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The Native Sacramento Valley Red Fox

Radio-collared adult male Sacramento Valley red fox,
north of Capay, Yolo County, Photo taken by Ben Sacks, 3/31/2010

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Abstract

It was recently determined that the Sacramento Valley red fox (*Vulpes vulpes* ssp. nov.; Sacks et al. 2010), previously considered an introduced species, is indigenous to California and phylogenetically most closely related to the state-threatened Sierra Nevada red fox (*Vulpes vulpes necator*). Also occurring in lowland areas of the state are introduced red foxes, which derive largely from fur farm stock exhibiting ancestry from an admixture of diverse and phylogenetically distant sources. We researched the current status of the Sacramento Valley red fox, including hybridization with introduced foxes, using noninvasive genetic sampling approaches and opportunistic collection of carcasses. Due to the apparent sparseness of red foxes, search efforts were concentrated in locations where we received credible sighting reports, following broadcast solicitations for this information from the public. Objectives were to describe the current range of the native Sacramento Valley population relative to the introduced red fox population, including hybrid zones, and to compare morphometric, life-history, and habitat affinities. Within the native population, we also investigated genetic substructure and diversity, and pathogen exposure. Results can be summarized as follows:

(1) Based on genetically verified samples, we estimated the current range of the native Sacramento Valley red fox to span the Valley from Cottonwood to the Delta, west of the Sacramento River, and Chico to Sacramento, east of the Sacramento River. Hybridization with introduced red foxes was observed, primarily on the southern and southeastern margins of the range, possibly facilitated by low densities of native foxes in these areas. A tentative hybrid zone was designated where it appears most hybridization has occurred. The largest continuous span of native samples was centered on the historical range. All red foxes south of the American River and Delta and west of the Sacramento Valley (Sonoma County) were found to be nonnative.

(2) Although substructure within the native population was detected, it appeared to reflect heterogeneity in red fox distribution on the landscape rather than stable barriers to gene flow. Genetic diversity, indexed by heterozygosity in 33 microsatellite loci, was relatively uniform throughout the native range (H_e = 0.63), which was lower than in the hybrid zone (H_e = 0.70) or nonnative range (H_e = 0.69). Thus, the native Sacramento Valley red fox appears to consist of a single population.

(3) Sacramento Valley red foxes were significantly longer (total body length, tail length, ear length, hind foot length) than nonnative red foxes but the two populations had similar body masses. Native and nonnative lowland red foxes could be correctly differentiated approximately 85% of the time based on discriminant functions of body mass and total body length. Additionally, the Sacramento Valley red fox and native mountain foxes, although significantly

different in size, exhibited similar allometric proportions, which differed from Midwestern red foxes; nonnative red foxes clustered closer to Midwestern than native red foxes. In general, the phylogenetically related Sacramento Valley red fox and mountain red foxes were lankier than other red foxes examined in this study.

(4) Whelping dates were estimated from body mass and hind-foot length of pups according to previously established growth curves. Both Sacramento Valley and nonnative red foxes exhibited estimated peaks in whelping around the first of March, although variability was higher in the nonnative sample.

(5) Sacramento Valley red fox den sites were disproportionately associated with grasslands and away from flooded agriculture and wetlands. These findings agree with historical observations, which indicate that red foxes were once abundant in grassland portions of the Valley that were elevated above the flood plain. Given both a 65% decline in Valley grasslands since historical times and genetic (and anecdotal) evidence that Sacramento Valley red fox experienced a population decline over the same period, it seems likely that the Sacramento Valley red fox distribution in California has been tied to the distribution of grasslands. The apparent avoidance of wetlands by native red foxes also could mark an important difference from nonnative red foxes, which commonly impact endangered ground-nesting birds in coastal wetlands. Also in contrast to nonnative red foxes, native den sites were not found in heavily urbanized areas. Finer scale studies of habitat use within home ranges and habitat-specific estimates of survival and reproduction are needed to more precisely determine critical habitat characteristics for the Sacramento Valley red fox.

(6) The number of pups directly observed at den sites averaged 3.2, representing a minimum estimate of litter size. Genetic analyses identified an estimated average of 2.3 adults and 5.3 pups at den sites. These estimates are comparable to those for other red fox populations. Although we did not systematically investigate or quantify pup survival, a seemingly large number of pups was found dead considering that they were opportunistically discovered. Although most were hit by cars, many were found nowhere near roads and too long post-mortem to determine causes of death. Without quantitative estimates of pup survival, recruitment, and adult survival, the significance of observed pup mortality cannot be assessed. Future studies are needed to investigate population growth rate, along with sensitivity/elasticity of vital rates and rates of specific causes of mortality.

(7) Based on serological tests and DNA tests of feces, native red foxes exhibited exposure to or active infection with several pathogens potentially causing morbidity or mortality in canids, including CDV and CPV-2. Our small serological sample size combined with apparently low sensitivity of fecal PCR surveillance

for CPV-2 prevent us from assessing potential effects of these pathogens on the Sacramento Valley population, but future surveillance is warranted, especially in the context of cause-specific mortality studies. Disease should be considered among the list of potentially important factors affecting the population.

Spatial distributions of native and nonnative red foxes, along with genetic and morphometric criteria, indicate that despite limited interbreeding where the two populations come into contact, the native Sacramento Valley red fox presently retains most of its genomic integrity. Thus, while introgression occurs and could pose a greater threat in the future, some type(s) of reproductive barrier appear(s) to be in place. Reproductive phenology, which was similar between the two populations, was ruled out as a barrier to first-generation hybridization. However, the possibility remains that reproductive timing or other traits affecting fitness could be altered in F1 individuals, potentially reducing the frequency of backcrosses. Understanding mechanisms that have thus far prevented nonnative red foxes penetrating the range of native red foxes (with or without interbreeding) could be key to assessing threats from nonnative red foxes in the future.

The Sacramento Valley red fox appears to satisfy at least two criteria of a California State Species of Special Concern: (1) “is experiencing, or formerly experienced, serious (noncyclical) population declines or range retractions (not reversed) that, if continued or resumed, could qualify it for State threatened or endangered status.” and (2) “has naturally small populations exhibiting high susceptibility to risk from any factor(s), that if realized, could lead to declines that would qualify it for State threatened or endangered status.” Three areas requiring future research were identified to assess the condition of the Sacramento Valley red fox subspecies with respect to criteria for State threatened or endangered status: (1) threats posed by hybridization with nonnative red foxes, (2) habitat relationships, occupancy, and abundance, including interspecific relationships with coyotes and gray foxes, and (3) population growth rate (survival, recruitment) and cause-specific mortality.

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Introduction

Both native and introduced (nonnative) red foxes (*Vulpes vulpes*) occur in California. Until recently, red foxes inhabiting the Sacramento Valley were thought to be introduced, putatively from the Midwest (Grinnell et al. 1937; Gray 1975; Roest 1977; Jurek 1992; Lewis et al. 1999). Recent genetic work, however, determined that these foxes were native and phylogenetically related to the state-threatened Sierra Nevada red fox (*V. vulpes necator*; Perrine et al. 2007; Sacks et al. 2010). Despite their shared ancestry, foxes of the Sacramento Valley are larger than the Sierra Nevada red fox (Grinnell et al. 1937; Roest 1977; this study); they occur in a distinct climatic zone with distinct habitats, competitors, and prey, and differ in functional regions of the mtDNA (Roest et al. 1977; Sacks et al. 2010). Consequently, the Sacramento Valley red fox has been proposed as a distinct subspecies (*V. vulpes* ssp. nov.; Sacks et al. 2010).

In the 1960s through 1980s, red foxes were reported from southern parts of the Sacramento Valley, San Joaquin Valley, and coastal areas where they had not previously been known to occur (Gray 1975, 1977; Schempf and White 1977; Gould 1980; Gogan et al. 1986), and by the early 1990s, lowland red foxes had become established in significant numbers over a wide area of lowland California, including Southern California (Burkett and Lewis 1992; Jurek 1992; Lewis et al. 1993, 1999). Genetic studies have since confirmed that foxes throughout these newly colonized areas were nonnative (Perrine et al. 2007; Sacks et al. 2010). In particular, they appear to stem largely from fur farm stock (possibly augmented by other translocated sources), reflecting an admixture of principally Alaskan and Southeast Canadian ancestry (Aubry et al. 2009; Sacks et al. 2010; Statham et al., submitted).

Prior to the genetic studies differentiating native from nonnative red foxes, the growth of the red fox range throughout the California lowlands was viewed as an expansion of the Sacramento Valley population, albeit one augmented by independent introductions (Lewis et al. 1999). However, it is now clear that the Sacramento Valley red fox population remains endemic to its approximate historical range (Perrine et al. 2007; Sacks et al. 2010). Moreover, anecdotal and genetic evidence suggest that the Sacramento Valley red fox has declined considerably in abundance from its historical numbers (Borrel 1924, unpublished field notes; Sacks et al. 2010). Otherwise, little is known of the status of this population or of the relative importance of potential threats to its persistence. Therefore, basic information of the status and ecology of this subspecies is needed to guide efforts aimed at its management and conservation.

This report on the Sacramento Valley red fox corresponds to Agreement Nos. P0780029 and P0685904 (subgrant HBSDF12). Here, we describe the current range of the Sacramento Valley red fox, including its relation to nonnative populations, population genetic diversity, and distribution of reproductive den sites relative to habitat types. Data are also presented on morphometrics, reproductive phenology, and potential exposure to pathogens.

Study Area

Our principal region of interest was the Sacramento Valley, but we also obtained reference samples from the coastal valleys of Sonoma County, the San Joaquin Valley, and coastal areas in the vicinity of San Francisco, Monterey, and Morro Bays. The Sacramento Valley represents the northern portion of the Central Valley of California. It is separated from the southern portion, the San Joaquin Valley, by the Sacramento-San Joaquin River Delta and the American River. The Sacramento Valley is bordered to the west by the North Coast Ranges, to the north by the Siskiyou Mountains, and to the east by the Sierra Nevada and southern Cascade Ranges. The Capay Valley, containing Cache Creek, is continuous with the Sacramento Valley and we therefore considered it part of the potential range of the Sacramento Valley red fox and included in the study. We also investigated reports of red fox occurrence in the foothills of the surrounding mountain ranges.

Historically, the Sacramento Valley contained a large flood plain northeast and south of the Sutter Buttes (or "Marysville Buttes"), an isolated group of volcanic peaks reaching 650 m in elevation and located between the Feather and Sacramento Rivers; each of these rivers supported dense riparian forests up to 5 miles wide (Thompson 1961; Gipson 1975). To the west of the Sacramento River riparian corridor were marshes lined on either side by slightly raised ground supporting grasslands (Nelson et al. 2003). Today, the landscape of the Sacramento Valley is much changed, with levees containing the rivers, tributaries, and canals and >90% of the historic riparian forests gone. In the lowest elevations of the valley, flooded agriculture has largely replaced naturally flooded lands and former grasslands, while in the more upland areas, much of the grasslands have been replaced by dry cropland, vineyards, and orchards (Nelson et al. 2003). Remaining grasslands are principally used as rangeland for livestock; the composition of grass and forb species has changed dramatically over the past 150-200 years, and is currently dominated by annual exotics (Barbour et al. 2007).

Materials and Methods

Samples.—We attempted to obtain biological samples from red foxes from throughout the Sacramento Valley and surrounding lands, including road-killed, trapped, or otherwise obtained carcasses or live individuals. Because red foxes can disperse over hundreds of kilometers, however, the occurrence of a fox carcass was not necessarily a good indicator of reproductive habitat (Allen and Sargeant 1993). Therefore, we made a special effort to find and locate reproductive dens or rendezvous sites (hereafter referred to as "den sites"). We established a web site to which members of the public could report sightings of red fox (http://foxsurvey.ucdavis.edu/) and broadcasted requests for sighting information through various news outlets. We concentrated these efforts during March through May of each year (2007—2009), when pups and provisioning adults would be most visible and likely to be seen in the vicinity of den sites. Sightings were then followed up by ground searches for den sites. Once dens were discovered, feces from both adults and pups were collected and preserved in 4 parts 95-100% ethanol to 1 part fecal matter and saved for genetic analyses,

parvovirus testing, and future parasitological examination and dietary analysis. Remote video cameras and field observations were used to estimate minimum litter sizes (i.e., the largest number of pups observed at one time). Residents living in the vicinity of den sites were asked to contact us if they became aware of road-killed foxes. Additionally, we contacted road maintenance, agricultural extension, and animal control agencies in counties within the study area to seek assistance in discovery of road-killed red foxes. DNA samples (buccal swabs, blood, feces) were collected from red foxes from wildlife rehabilitators when capture locations were known. For morphometric comparisons, necropsy data for a sample of 190+ nonnative red foxes primarily from the San Francisco Bay and Monterey Bay areas were also used (B. N. Sacks, unpublished data).

