon the evolutionary history of the native and nonnative red fox populations, we predict that specific genes likely confer fitness advantages and may be selectively introgressed across the stable hybrid zone. The nonnative red fox population is derived from phylogenetically divergent (~20-30 kya), eastern Canadian and Alaskan lineages. They were bred in fur-farms for decades, first in Canada and then in California, before their release in the 1950s⁴. We predict there are certain genes that were selected for in captivity (e.g. tameness, high reproductive rates) that may now be selectively introgressed into the native SVRF population.

Proposed Future Research

- We will collect genetically independent tissue samples from
 - 50 native SVRF
 - 50 nonnative red foxes
 - 30 red foxes from within the stable hybrid zone
- We will use a reduced representation genotyping-by-sequencing (GBS) approach to identify single nucleotide polymorphism (SNP) variants and outlier loci, elucidating potential candidate regions under selection⁵.
- We will also incorporate spatial, phenotypic and environmental data to conduct a genomic cline analysis which will enhance outlier detection⁶.
- We will then align this reduced set of SNPs to the previously annotated dog and red fox genomes to identify regions that may be associated with selection to captivity in the nonnative red fox⁷.

Prior Results (2007–2017)

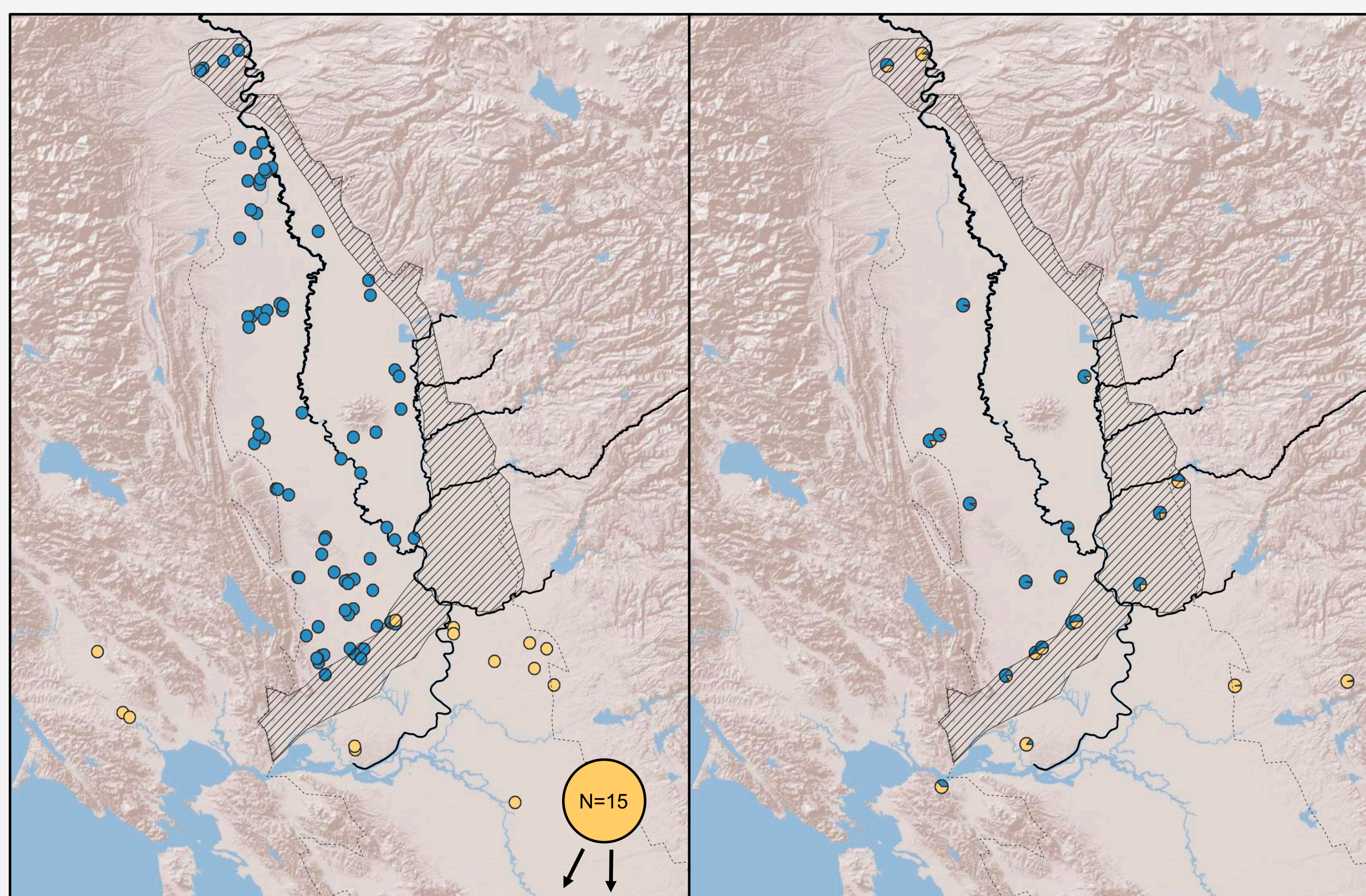


Figure 1. Locations of red fox samples with ancestry assigned fully or partially to native and nonnative populations. (A) 2007–2015 samples assigned to their home population as pure (>98%) native Sacramento Valley red foxes (blue circles) or nonnative foxes (yellow circles); Large yellow circle reflects 15 pure nonnative samples from further South⁴. (B) 2007–2015 samples identified as hybrids, with pie charts indicating estimated proportions of native (blue) and nonnative (yellow) ancestry.