Laboratory DNA methods have been detailed in several publications, including fecal (and other) DNA extraction (Moore 2009; Sacks et al. 2010, submitted.), microsatellite marker development (Moore 2009; Moore et al. 2010), SNP development and genotyping (Sacks and Louie 2008; Sacks et al. 2009; Sacks et al., submitted.), microsatellite genotyping (Sacks et al. 2010), and mtDNA sequencing (Perrine et al. 2007; Aubry et al. 2009; Sacks et al. 2010, submitted.).

Genetic data analysis.—Identities of individual genotypes were assessed based on microsatellite genotypes for 33 loci, with fecal genotyping error rates estimated at 1% false alleles and 2.3% allelic dropout (Sacks et al., submitted). Because numbers of individuals can be overestimated if genotyping error is not accounted for, we considered any two genotypes with >85% of alleles matching to be from the same individual. This cutoff was justified based on the following analytical and empirical criteria. First, the genotyping error rate (3.3% overall) was used to calculate the binomial distribution of expected numbers of allele matches between genotypes of the same individual, which indicated that 99.9% of such pairwise comparisons were expected to share >89% of their alleles. Second, the observed distribution of numbers of matches for all pairwise combinations of genotypes was strongly bimodal, with most genotypes (including close relatives) sharing <70% of their alleles, and a small number of pairs sharing 90—100% of alleles, presumed to be duplicate samples, i.e., from the same individual (B. N. Sacks, unpublished data).

Once genotypes were assigned to individuals (regardless of the number of times individuals were sampled), the total number of individuals was assessed. Because we attempted to sample all individuals from family groups around den sites, the sample was nonrandom (i.e., close relatives were oversampled). Therefore, for population level analyses, we selected 1-3 unrelated individuals per den site (e.g., the breeding pair and a trespassing disperser) and further genotyped these samples, along with non-den-related road kills and other isolated samples, at 51 SNP markers (Sacks et al. 2009, submitted). The resulting independent data set was used, along with previously collected samples, to assign native, nonnative, and hybrid status to samples, den groups, and regions in the Valley (Moore 2009; Sacks et al., submitted). The methods and results of this study were detailed elsewhere (Moore 2009; Sacks et al., submitted).

Briefly, this involved admixture analyses implemented in program Structure (Pritchard et al. 2000) and simulation of various classes of hybrid genotypes (F1, F2, back-cross, etc.) to assess statistical power and probabilities of Type I errors (Sacks et al., submitted.).

The independent samples from the native population in 2007--2009 were then used to estimate genetic substructure. Individuals determined in the previous analysis to be hybrids were excluded from these analyses. We used program Structure, which apportions ancestry of each multilocus genotype (i.e., individual) into a pre-specified number (k) of genetic clusters that minimizes genetic variation within each cluster. Strongly structured populations are indicated when most individuals are assigned most of their ancestry in one or the other genetic cluster and are spatially separated according to those genetic clusters. Conversely, weakly structured or unstructured (i.e., a single randomly interbreeding population) populations are indicated when most individuals are assigned to multiple clusters and, therefore, are not spatially segregated by genetic cluster. We investigated structure according to k = 2 and k = 3 clusters based on optimizing average (across 5 runs) log probabilities of the data at k = 1—4 (Pritchard et al. 2000). To maximize the sample size with respect to individuals, we performed these analyses using microsatellite genotypes of 61 independent pure-native foxes. We also performed the analyses using all 84 markers on a smaller number of individuals (n = 39) for which we had both microsatellite and SNP genotypes and found no qualitative differences (results not presented). Lastly, similarly to Sacks et al. (2010) but with a larger sample size (both loci and individuals) here, we estimated N_e using a bias-corrected linkage-equilibrium estimator calculated in LDNE (Waples 2006; Waples and Do 2008). We assumed a monogamous mating system, excluded alleles with frequencies <0.05, and used jackknife-based confidence intervals (Waples and Do 2008). To ensure that sample size exceeded 60 individuals (Tallmon et al. 2010) and to avoid use of physically linked markers (Sacks et al., submitted), we used only microsatellites for this analysis.

Morphometrics.—Two sets of morphometric comparisons were conducted based on body mass and external measurements (total body length, tail length, hind foot length, ear length from notch to tip). First, for genetically confirmed native and nonnative red foxes, *t*-tests were used to compare external measurements individually, and discriminant analyses were performed to assess morphometric differentiability based on combined morphometric variables. Hybrid individuals were excluded from these analyses. Analyses were conducted separately for males and females.

Second, we conducted morphometric comparisons among multiple subspecies and populations. Although Roest (1977) conducted a morphometric analysis of skulls of Sacramento Valley red foxes, Sierra Nevada red foxes, and other populations, including from the Midwest, the comparison apparently was confounded by the inclusion of nonnative (or hybrid) red foxes with the Sacramento Valley red fox. Recent molecular analyses indicate that at least 4 of the red foxes apparently included in Roest's sample

of 19 “Sacramento Valley red foxes” had nonnative haplotypes, including two from the Davis area (Sacks, unpublished data; WFB-10, WFB-17, UC Davis museum) and two from Richvale (B. N. Sacks et al., submitted.; M-1639, M-1640, Cal Poly San Luis Obispo museum). Moreover, Roest (1977) pooled males and females, which, given the substantial sexual dimorphism in red foxes (e.g., Storm et al. 1976), obscures differences among populations. Lastly, no analysis was conducted of post-cranial external measurements.

Therefore, we conducted sex-specific comparisons of external measurements of genetically confirmed Sacramento Valley red foxes, California nonnative red foxes, Sierra Nevada red foxes (*V. v. necator*), Cascade (*V. v. cascadensis*) red foxes, and Midwestern populations from east (Illinois) and west (Iowa) of the Mississippi River. The nonnative California sample consisted of 138 adults from coastal areas spanning San Luis Obispo north to the San Francisco Bay and inland to the northern San Joaquin Valley near Stockton (B. N. Sacks, unpublished data). Data for other populations were drawn from dissertations (Aubry 1983; Perrine 2005), published museum records (Grinnell et al. 1937), and published field studies (Storm et al. 1976). The Sacramento Valley red foxes used here included only those collected in this study, but should be augmented in the future with existing measurement data used by Roest (the native portion of his sample) and additional individuals housed in various museum collections.

Reproductive phenology.— As with other canid species, the lengths of phases of the estrous cycle, gestation period, and weaning periods are relatively invariable among populations of red foxes (Hayssen et al. 1993; Sacks 2005). Further, the seasonal timing of reproduction (e.g., ovulation) is highly synchronized within populations (Cavallini and Santini 1995). However, seasonal timing can vary substantially among populations (Storm et al. 1976; Cavallini and Santini 1995). Therefore, we focused on assessing the timing of parturition. We estimated parturition dates from body masses and hind-foot lengths of pups using Richardson’s growth curve and regression equations based on data from known-age male and female red foxes (Johnson et al. 1975; Sargeant 1978). Because growth rates become more variable after 12 weeks of age, only pups weighing $\leq$2.6 kg (corresponding to approximately 12 weeks of age) were used. We used live pups obtained opportunistically (animal control agencies, wildlife rehabilitators, or various incidental sources) and freshly recovered road-killed pups.

Reproductive Habitat.—To assess habitat selection at the landscape scale, the habitat associated with each native (as confirmed from genetic analyses) den site was characterized and compared to that of >3,000 random locations throughout the Sacramento Valley. Analyses were based on habitat composition of “locations” (den site and random), defined as 1-km^2 (i.e., radius = 564 m) circular plots centered on the den site or random point. Two comparisons were conducted. First, for each habitat class (described below), a Yates-corrected chi-square goodness-of-fit test was used to compare observed numbers of den locations containing the habitat class to the number

expected based on the proportions of random locations containing that habitat class. This analysis was primarily useful to assess proximity to important features that did not necessarily compose a large amount of area (e.g., human facilities). Second, for each habitat class, the average composition (e.g., %cover of grass) was compared between den locations and random locations. Average composition of den locations differing by $\geq$1.96 standard errors from average composition of random locations was considered statistically significant. This analysis offered a more statistically powerful way to assess selection of more extensive habitat types.

Habitat classes were based on the California Central Valley Wetlands and Riparian GIS data layer, a vegetation coverage based on 1997 Landsat imagery, projected in Teale Albers NAD83 in Vector format (CDFG 1997). This layer included 17 vegetation classes, pooled for the present study into the following 7 classes: (1) Wetland (Seasonally Flooded Estuarine Emergents, Permanently Flooded Estuarine Emergents, Tidal Estuarine Emergents, Seasonally Flooded Palustrine Emergents, Permanently Flooded Palustrine Emergents, Tidal Flats), (2) Barren (Non-Tidal Flats, Barren), (3) Flooded Agriculture (Flooded Agriculture, Seasonally Flooded Agriculture), (4) Dryland agriculture (Non-Flooded Agriculture, Orchards/Vineyards), (5) Woodland (Riparian Woody, Non-Riparian Woody), (6) Grass, (7) Human facilities (Other). Details on these classes, resolution, and interpretation of satellite imagery can be found at http://www.dfg.ca.gov/biogeodata/gis/clearinghouse.asp. Analyses were conducted using ArcView (v 3.2).

Pathogen surveillance.—Exposure rates to selected pathogens potentially causing morbidity or mortality in canids were examined by Mourad Gabriel at the Canid Diversity and Conservation Laboratory (Center for Veterinary Genetics, UC Davis) via immunofluorescent antibody assay (IFA) test, including positive and negative controls from dogs of specific pathogen free (SPF) colonies. The serological panel included canine distemper virus (CDV), parvovirus (PV), which included CPV-2 and feline panleukopenia virus (FPV), canine adenovirus-2 (CAV-2), canine herpes virus (CHV), *Neospora caninum* (NC), and *Toxoplasma gondii* (Toxo). Additionally, fecal DNA was tested for active infections with PV using a nested polymerase chain reaction (PCR) procedure (Hirasawa et al. 1994), followed by direct sequencing to differentiate CPV-2 from FPV.

Unless otherwise stated, statistical analyses were performed using Systat (v 9.0, SPSS, Inc.).

Results

Samples.—We identified 51 reproductive den sites during 2007—2009 (Fig. 1, Table 1). From these den sites, we collected >800 scats and 38 tissue samples associated with opportunistically recovered carcasses or live-captures. Additionally, 29 non-den-related samples were collected (Fig. 1). In total, samples resulted in 611 microsatellite genotypes for 299 distinct individuals.

Range delineation and hybridization with nonnative red foxes.—Genetic samples obtained during 2007—2009 verified the presence of red foxes, west of the Sacramento River, from Cottonwood in the North to Montezuma Hills in the Southwest and, east of the Sacramento River, north to Chico and south to Sacramento (Fig. 1). We received several seemingly credible reports of red foxes in the Capay Valley and strongly suspect their presence there, although we did not confirm it. No red fox samples and few reports (most of which were genetically or photographically confirmed to be of gray fox, *Urocyon cinereoargenteus*) were collected in the foothills, suggesting that native red foxes were confined to the Valley bottom. However, nonnative red foxes were verified previously in the East Bay Hills (n = 2; L. Frank, B. Sacks) and one used in this study was purportedly collected by a rehabber in Jackson.

Based on 142 independent samples, mtDNA (Fig. 2) and nuclear DNA (Fig. 3) indicated that native and nonnative red fox populations remained largely distinct, yet hybridized in a restricted zone (Moore 2009; Sacks et al., submitted). Although more sampling is needed to precisely delineate and characterize hybrid zones, most hybrids were detected at the southern end of the Sacramento Valley (Fig. 3). West of the Sacramento River, south of I-80, includes one hybrid zone, apparently a cline where red foxes directly south of I-80 are mostly or all native and those in the Montezuma Hills south of Highway 12 are hybrids with predominantly nonnative ancestry (Fig. 3). To the east of the Sacramento River, samples were sparser (probably because red foxes were generally scarcer), but suggest that hybrids may have been scattered farther north than on the west side. Although nonnative introgression also was detected in Cottonwood, west of the Sacramento River, the route of nonnative gene flow likely was from east of the river (Fig. 4). The basis for this surmise is that a large sample to the south of Cottonwood, west of the river, reflected little if any nonnative introgression and, while the Sacramento River poses a significant barrier to gene flow at its southern end, the high frequency of bridges spanning the River at the north end of the Valley likely facilitate dispersal across it.

Population genetic structure, diversity, and effective size.—Based on specification of k = 2 or 3 genetic clusters within the Sacramento Valley population (i.e., excluding hybrids and nonnative foxes), there appeared to be a small degree of structure, primarily in the south end of the Valley (Fig. 5). Based on unidirectional F_{ST} estimates between these clusters, at k = 2, the light blue cluster (as per Fig. 5) received less gene flow from the dark blue cluster (F_{ST} = 0.091) than vice versa (F_{ST} = 0.004), and, at k = 3, the light blue cluster received less gene flow from the purple and dark blue clusters (F_{ST} = 0.101) than did the dark blue or purple cluster from the other two (F_{ST} = 0.054, 0 033, respectively). These findings suggest that the predominant directions of gene flow were out of the south and southwest to the north and east. Although there was no evidence that the Sacramento River posed a significant barrier to gene flow, the small number of samples east of the River also occurred near major roads with river crossings (SR 20 and SR 113). Because genetic clusters did not correspond to any

obvious landscape barriers, it seems likely that substructure simply reflected heterogeneity in the distribution of red foxes across the landscape, possibly due to habitat or possibly due to chance, and will not necessarily remain a stable pattern. There was little evidence of population structure within the native population throughout most of the north-south length of the range. Genetic diversity, assessed in terms of observed and expected heterozygosity, also was nearly identical in the two Sacramento Valley native genetic clusters, but was considerably lower throughout the native portion of the range than in the hybrid zones or in the nonnative population (Table 2). Overall, we found little evidence to support the presence of multiple population units within the native subspecies. Moreover, the relative uniformity of genetic diversity throughout the native range, except for the hybrid zone, suggests that nonnative genetic introgression was limited, at least with respect to selectively neutral genetic variation. Based on the Sacramento Valley native sample (n = 61), the N_e estimate was 46 breeding individuals (95% jackknife confidence interval = 40—52), similar to a previously estimated 49 (29—79, Sacks et al. 2010).

Morphometric comparison.—Adult Sacramento Valley and nonnative red foxes did not significantly differ in body mass for either males or females, but Sacramento Valley red foxes were significantly larger than nonnative red foxes according to all external measurements in males and in all but one measurement in females (Table 3). A stepwise elimination procedure identified two variables, body mass and total body length, for use in discriminant analyses. The discriminant function for males was 22.889 + 1.551*body mass (kg) + 0.290*total body length (cm); the discriminant function for females was 30.239 + 1.785*body mass (kg) - 0.377*total body length (cm). To avoid over-fitting of models, exclusion of other variables was necessary due to the high correlation among linear body measurements. A leave-one-out, jackknife cross-validation analysis indicated classification of red foxes to the correct population for 83% of males and 84% of females.

To assess the morphometric relationships among a broader range of populations, average total body length was plotted against average body mass in these and 4 other populations. Body mass and linear dimensions were very similar between the two native mountain red fox subspecies (Cascade and Sierra Nevada red foxes) and did not differ significantly (although larger sample sizes might reveal small differences in the future). Therefore, these samples were combined for the present analysis. Two important results were apparent. First, the California nonnative red foxes clustered most closely with Midwestern red foxes (Fig. 6), consistent with what is known of their phylogenetic ancestry (Aubry et al. 2009; Sacks et al. 2010; Statham et al. submitted). Second, although Sacramento Valley red foxes were considerably larger in both dimensions than the mountain foxes (and are also larger in body length than Midwestern foxes), the allometric relationship was very similar for these three native western subspecies (Fig. 6), consistent with their close phylogenetic relationship (Perrine et al. 2007; Aubry et al. 2009; Sacks et al. 2010).

Reproductive phenology.—Table 4 shows the estimates for parturition dates (whelping dates) of pups in both native and nonnative populations according to both methods, indicating late February and early March as the peak. No differences in timing of reproduction were apparent between the native and nonnative populations, although variation was greater in terms of both body-mass dates and hind-foot dates in the nonnative (SD = 16.4, 15.7 days, respectively) than native population (SD = 10.2, 7.0 days). Although our whelping date estimates were based on growth curves adopted from a Midwestern population, adult body masses were similar among lowland California and Midwestern populations (e.g., Fig. 6), supporting our application of this approach based on body mass.

Litter size, recaptures, and pup mortality.— Based on a subset of scats (n = 351) collected early enough in the pup-rearing season to confidently differentiate pup scats from adult scats, 70% (n = 247) were from pups, few of which were sampled in subsequent years (see below). The average numbers of pups observed directly or via remote video at native (and hybrid) den sites (2007, 2008) indicated average minimum litter sizes of 3.2 (SD = 1.2) pups (n = 25 litters; Table 5a-c). To assess numbers of individuals identified from scats collected from den sites in any one year (which included pups and adults), only dens for which $\geq$10 scats were successfully genotyped were used, indicating an average of 7.6 individuals (SD = 2.8) from 25 den sites with an average of 18.2 scat genotypes per den site (i.e., 2.4 genotypes per individual). Thus, a crude estimate of average number of pups genotyped at dens is 5.3 pups per litter (i.e., 70% * 7.6). In the future, fecal genotype-based mark-recapture methodologies should be used to obtain more accurate estimates of litter size along with associated confidence intervals.

Few individuals were sampled in multiple years (Table 6). Of these, all four individuals initially sampled as adults were sampled at the same den site 1 or 2 years later. The 6 individuals initially sampled as pups were split, with 3 individuals sampled in their natal den sites and the other 3 sampled at different den sites. Two of these individuals, including a hybrid female from Dixon, formed a pair and produced an unusually late litter (apparently whelped in late April) in 2008. The den was not active in 2009 and the female was located a couple of miles away on the UC Davis campus; no evidence of reproduction was found in 2009. Overall, the low number of recaptures of pups among years suggests that most individuals dispersed or died.

We collected 28 carcasses of pups near den sites, where causes of mortality included automobile (n = 14), shooting (n = 2), horse-trampling (n = 1), killed by a dog (n = 1), and unknown causes (n = 10). The number of pups found dead near dens, especially those that died of unknown causes, seemed high given that we did not actively search for carcasses and did not intensively monitor most dens.

Habitat selection.—Inspection of native Sacramento Valley red fox den sites plotted on a vegetation map of the Sacramento Valley suggested a general association with grasslands and avoidance of flooded agriculture and wetlands (Fig. 7). Indeed,

statistical comparison of the areas surrounding den sites to random points in the Valley supported this association (Fig. 8). A significant positive association of den sites with grasslands was indicated both in terms of the frequency that dens were located in proximity to grasslands as well as by the amount of grasslands found in the vicinity of den sites. Avoidance of flooded agriculture for den-site placement was similarly supported by both tests, but the relationship was significant only with respect to the amount of flooded agriculture in the vicinity of den sites (Fig. 8b). Lastly, human facilities were found in proximity to den sites more frequently than expected by chance (Fig. 8a). The association was probably even stronger than indicated because human structures <0.81 ha were not represented in the vegetation coverage (CDFG 1997). On the other hand, because we were more likely to find dens in proximity to humans, these findings do not indicate that Sacramento Valley red foxes did not also den in areas far from human structures. Studies designed specifically to assess presence-absence or abundance systematically across the range of habitat variables are required to assess this possibility.

Pathogen surveillance.—The IFA tests for native Sacramento Valley red foxes are shown separately for post-mortem samples (n = 21) taken from the heart or thoracic cavity during necropsy and serological samples taken from live individuals (n = 9; Table 7). Except for PV, for which exposure was detected in one post-mortem sample, all detections were from the smaller sample of blood taken from live animals. Therefore, despite small sample size, the latter sample provided a more accurate assessment of exposure in the population. Exposure to 5 pathogens was detected in 1 to 3 of the 9 individuals. Although PV exposure was not detected in this sample, the nested PCR tests for active PV infection of a much larger number of feces (n = 574) indicated the presence of parvovirus in the population (Table 8). The test itself detects many parvoviruses; direct sequencing of 12 of the PCR-positive samples indicated that 8 (67%) detections were of CPV-2 and 4 (33%) were of FPV. Positive cases were found scattered widely, with no evidence of spatial clustering. Necropsies did not detect any canine heartworm (*Dirofilaria immitis*) in any of 12 adult native red foxes for which cardiopulmonary tissue was sufficiently intact to examine.

Discussion

A thorough status assessment of the Sacramento Valley red fox requires knowledge of the current range, abundance, and demographic parameters (e.g., survival, reproduction, and causes of mortality), all of which must be understood in the context of habitat requirements and availability, as well as emergent threats associated with recent anthropogenic activities. This report summarizes our findings based on a 3-year study intended as a first step in obtaining this knowledge. In particular, we focused on determining current range, comparisons to and interrelations with nonnative red foxes, and habitat associations of the native subspecies. Although we also presented preliminary data on minimum litter size, pup mortality, and pathogen exposure, future studies will be required to adequately assess demographic health, life history, home

range and habitat use, food habits, dispersal, cause-specific mortality, and habitat occupancy or overall abundance. Obtaining this basic information is essential to effective management and conservation of the native subspecies.

Hybridization.—Nonnative red foxes may represent the most immediate threat to the native population, primarily through hybridization, but possibly also competition and disease transmission. Because we have treated this topic in depth in a separate manuscript (Sacks et al., submitted), only a few salient points will be addressed here. First, what are the policy implications of hybridization of the native Sacramento Valley population? At present, state and federal endangered species policies address this question on a case-by-case basis (Haig and Allendorf 2006). Based on the guidelines set forth by Allendorf et al. (2001) for this purpose, however, the answer would seem straightforward. Because the Sacramento Valley red fox is a native and endemic subspecies, the population clearly warrants conservation even if hybridization with nonnative red foxes were "widespread" (Allendorf et al. 2001). Moreover, our findings suggest that hybridization was relatively localized and likely has changed little in the past several decades, suggesting hybridization is or has been confined to a relatively small portion of the native population. Thus, of greater concern is an assessment of the biological threats of hybridization to the native subspecies and the corresponding implications for management.

At present, threats associated with hybridization are largely speculative, requiring additional research to evaluate effects on fitness (among others), and monitoring to assess whether the hybrid zone could be moving or expanding. Although hybridization appears to be localized and potentially maintained in stable hybrid zones, understanding the mechanisms for this maintenance is important for predicting and managing potential changes to these conditions in the future. Moreover, nonnative genes can make their way into the native population by way of backcrossing (i.e., introgression), the extent and effects of which are presently unknown. Mapping the native, hybrid, and introduced ranges of red foxes was an essential first step, both in assessing threats of hybridization itself, and to the remainder of our objectives, which depended on clearly distinguishing among these superficially cryptic populations.