Selective Introgression – How It Works

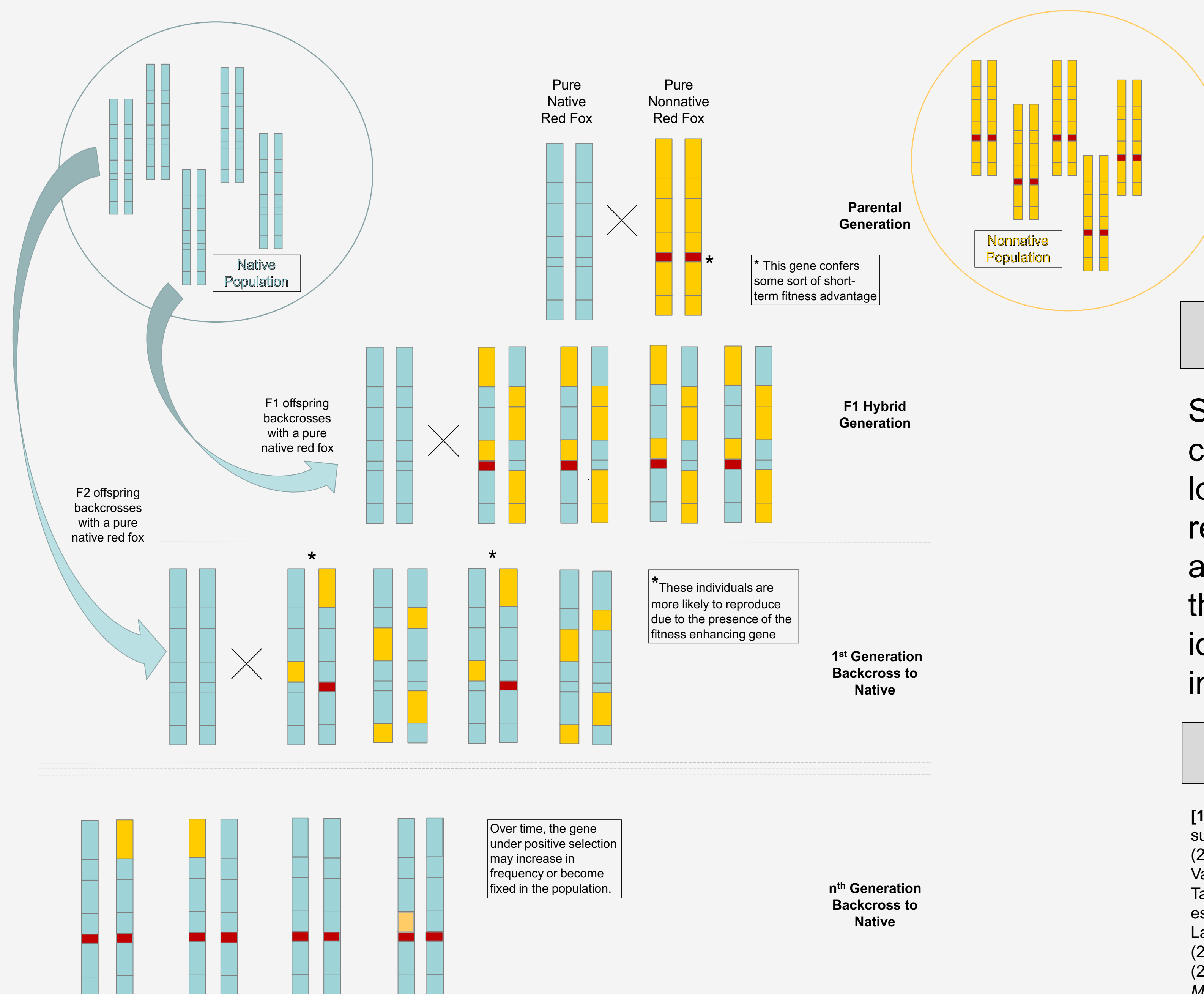


Figure 2. This image shows an active den within the currently identified hybrid zone. From 2014-2016, this fully nonnative vixen (female) was paired up with a fully native raynard (male) and the two have produced F1 hybrid offspring each year. If these pups successfully breed with fully native red foxes, generations of backcrossing can occur.