Morphometrics.—Morphometric analyses were concordant with genetic analyses in reflecting distinctions between native Sacramento Valley red foxes and nonnative red foxes, consistent with what we know of the ancestry of both populations (Perrine et al. 2007; Aubry et al. 2009, Sacks et al. 2010; Statham et al. in review). Although nonnative haplotypes originated from both eastern and Alaskan (or western Canadian) stocks, the majority were from the East, consistent with the morphometric clustering of these foxes with those from Illinois and Iowa. Although Roest (1977) concluded that Sacramento Valley red foxes were morphometrically similar to Eastern populations, as mentioned earlier, his sample was confounded by inclusion of nonnative red foxes and was weakened by pooling of both sexes. Moreover, Roest's (1977) conclusion was based strictly on univariate skull measurements, which indicated similar size ranges.

His multivariate plots of skull measurements as well as his discriminant assignments did not support this conclusion, but rather indicated the Sacramento Valley sample to be as distinct, or more so, as other subspecies. Our findings with respect to external measurements agreed qualitatively with Roest's (1977) that the Sacramento Valley red fox differed most substantially in size from the mountain subspecies (at least, Sierra Nevada and Cascade red foxes). However, consideration of body size and mass dimensions together in our analysis showed that both native California (and Cascade) subspecies shared a similar allometry that was distinct from Midwestern populations. In essence, both native California subspecies (along with the Cascade red fox) are lankier than eastern and nonnative populations.

Current range of the Sacramento Valley red fox.—The current range of the Sacramento Valley red fox population extends throughout most of the Sacramento Valley, but appears free of hybridization with nonnative red foxes primarily on the west side of the Sacramento River between I-80 and Red Bluff (Figs 2—4). Except for Cottonwood, at the far north of the Valley, most hybrids occurred to the south closer to the nonnative population. Cottonwood is situated in a low, isolated patch of Valley carved by Cottonwood Creek and is isolated from the remainder of the Sacramento Valley to the south by foothill woodland, a habitat in which we never found native red foxes. On the other hand, nonnative red foxes, which have been observed on occasion in foothill habitat (e.g., in the East Bay Hills, B. N. Sacks, personal obs.), possibly have greater access to Cottonwood. Because our method of sample collection was opportunistic, firm conclusions about relative abundance are impossible. However, based on our considerably unequal sample sizes, which may reflect unequal abundance, red foxes appeared more abundant west than east of the Sacramento River. Low fox abundance east of the Sacramento River also would be consistent with the greater portion of nonnative ancestry we observed there and with the distribution of previous sighting reports of red foxes in the Sacramento Valley (Gray 1975; Lewis et al. 1999). It is also the case that many more fur farms were located east of the Sacramento River in the early to mid 20th century (Lewis et al. 1999) and anecdotal reports suggest that nonnative red foxes may have been introduced to Rancho Cordova and east of Knights Landing in the 1960s (Appendix A). In the future, occupancy surveys (e.g., MacKenzie et al. 2006) will be necessary to accurately assess the distribution of red foxes in the hybrid zones and east of the Sacramento River, as well as across habitat types in the primarily native portion of the range.

Current abundance.—Although an estimate of current population size was beyond the scope of the present project, genetic evidence indicates a decline in abundance relative to historical levels (Sacks et al. 2010, more below). Additionally, several lines of evidence suggest that the population was sparse during our study. First, the current genetic effective population size was approximately 50 breeding individuals (Sacks et al. 2010; this study). This estimate was clearly lower than the actual population size at the time of this study, as we were aware of approximately 80

native breeding individuals and probably did not account for the majority of the population. Nevertheless, such a low genetic effective population size implies that the population abundance has reached low levels in the past and underscores its potential vulnerability in the future. Moreover, it is the genetic effective population size rather than census size (which fluctuates seasonally and annually and includes pre-recruitment individuals) that determines evolutionary potential or risk of inbreeding depression (e.g., Tallmon et al. 2010). Second, the distribution of red fox den sites appeared to be highly discontinuous, with small clusters of red foxes in some areas (e.g., Woodland, Willows) and apparently isolated den sites in others (Davis, Chico). Third, the lack of clear genetic structure throughout a large portion of the Sacramento Valley implies high dispersal, which is typically associated with low density populations (Allen and Sargeant 1993; Schwartz et al. 2005). Anecdotal evidence further suggests declines in red fox abundance since the 1970s (see below). Preliminary remote camera surveys successfully detected red foxes at control sites where we had previously confirmed their presence but failed to detect them in random locations in apparently suitable habitat (Appendix B). In the future, similar but more extensive surveys are needed to assess the spatial distribution of red foxes in the native range as well as in hybrid zones. Ideally, such surveys would simultaneously test models of habitat suitability and assess habitat occupancy, along with correlations with other mesocarnivores, particularly coyotes (*Canis latrans*) and gray foxes (see below). Additionally, the estimate of genetic effective population size presented here can be used as a basis to monitor trends over time, after about 10 years (Tallmon et al. 2010).

Historical abundance and range.—Available evidence suggests that Sacramento Valley red foxes were more abundant historically than today, especially throughout grasslands west of the Sacramento River, but also in the vicinity of the Sutter Buttes, east of the Sacramento River. Sacks et al. (2010) found significant declines in both mitochondrial and nuclear genetic diversity between historical museum and modern Sacramento Valley red fox samples. In addition, based on a larger modern sample and more nuclear markers, we detected a highly significant signature of a genetic bottleneck in the past. These indicators of population decline coincide with a loss of 65% of grassland area (i.e., irrespective of species composition) in the Sacramento Valley since historical times (Fig. 9), as calculated by Nelson et al. (2003). Although Grinnell et al. (1937) were suspicious of the origins of the Sacramento Valley population due to the distinctiveness of the habitat and climate relative to that associated with the Sierra Nevada red fox, in retrospect, their notes and the notes of other earlier naturalists are informative. It seems apparent that by the 1920s, when Grinnell et al. (1937) first became aware of Sacramento Valley red foxes, the population had already declined considerably in numbers since the late 1800s.

The earliest report of red foxes in the Sacramento Valley we are aware of was from J. S. Newberry in his 1857 “Report of the zoology of the route (for a railway connecting San Francisco to the Columbia River),” where he stated

> "…the red fox inhabits all parts of OR and CA [*meaning north of Sacramento*], but I suspect it less abundant in the central and southern portions of CA than further north. " [*transcribed and communicated by J. D. Perrine, UC Berkeley Museum of Vertebrate Zoology*]

This statement, which refers to an expedition northward through the Sacramento Valley into the Siskiyou and Cascade Ranges, suggests red foxes were encountered in the Sacramento Valley, although apparently not as commonly as in the mountains northward to the Deschutes Basin of Oregon. Later field notes were more precise. Apparently unknown to Grinnell and colleagues, J. H. Gaut's (1906) notes describe the trapping of a cross-pelage red fox (verified by photograph taken by MJS) in 1906 in St. John, CA, historically a town in northern Glenn County just east of where Orland is currently located. This specimen was accessioned in the National Museum of Natural History (USNM-146294), along with accompanying field notes and was verified to have a native haplotype (Sacks et al. 2010). Referencing red foxes in northern Glenn County, Gaut wrote

> "…they were reported to be fairly numerous….No records of these little foxes occurring on the east side of the Sacramento River could be secured. The open rolling plains on the west side of the river all the way to the eastern foothills of the coast ranges are undoubtedly inhabited by these little foxes." [*transcribed and communicated by R. Fisher*, *National Museum of Natural History*]

This description suggests that the Sacramento River, including an 8-km-wide riparian forest, could have served as an eastern range boundary for the Sacramento Valley red fox. If so, this would imply that any sporadic historical connectivity with the Sierra Nevada red fox (Sacks et al. 2010) would have been to the Mount Shasta population, e.g., linked by occasional dispersal along the Sacramento River, rather than the Lassen population to the east, which was slightly closer to the Sacramento Valley. On the other hand, red foxes apparently occurred east of the Sacramento River farther south (Grinnell et al. 1937), so it seems likely that Gaut's explorations to the east were not especially thorough and therefore do not support presumption of red fox absence in the northeastern Sacramento Valley.

Regardless of their occurence in the northeastern Sacramento Valley, Gaut's description of red fox abundance west of the Sacramento River is complemented by Joseph Grinnell's (Grinnell et al. 1937) and Adrey Borell's findings further to the south, which indicate dense populations along large tracts of continuous upland habitat. For example, describing his interview with Sam Lamme during December, 1924, Borell states

> "He is 50 years of age and has spent most of his life in this part of the country, hunting for market, ranching and running duck clubs and trapping. There used

to be a great many red fox on the plains between Butte Cr and Marysville [= *Sutter*] Buttes. He judged that he had killed 100 red foxes in that district when he was about 20 years old. Never saw a cross or black fox. During high water, these foxes took to the knolls and levees. Here the hunters went with boats and easily killed great numbers of them. Now they are all gone from that district, he has not known of one being there for several years. He never knew of one being taken in the Buttes proper. Mr. Lamme thinks these foxes are entirely different than the high Sierra Red Fox, he says that these are larger and lighter in color. He said that all the Old Timers told of foxes being there when they came." [*transcribed and communicated by J. D. Perrine, UC Berkeley Museum of Vertebrate Zoology*]

Unfortunately, the extent of the range is more difficult to assess due to a paucity of historical reports of wildlife from Yolo and Solano Counties to the south and Shasta County to the north. Grinnell et al. (1937) estimated the historical range to extend into Yolo County but not Solano County. Based on the historical distribution of grasslands south into Solano County (Nelson et al. 2003) and the lack of obvious dispersal barriers, it seems likely that red foxes occurred as far south as they do (in hybrid form) today (Fig. 9). East of the Sacramento River, however, there were relatively little valley grasslands south of what is now Chico, north of the Feather River. Although there was much grassland south (east) of the Feather River, the only evidence that red foxes occurred here until much later was an unverified record in southern Sutter County (Fig. 9, black circle). Even by the 1970s and 1990s, red fox sightings suggest they were rare or nonexistent south of the Feather River (Gray 1975; Lewis et al. 1999). We received few reports of foxes in this area and the only samples we genotyped in this area (north of Sacramento) were hybrids (Sacks et al., submitted). A long-time (>15 years) coyote trapper in Yuba County mentioned in 2005 and again in 2008 that he had never come across red foxes on Beale Air Force Base, which contains one of the most extensive tracts of remaining valley grasslands between the Feather and American Rivers (M. Frederick, USDA/APHIS/Wildlife Services, pers. comm.). The red foxes commonly observed since the 1970s south of the American River apparently are all nonnative (Sacks et al. 2010, this study).

That we stumbled upon Gaut's field notes and specimen accessioned in the National Museum in 1906, unknown to Grinnell and colleagues, suggests that a more systematic investigation of historical documents in the future might turn up additional information allowing the historical range to be better documented. Inspection of archaeological sites also could potentially provide additional records of red fox in the Sacramento Valley. At present, our best estimate is that the current and historical ranges of the Sacramento Valley red fox were similar and only slightly different from the putative range estimated by Grinnell et al. (1937) (Fig. 10). In particular, it is not clear that red foxes were historically present south and east of the Feather River or that they were necessarily absent from Solano County or Cottonwood and vicinity. Nevertheless, the magnitude of our current range estimate was similar to that of both our and

Grinnell's et al. (1937) historical range estimates. Thus, the decline in abundance discussed above apparently reflects a reduction in the average density of red foxes throughout their range rather than a reduction in the range limits per se.

Habitat use.—Our most important findings with respect to habitat use were that den sites were positively associated with grasslands and negatively associated with flooded agriculture and wetlands. These results are consistent with what we know of the historical distribution of red foxes in the Sacramento Valley. For example, in the late 1800s to 1920s, red foxes were commonly found denning in dug-out ground squirrel (*Spermophilus beecheyi*) burrows on uncultivated ridges and they avoided the lower areas more prone to seasonal flooding (Grinnell et al. 1937; J. H. Gaut, 1906, field notes). During our study, we also noted that many den sites appeared to be excavated ground squirrel burrows. Moreover, the aforementioned co-occurrence of the loss of 65% of grasslands from the Valley and decline in genetic diversity of Sacramento Valley red foxes (Nelson et al. 2003; Sacks et al. 2010) support this association. The avoidance of wetlands (cultivated or otherwise) by native red foxes apparently marks a distinction with nonnative red foxes, which have commonly been associated with impacts on several endangered prey species in coastal wetlands (Burkett and Lewis 1992; Jurek 1992). Moreover, many nonnative red fox pups were collected from the salt marshes of the San Francisco Bay, indicating that nonnative red foxes used these wetlands (e.g., levees) as reproductive habitat (B. N. Sacks, unpublished data). We did not, however, investigate whether nonnative red foxes were similarly associated with inland wetlands, for example in the Delta. Therefore, it is unclear whether landscape-scale differences in habitat selection for wetlands in particular or presence/absence in coastal regions in general best explains the observed differences in wetland use by native and nonnative red foxes. Regardless of the scale responsible for these differences, however, the result is that the nonnative red fox has invaded these sensitive habitats and, for reasons unknown, the native subspecies has not.

The observed association of den sites with human facilities also warrants comment. This finding could partly reflect a bias in our sampling, reliance on sighting reports, in that we were more likely to hear reports of foxes with den sites close to human facilities. Additionally, however, it probably reflects a tendency for foxes to seek out human facilities, possibly as a strategy for avoiding coyotes. For example, we documented several dens under sheds or woodpiles, in culverts, road cuts, and between buildings. Radio-collared individuals also were usually located in edge habitat sandwiched between human facilities and open agricultural expanses and apparently avoided areas farther from human structures unless heavy cover was nearby (Sacks et al., unpublished data). While it was not uncommon to find den sites on the edge of small towns, however, we did not find native den sites in highly urbanized locations as we did with nonnative red foxes, e.g., in South Sacramento. Lewis et al. (1993) also documented a dense population of nonnative red foxes in urban Southern California and nonnative red foxes are commonly found in urbanized parts of Bakersfield (B. Cypher, CSU Stanislaus, Endangered Species Recovery Program, pers. comm.).

Based on findings in other parts of North America where red foxes and coyotes co-occur, it is likely that red foxes use proximity to human structures as a way of avoiding coyotes, which are likely important determinants of red fox distribution and abundance (Dekker 1983; Sargeant et al. 1987; Sargeant and Allen 1989; Gosselink et al. 2003; Van Etten et al. 2007). Gray foxes also could affect the distribution and abundance of Sacramento Valley red foxes, for example, through exploitative competition, e.g., resulting in exclusion from riparian or patches of dense vegetation capable of providing refuge from coyotes. However, direct interference from coyotes is probably far more significant than exploitative competition with gray foxes. Red fox abundance apparently declined in the Sacramento Valley since the 1970s concomitant with an increase in coyote abundance, the latter likely resulting from the federal ban in 1972 on widespread use of toxicants for predator control (Sacks and Neale 2007). A study conducted in 1977 on the Sacramento River National Wildlife Refuge, where Grinnell et al. (1937) had previously documented red foxes, reported 6 red fox dens and hundreds of red fox scats, and found little evidence (1 putative coyote scat) of coyote presence (Moore 1982). More recently, a supervising biologist stationed at this refuge reported that he had never seen or heard of a red fox on the refuge during his tenure there (1989—2007), although coyotes were abundant (M. Wolder, USFWS, personal communication). Another long-time resident of Glenn County (a 50-year-old man in 2007) mentioned having seen red foxes almost daily when he was young but not having seen one in 20 years, until discovering a den southwest of Williams in 2007; he also reported observing the opposite trend in coyotes (J. Lausten, Maxwell resident, personal communication). A professional coyote trapper, also a life-long resident of Glenn County, communicated similar observations although he also was aware of several current red fox dens in the area (D. Davis, USDA/Wildlife Services, personal communication). Finally, corresponding increases in coyote abundance and declines in red fox abundance have been well-documented in other regions since the 1972 federal restrictions on coyote control (Gosselink et al. 2003).

More directly, during the present study, we obtained several anecdotal reports or observation suggesting that coyotes sometimes chased or otherwise antagonized red foxes, in some cases possibly causing failure of red fox dens (Appendix A). We also observed red fox dens frequently in proximity to dogs. In one case, a pup was killed by a dog (Red Bluff) and, in another, red foxes relocated a den after a landowner reported that his dogs chased an adult fox (Willows). However, other residents reported that their dogs tolerated or appeared uninterested in red foxes denning on the property, in which case dogs may have provided some protection from coyotes. Studies that have obtained detailed data on red fox and coyote interactions suggest that they range in space and time, from tolerance to killing, depending on habitat, food scarcity, and other factors (Sargeant et al. 1987; Sargeant and Allen 1989; Gese et al. 1996; Gosselink et al. 2003). Studies of sympatric kit foxes (*V. macrotis mutica*) and coyotes in California further indicate that such habitat-mediated effects on interactions result in differential fox survival rates (Nelson et al. 2007). Thus, contemporary effects of coyotes on the Sacramento Valley red fox population are likely to be complex and habitat-dependent.

It is a matter of speculation as to how red foxes historically co-existed with coyotes in the Sacramento Valley. It is possible that the once extensive riparian forests provided edge habitat with a similar protective function. Native Americans and their dogs also might have provided some refuge for red foxes from coyotes. An especially intriguing hypothesis is that the considerably larger body size of Sacramento Valley red foxes relative to the closely related Sierra Nevada red foxes (which historically occurred where coyotes were scarce) reflects an adaptation to co-existence with coyotes. Future studies clearly are needed to investigate the nature and importance of interspecific interactions of Sacramento Valley red foxes with coyotes and gray foxes in the context of habitat.

Pathogens.— Our sample size of sera was too small to estimate pathogen-specific antibody prevalence. Likewise, despite the relatively large sample size for our fecal PCR test for parvovirus shedding, this test was apparently a very inefficient way to assess the presence of the pathogen at a den site. Although we tested multiple scats for several positive individuals, we never obtained positive tests in >1 of these samples per individual nor did we obtain positive results >1 time at any den. This inefficiency can probably be explained by observations that red foxes experimentally inoculated with CPV-2 shed the virus in feces only sporadically (Barker et al. 1983). Nevertheless, the fact that we detected this pathogen at 32% of the native dens suggests that CPV-2 could be widespread in the population despite our failure to detect antibodies in any of the 9 sera. Moreover, we detected antibodies to the other 5 pathogens, most noteworthy, canine distemper virus, *Toxoplasma gondii*, and *Neospora caninum*.

Exposure to canine distemper has been reported in low frequency (<5%) in other wild red fox populations (Davidson et al. 1992; Truyen et al. 1998) and has been the greatest disease concern for red fox fur farms (Rikula et al. 2001). However, epizootic mortality, as can occur in gray foxes and Island foxes (*U. littoralis*) (e.g., Clifford et al. 2006), has not been reported in red foxes (Davidson et al. 1992; Little et al. 1998). In the early 1980s, parvovirus (CPV-2) caused epidemic mortality in wild and domestic canid populations, including in California (Thomas et al. 1984; Windberg 1995; Sacks and Neale 2007). More recently, however, CPV-2 has been found to be endemic in other North American red fox populations and California kit fox and island fox populations, with >75% seroprevalence, without necessarily causing acute effects on the population (Barker et al. 1983; McCue and O'Farrell 1988; Davidson et al. 1992; Clifford et al. 2006). On the other hand, endemic CPV-2 has been associated with chronic effects, including reduced juvenile survival in wolves (Mech et al. 2008). Moreover, CPV-2 may exacerbate effects of other pathogens, such as *T. gondii* (Clifford et al. 2006), exposure to which we detected in half of the 6 sera tested. We observed cats, the definitive hosts of *T. gondii*, frequently in the vicinity of red fox dens, probably due to their tendency to be located near human structures. Our detection of antibodies to *Neospora caninum* also was noteworthy as this pathogen, carried by dogs and coyotes, is known to cause acute neurological disease in dogs and has been observed also in red foxes (Dubey 2003). Heartworm is probably not an important concern

because the primary habitat in California for canine heartworm transmission occurs in foothill woodlands (Sacks et al. 2004). Future studies should continue to monitor exposure of red foxes to potential pathogens, but will be most informative in the context of systematic studies of cause-specific mortality.

Conclusions, Recommendations, and Future Research Needs

The Sacramento Valley red fox is an endemic subspecies native to California (Perrine et al. 2007; Sacks et al. 2010). Results from the present study further support the genetic, phenotypic, and ecological distinctiveness of the Sacramento Valley red fox both from the Sierra Nevada red fox and from nonnative red foxes. Whether the Sacramento Valley population is currently stable, in decline, or increasing cannot be assessed from existing data and should be investigated with high priority. Nevertheless, the apparent decline in abundance from historical levels, associated loss of valley grasslands, generally low genetic effective population size, apparently sparse distribution, restricted range, and hybridization with nonnative foxes suggest this population is vulnerable. At present, the Sacramento Valley red fox appears to satisfy at least two criteria recommending it as a California State Species of Special Concern (Comrack et al. 2008): (1) “is experiencing, or formerly experienced, serious (noncyclical) population declines or range retractions (not reversed) that, if continued or resumed, could qualify it for State threatened or endangered status.” and (2) “has naturally small populations exhibiting high susceptibility to risk from any factor(s), that if realized, could lead to declines that would qualify it for State threatened or endangered status.”

While current information is insufficient to devise a comprehensive conservation strategy (and additional research is therefore critical), some tentative conclusions seem warranted. Although our understanding of the habitat requirements of the Sacramento Valley red fox is superficial, our findings suggest it can be enhanced though grassland preservation, including the mammalian and avian prey base, especially in proximity to escape cover (e.g., blackberry thickets). Moreover, because it seems likely that red foxes historically used similar cover types to avoid coyotes, encouragement of such cover in grass and rangelands could provide important refuges from coyotes. The apparent affinity of modern-day red foxes for grasslands at the edge of or in proximity to human structures may substitute to some extent for historical modes of protection from coyotes, but also potentially exposes red foxes to a host of alternative threats, including feeding by well-meaning residents, depredation of chickens owned by well-defended residents, exposure to pathogens carried by domestic animals, secondary poisoning associated with rodenticides, and proximity to roads and, therefore, high vehicle mortality. Thus, public outreach and education also may be especially important conservation tools for this species which inhabits a landscape composed chiefly of privately owned land. Specific recommendations for land management likely to benefit Sacramento Valley red foxes include avoidance of rodenticide use, planting or maintaining hedgerows, woodlots, riparian and brushy vegetation in upland areas likely to provide prey habitat and escape cover, securing pet food, poultry, and pets, refraining

from feeding red foxes intentionally or otherwise, and, in the vicinity of (e.g., 100 m) den sites, especially during February through March, avoid offroad vehicle use, disking, grading, construction, and excessive irrigation likely to flood dens (see also CDFG 2009). Lastly, focal efforts by appropriate agencies/personnel to remove nonnative red foxes from locations where hybridization occurs could potentially help stem nonnative introgression, although more information on movement corridors would be helpful in selecting target locations.

Ultimately, a comprehensive conservation strategy for the Sacramento Valley red fox and status assessment require additional information, in particular, corresponding to 3 areas: (1) threats posed by hybridization with nonnative red foxes, (2) detailed habitat relationships, occupancy, and abundance, including interspecific relationships with coyotes and gray foxes, and (3) population growth rate (survival, reproduction) and cause-specific mortality.

Personnel and cooperators

Graduate student researchers included Marcelle Moore (CSUS, MS graduate), Gina Tarbill (CSUS, MS student), Karen Converse (CSUS, MS student), and Mourad Gabriel (PhD student at UC Davis). Field work was coordinated by B. Sacks, M. Statham, and H. Wittmer and laboratory work by B. Sacks and M. Statham. M. Moore's thesis was completed in August 2009 and dealt with assessing and quantifying hybridization of native and nonnative red foxes. G. Tarbill and K. Converse completed a pilot project using camera stations to detect red foxes in un-surveyed locations. K. Converse's MS thesis is in progress, using noninvasive genetic tools to assess multiannual turnover of breeding foxes and social relationships within established resident territories. M. Gabriel conducted surveillance for pathogens. Several DFG biologists, managers, veterinarians, and scientific aids contributed significantly to field work and other aspects of the project, including Armand Gonzales, Terri Weist, Pete Figura, Steve Burton, Jennifer Carlson, Jamie Gannon, Karen Converse, and Pam Swift. Numerous student interns and assistants from CSUS, UC Davis, American River College, and the community also contributed to field and laboratory duties, including K. Ahrens, W. Bachman, A. Brodsky, S. Brown, R. Chhokar, M. Croom, A. Davignon, L. Douglas, J. Draper, Y. Ferreira, T. Fleming, R. Gutstein, M. Hancock, J. Krantz, C. Laursen, E. Long, D. Lytle-Hoover, A. Richards, J. Schaefer, Z. Smith, Q. Voyce, J. Wallace, P. Williams, and L. Wong.