Conservation Implications

Short-term fitness benefits may result in fixation of nonnative genes, which could have negative long-term consequences for both the native foxes (i.e. loss of locally adaptive alleles) and the ecosystem as a whole. We have recorded instances of SVRF, historically a grassland species, using highly atypical habitat types (e.g. flooded agriculture, wetland), more similar to those used by the nonnative population throughout California⁸. We hope to identify whether this is a result of specific nonnative genes being introgressed into the native SVRF population.

References

[1] Sacks, B. N., M. Moore, M.J. Statham, H.U. Wittmer. 2011. A restricted hybrid zone between native and introduced red fox (*Vulpes vulpes*) populations suggests reproductive barriers and competitive exclusion. *Molecular Ecology* 20: 326–341 [2] Preckler-Quisquater, S., Batter, T., Anderson, S., Sacks, B. (2015) *The Wildlife Society Western Section Conference*. Increasing distribution of non-native red fox genes within the range of the native Sacramento Valley red fox (*V.v. patwin*)? [3] McGinnity P., Prodohl, P., Ferguso, A., Hynes, R., Maoloidigh, N., Baker, N., Cotter, D., O’Hea, B., Cooke, D., Rogan, G., Taggart, J., Cross, T. (2003) Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proceedings of the Royal Society: Biological Sciences*. 270: 2443-2450 [4] Sacks, B. N., Brazael, J. L., & Lewis, J. C. (2016). Landscape genetics of the nonnative red fox of California. *Ecology and Evolution*. [5] Larson, E. L., Andrés, J. A., Bogdanowicz, S. M., & Harrison, R. G. (2013). Differential introgression in a mosaic hybrid zone reveals candidate barrier genes. *Evolution*. [6] Stankowski, S., Sobel, J. M. and Streisfeld, M. A. (2017). Geographic cline analysis as a tool for studying genome-wide variation: a case study of pollinator-mediated divergence in a monkeyflower. *Molecular Ecology*, 26: 107–122 [7] Kukekova et al. (unpublished) [8] Sacks, B. N., Statham M., Wittmer, H.U. (2017). A Preliminary Range-Wide Distribution Model for the Sacramento Valley Red Fox. *Journal of Fish and Wildlife Management*, 8:28-38.

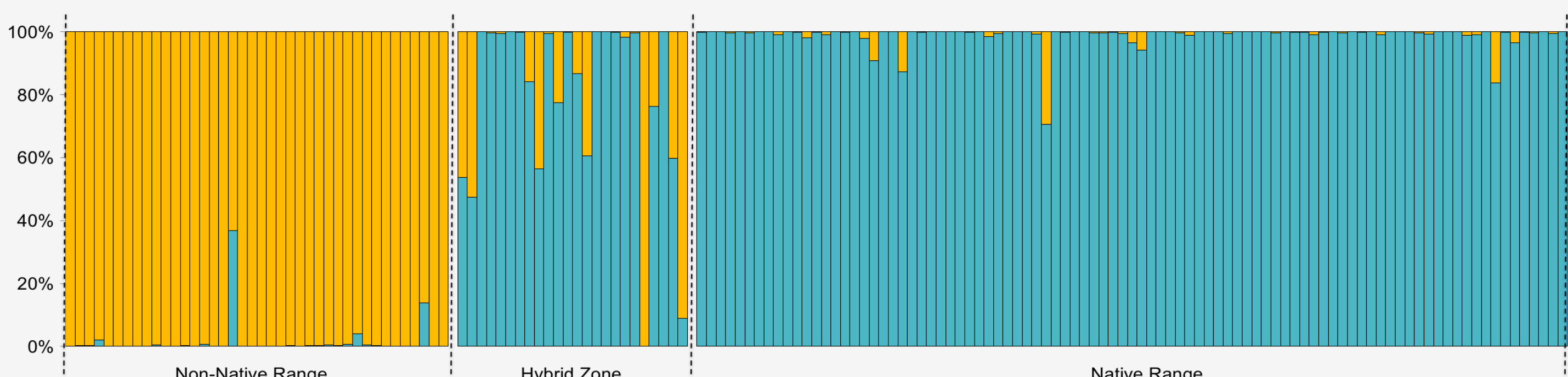


Figure 2. Distribution of estimated proportions of ancestry (q) according to admixture analysis at $K = 2$ with prior information using nuclear DNA. Analyses were conducted with multilocus genotypes composed of 33 microsatellite loci in program STRUCTURE based on 150,000 post-burn-in Markov Chain Monte Carlo cycles. Nonnative ancestry shown in yellow. Native ancestry shown in blue.

Acknowledgements

We thank David Wright and Canh Nguyen of the California Department of Fish and Wildlife (CDFW) for cooperation and assistance as well as the many private landowners who granted us access to conduct research activities on their property. We also thank Zachary Lounsbury and the many student interns for their lab and field efforts. This work was funded by the United States Fish and Wildlife Service, CDFW, and UC Davis Mammalian Ecology and Conservation Unit of the Veterinary Genetics Laboratory. For more information about our research or to report a red fox sighting, please visit <http://foxsurvey.ucdavis.edu>.