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Table 1. Approximate locations (<1.9 km) and status of 51 red fox reproductive den or pup rendezvous sites found in the Sacramento Valley and vicinity during 2007--2009.

Population[1]	Den name	Den ID	Lat[2]	Lon	Status (07/08/09) [3]
Native range			XXX	XXX	
	Davis1	1	XXX	XXX	a/a/a
	Davis2	2[1]	XXX	XXX	?/a/i
	Woodland1	3	XXX	XXX	a/i/i
	Woodland2	4	XXX	XXX	i/a/a
	Madison1	5	XXX	XXX	a/a/a
	Zamora1	7	XXX	XXX	a/a/a*
	Esparto1	9	XXX	XXX	a/a/i
	Vacaville1	10	XXX	XXX	a/a/a
	Vacaville3	11	XXX	XXX	a/?/i
	Vacaville2	12[1]	XXX	XXX	a/a/i
	Yolo1	13	XXX	XXX	a/a/?
	Dixon1	14[1]	XXX	XXX	a/a/?
	Woodland3	15	XXX	XXX	a/a/i
	Arbuckle1	17	XXX	XXX	?/a/?
	Chico1	19	XXX	XXX	a/?/a
	Red Bluff1	21	XXX	XXX	a/i/i
	Williams1	22	XXX	XXX	a/?/?
	KnightsLanding1	23	XXX	XXX	?/a*/?
	Arbuckle2	27	XXX	XXX	?/?/a
	Williams2	28	XXX	XXX	?/?/a
	KnightsLanding2	29	XXX	XXX	?/?/a
	Dixon2	30	XXX	XXX	?/a*/?
	Dixon3	31	XXX	XXX	?/?/a
	SutterButtes1	32	XXX	XXX	a*/a*/a
	Cottonwood1	33	XXX	XXX	?/?/a
	Grimes	34	XXX	XXX	?/?/a
	Willows1	35	XXX	XXX	?/?/a
	Willows2	36	XXX	XXX	?/?/a
	Live Oak den	38	XXX	XXX	?/a*/a
	Cottonwood2	39[1]	XXX	XXX	?/?/a
	Vacaville4	40	XXX	XXX	a*/a*/a
	Williams3	43	XXX	XXX	?/?/a
	Arbuckle3	44	XXX	XXX	?/a*/a
	Corning	46	XXX	XXX	?/?/a
	Gerber	50	XXX	XXX	?/?/a

Population[1]	**Den name**	**Den ID**	**Lat[2]**	**Lon**	**Status (07/08/09) [3]**
Native range					
	Orland	51	XXX	XXX	?/a*/a
	Willows3	52	XXX	XXX	?/?/a
	Willows4	53	XXX	XXX	?/?/a
	Willows5	54	XXX	XXX	?/?/a
	Willows6	55	XXX	XXX	?/?/a
	Willows7	56	XXX	XXX	?/?/a
	Yolo County Airport	58	XXX	XXX	?/?/a
Hybrid zone					
	Natomas1	18	XXX	XXX	?/a/?
	MontezumaHills1	20	XXX	XXX	a/?/?
	Bird Landing	37	XXX	XXX	?/?/a
Non-native range					
	Wilton1 (nonnative)	24	XXX	XXX	?/a/a
	Wilton2 (nonnative)	25	XXX	XXX	?/a/a
	SouthSac1	26	XXX	XXX	?/a*/a*
	Herald	42	XXX	XXX	?/?/a
	Wilton3 (nonnative)	57	XXX	XXX	?/?/a
	Martinez	59	XXX	XXX	?/?/a

[1] Three dens (2, 12, 14) with hybrid ancestry occurred just south of I-80, but north of the primary hybrid zone and one other occurred in Cottonwood (39).
[2]The precision of latitude-longitude coordinates presented in this table was intended to be as high as possible while protecting the privacy of individuals on whose residences den sites occurred.
[3]Status in years 2007 (07), 2008 (08), and 2009 (09); a = active, i = inactive, * = unconfirmed or determined through interviews with residents; ? = unknown status

Table 2. Expected (H_e) and observed (H_o) heterozygosity estimated from independent red fox samples in three zones relative to the Sacramento Valley, 2007--2009.

Zone	Subsample[1]	No. individuals	H_e (SD)	H_o (SD)
Native				
	Total native	61	0.63 (0.03)	0.58 (0.01)
	light blue cluster	36	0.62 (0.03)	0.58 (0.01)
	dark blue cluster	19	0.61 (0.03)	0.58 (0.02)
	Total in range	70	0.64 (0.03)	0.58 (0.01)
Hybrid zones		5	0.70 (0.03)	0.68 (0.04)
Nonnative		9	0.69 (0.03)	0.65 (0.03)

[1]Total number of native individuals (excluding hybrids) was further subdivided into genetic clusters ("light blue" or "dark blue") according to the Structure analysis at k =2 (Fig. 5) if their ancestry was estimated to be ≥80% in one or the other cluster (n = 55). The total in range additionally includes individuals with some nonnative ancestry as detected previously (Sacks et al., submitted).

Table 3. Comparison of body mass and standard external measurements between adult male and female native Sacramento Valley (SV) and nonnative introduced (I) California red foxes. Measurements of I red foxes were from B. N. Sacks (unpublished data).

	Males				Females			
	n (SV), *n* (I)	SV	I	*P*[2]	*n* (SV), *n* (I)	SV	I	*P*
Mass (kg)	12, 72	4.7	4.8	(0.72)	5, 58	4.0	4.1	(0.59)
TBL[1]	11, 79	108.8	104.3	<0.001	6, 59	104.5	99.3	<0.001
TL	11, 79	41.6	39.0	<0.001	6, 59	39.2	37.1	0.01
HF	11, 79	17.2	16.6	0.01	6, 59	16.2	15.9	(0.26)
EL	11, 79	9.5	9.1	0.02	6, 59	9.3	8.8	0.01

[1]TBL = total body length (cm), TL=tail length, HF=hind foot length, EL = ear length
[2]*P*-values based on 2-tailed *t*-tests; parentheses indicate nonsignificant comparisons.

Table 4. Estimates of whelping dates based on body mass and hind foot[1] measurements of pups from native and nonnative litters from lowland California.

	Body mass estimate			Hind foot estimate[1]		
	n	Average	95% CI	*n*	Average	95% CI
Native	11	5Mar	(26Feb--11Mar)	9	1Mar	(24Feb--6Mar)
Nonnative	19	8Mar	(28Feb--15Mar)	19	4Mar	(24Feb--12Mar)

[1]Estimate based on equations of Johnson et al. (1975), except 5 mm was first subtracted from our measurements of hind foot length (which included the claw) to bring estimates in line with those based on estimates from body mass. The body mass estimate was presumed less variable among populations based on morphometric comparisons of adults (see Table 3, Fig. 6).

Table 5a. Numbers of individual red foxes identified through genetic analyses and visual or remote video observation at dens in 2007.

Den ID	No. scats	No. genetic individuals	No. pups sighted
1	19	9	5
2	1	1	0
3	12	9	4
4	0	0	1
5	5	3	4
7	13	5	3
9	6	5	3
10	3	2	3
11	4	4	3
12	4	3	1
13	0	0	5
14	5	5	4
19	4	3	4
22	0	0	3

Table 5b. Numbers of individual red foxes identified through genetic analyses and visual or remote video observation at dens in 2008.

Den ID	No. scats	No. genetic individuals	No. pups sighted
1	20	9	3
2	24	8	3
4	17	5	3
5	14	7	11
7	11	5	1
9	2	2	3
10	7	4	5
12	13	6	4
13	3	3	4
14	--	--	2
15	16	6	3
17	0	0	2
18	3	3	0

Table 5c. Numbers of scats collected and individual red foxes identified through genetic analyses at dens in 2009.

Zone	Den ID	No. scats	No. genetic individuals
Native			
	1	42	15
	4	37	10
	5	21	8
	7	1	1
	10	19	7
	13	1	1
	19	14	5
	27	13	3
	28	17	7
	29	12	6
	30	1	1
	31	19	10
	33	3	2
	34	18	11
	35	5	3
	39[1]	1	1
	40	37	12
	43	4	2
	44	8	4
	46	14	9
	50	6	3
	51	4	2
	52	7	3
	54	5	3
	55	7	5
	56	11	7
	58	2	2
Hybrid			
	37	10	3
Nonnative			
	24	4	3
	25	1	1
	42	10	8

[1] Three dens (2, 12, 14) with hybrid ancestry occurred just south of I-80, but north of the primary hybrid zone and one other occurred in Cottonwood (39).

Table 6. Table of individuals genotyped in multiple years, indicating genetically determined sex (Moore et al. 2009), population, age (based on scat size), and locations sampled by year.

Individual ID	Sex	Population	Age 1st sampled	Nearest den or sample site 2007	2008	2009
5	M	native	adult	Esparto1	Esparto1	--
44	U	native	adult	Esparto1	Esparto1	--
36	F	native	adult	Davis1[1]	Davis1	Davis1
166	M	native	adult	Madison1	--	Madison1
18	M	native	pup	--	Davis1	Davis1
20	F	native	pup	--	Davis1	Davis1
203	F	native	pup	Zamora1	--	Zamora1
7	M	native	pup	Zamora1	Davis2[2]	--
10	F	hybrid	pup	Dixon1	Davis2[3]	UCD campus
46	M	native	pup	Davis1	Davis2[3]	--

[1]Female 36 was not directly sampled in 2007 but was determined via parentage analysis to be the mother of the pups sampled that year.
[2]Male 7 was sampled from a single scat near the Davis2 den in 2008 but was unrelated to parents and pups associated with that den site.
[3]Female 10 and Male 46 were found to be parents of the pups in the Davis2 den in 2008, which was not present in 2009. Female 10 was subsequently discovered in 2009 on the UC Davis campus, seen and sampled multiple times; no den associated with this female was discovered that year.

Table 7. Results of serological testing for exposure to selected canine pathogens in post-mortem blood (n = 21) and supernatant from EDTA whole blood or serum from live animals (n = 9) (M. Gabriel, unpublished data).

	Post-mortem blood		Sera (live animals)	
Pathogen (titer)	negative	positive	negative	positive
CDV[1] (1:8)	21	0	7	2
PV (1:8)	20	1	9	0
Toxo (1:64)	21	0	6	3
CAV-2 (1:8)	--	--	6	3
CHV (1:8)	--	--	8	1
NC (1:64)	--	--	6	3

[1]canine distemper virus (CDV), parvovirus (PV), *Toxoplasma gondii* (Toxo), canine adenovirus-2 (CAV-2), canine herpes virus (CHV), *Neospora caninum* (NC). Positive cutoff titers are indicated to the right of the pathogen.
Note: "PV" included CPV-2 and FPV

Table 8. Results of nested PCR tests for parvovirus (M. Gabriel, unpublished data) of 574 red fox feces collected from 49 den sites 2007—2009 in lowland California, organized according to whether dens were genetically identified as native (SVRF), hybrid, or nonnative.

	No. dens	No. scats	No. positive
Native	40	501	13
Hybrid	3	48	1
Nonnative	6	25	2

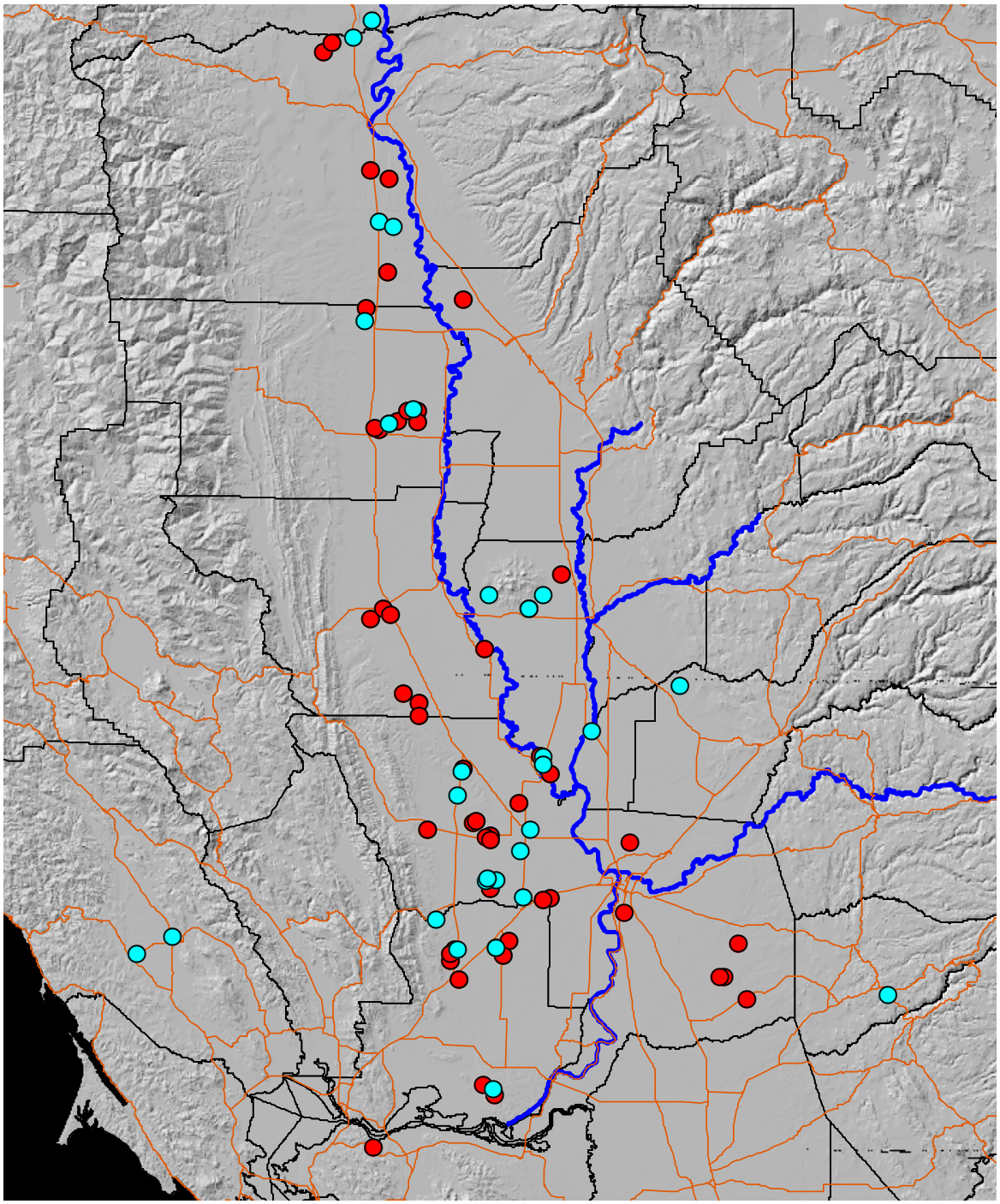


Figure 1. Red fox den sites (red circles, n = 51) and locations of non-den-related (e.g., road kills, live-captures) samples (blue circles, n = 29) from the Sacramento Valley and vicinity, 2007-2009. Also shown are major waterways (blue lines), county boundaries (black lines), major roadways (red lines), and topographic relief (California Gap Analysis project; http://www.biogeog.ucsb.edu/projects/gap/gap_data.html).

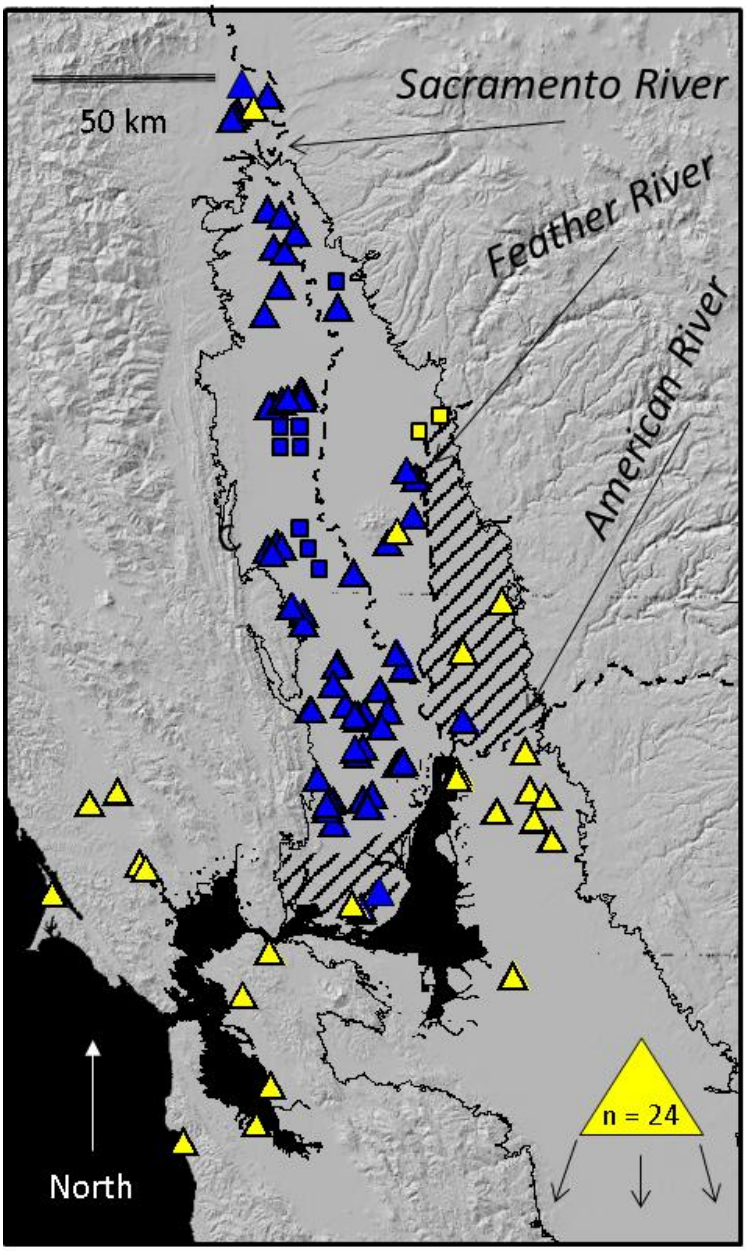


Figure 2. Mitochondrial (mtDNA) cytochrome *b* haplotype distribution for 142 modern (triangles) and 10 museum (squares, 1976—1977) red fox samples, indicating native (blue) or nonnative (yellow) origins (includes data from Sacks et al. 2010). Although mtDNA reflects matriline only, nuclear analyses (see Fig 3) indicate foxes sampled in the 2 cross-hatched zones in the southeast and southwest Sacramento Valley were hybrids. Nonnative red foxes occur in the San Joaquin Valley (SJV) and coastal lowlands north and south of the Bay. The large yellow triangle reflects 24 nonnative samples from south of the map extent (primarily from the SJV).

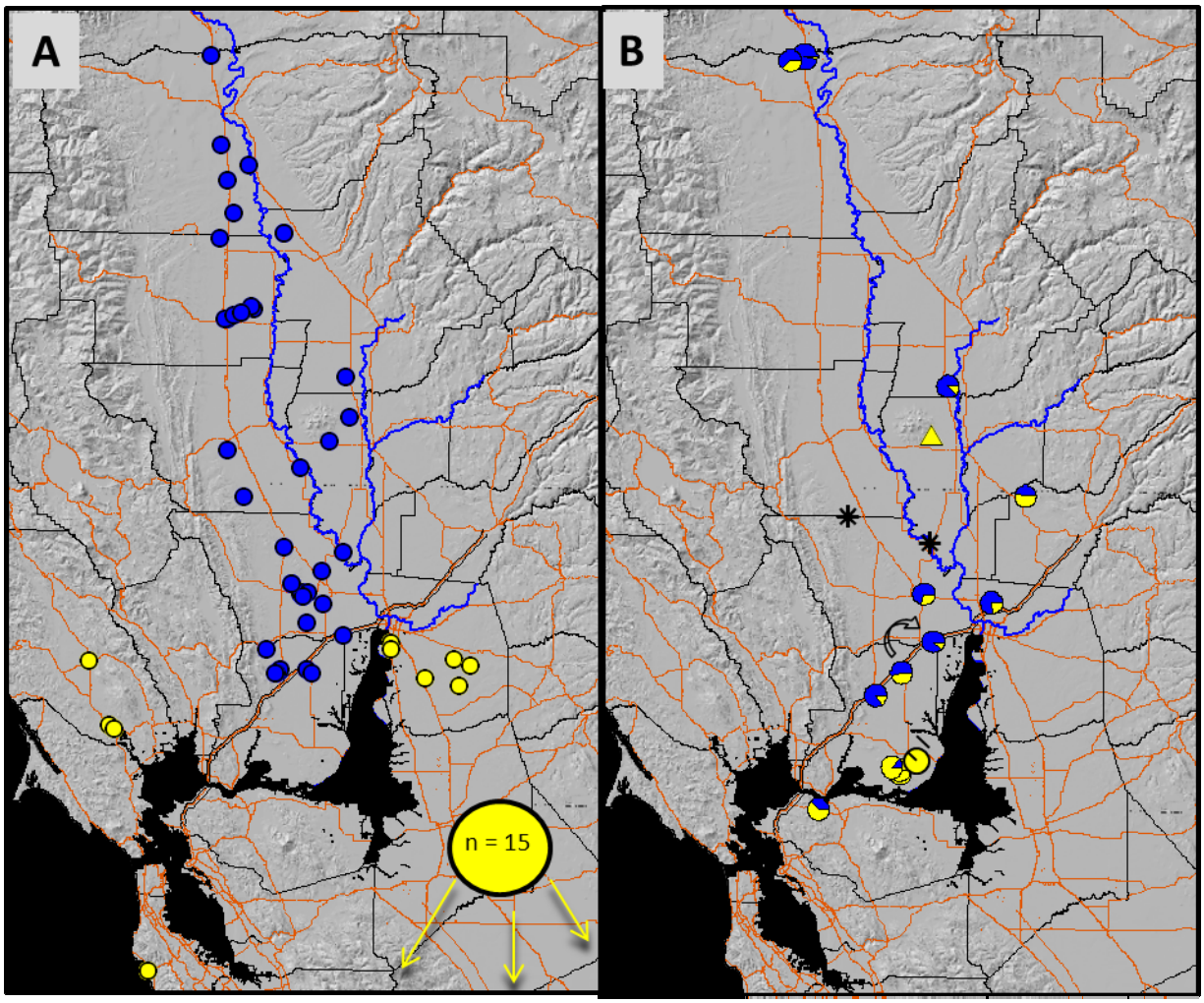


Figure 3. Locations of red fox samples with ancestry assigned fully or partially to native and nonnative populations based on 33 microsatellites and 51 SNPs (details in Sacks et al., submitted). County lines are shown in black, major roads in orange (I-80 by a double-line), and rivers in blue. (A) samples assigned to their home population as pure ($q > 0.97$, $q < 0.03$) native Sacramento Valley red foxes (blue circles) and nonnative red foxes (yellow circles); Large yellow circle reflects 15 samples from further south. (B) samples identified as hybrids, with pie charts indicating estimated proportions of native (blue) and nonnative (yellow) ancestry. Asterisks (*) indicate possible second- or third-generation backcrosses ($q = 0.94$—0.96). The yellow triangle indicates an individual that had a nonnative mtDNA haplotype but which had insufficient DNA to be genotyped at nuclear loci. The curved arrow indicates dispersal of a hybrid female from Dixon to Davis and her back-crossed offspring.

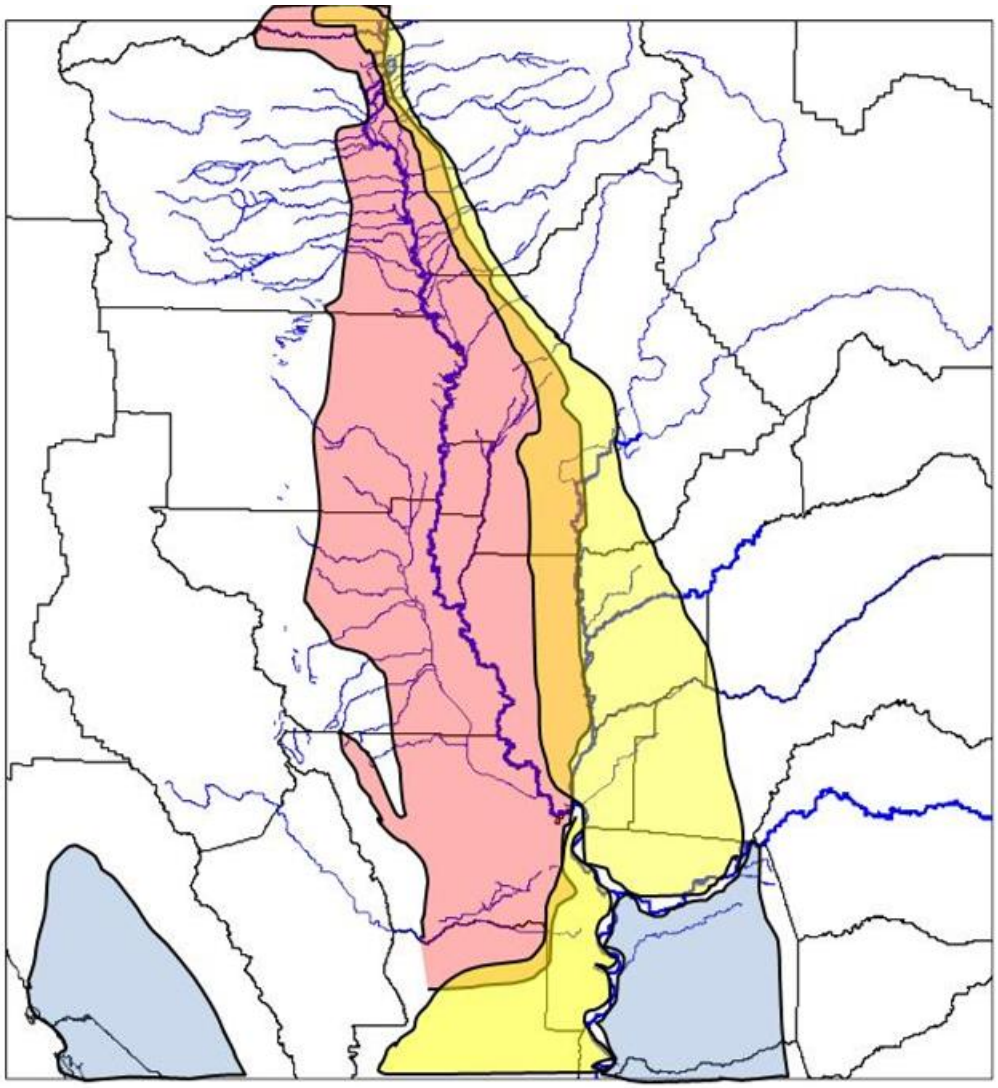


Figure 4. Estimated current range of the native Sacramento Valley red fox (red) along with hybrid zones (yellow), northern extent of nonnative range (blue), and areas of native-hybrid sympatry (orange). Fox density may be relatively low throughout most of the hybrid zones. Continuity of the eastern edge of the hybrid zone, as illustrated, is hypothetical; alternatively, hybrids at the north end of the range could reflect an isolated hybrid population.

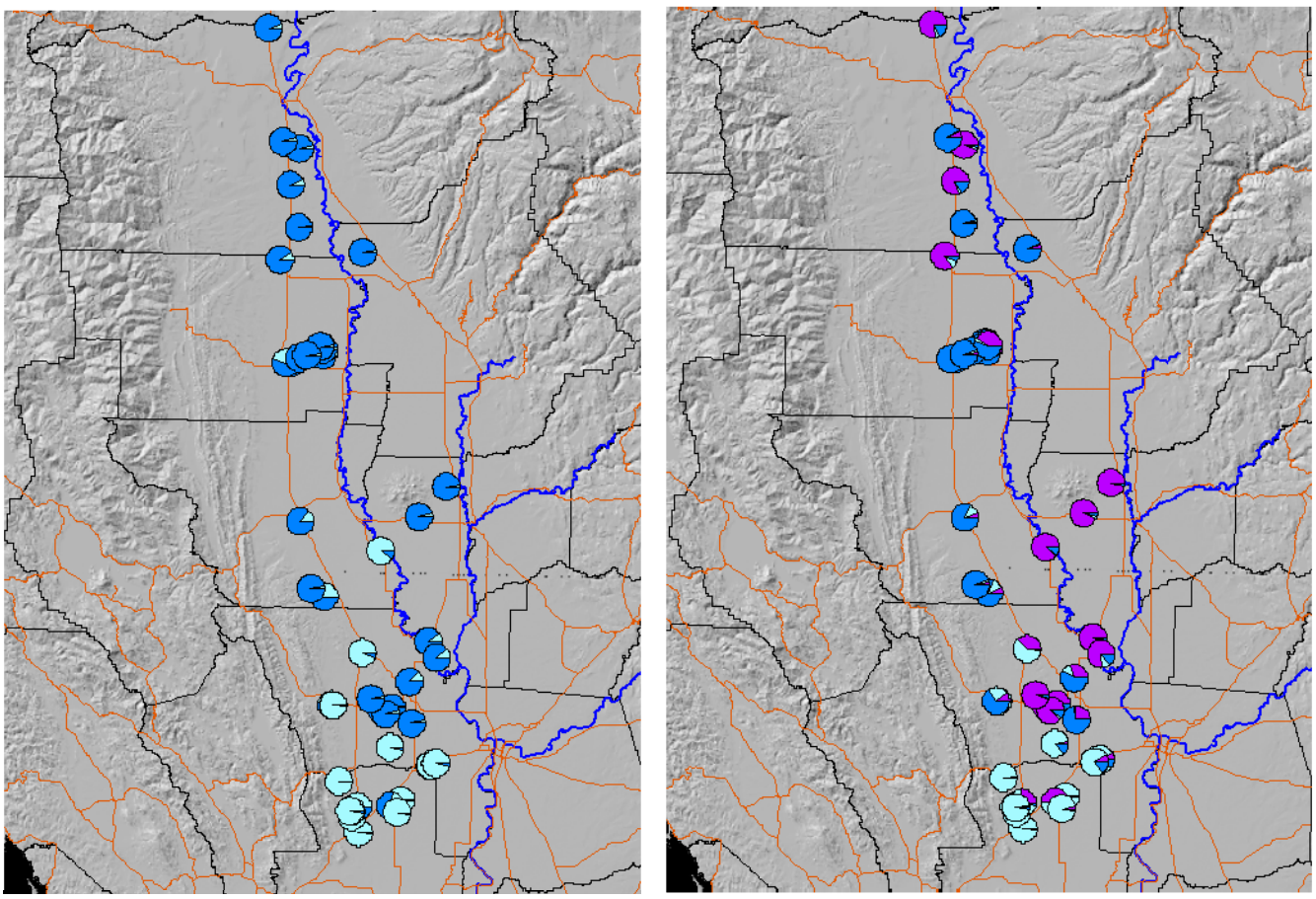


Figure 5. Population substructure within the native Sacramento Valley red fox based on analysis of 33 microsatellite loci in 61 independent samples collected 2007—2009 previously determined to have >98% native ancestry (blue circles in Fig. 3A). Pie charts reflect proportional assignment to k = 2 (left) and k = 3 (right) genetic clusters, estimated in program Structure according to the admixture model with no prior information and correlated allele frequencies (runs involved 20,000 cycles, of which the first 10,000 were discarded as burn-in). County lines are shown in black, major roads in orange, and rivers in blue.

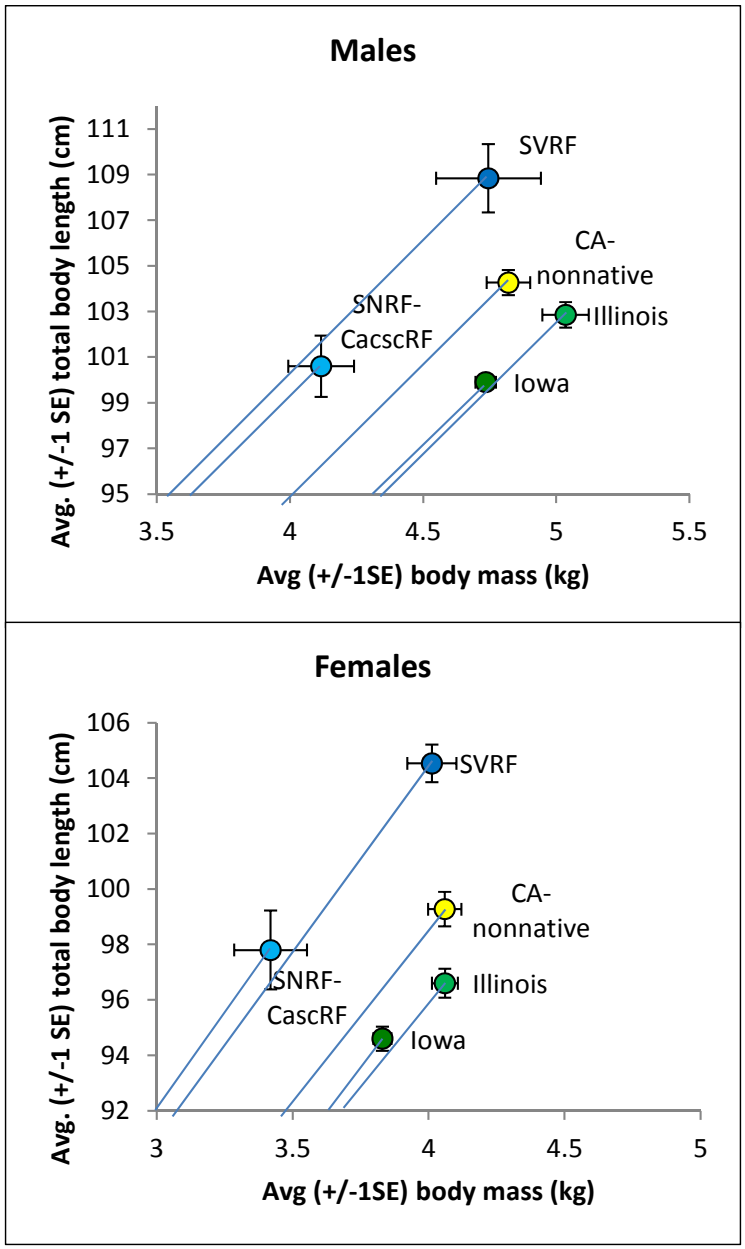


Fig. 6. Relationships between total body length and body mass of adults in native Sacramento Valley red foxes (SVRF), native Sierra Nevada and Cascade red foxes (SNRF-CascRF), California nonnative (CA-nonnative) red foxes, and Midwestern red foxes (Illinois, Iowa), shown separately for males and females. CA-nonnative red foxes cluster with Midwestern red foxes, especially those east of the Mississippi River (Illinois) and size differences are greatest between native mountain and valley subspecies. However, the native SNRF-Casc and SVRF exhibit similar allometry, distinct from that of Midwestern populations, with the nonnative California population somewhat intermediate. Lines indicate the allometric slope expected according to the terrestrial (and non-volant) mammal-specific scaling exponent, 0.334 (Silva 1998). (References for Iowa, Illinois, SNRF, and Cascade fox data are listed in the Methods section.)

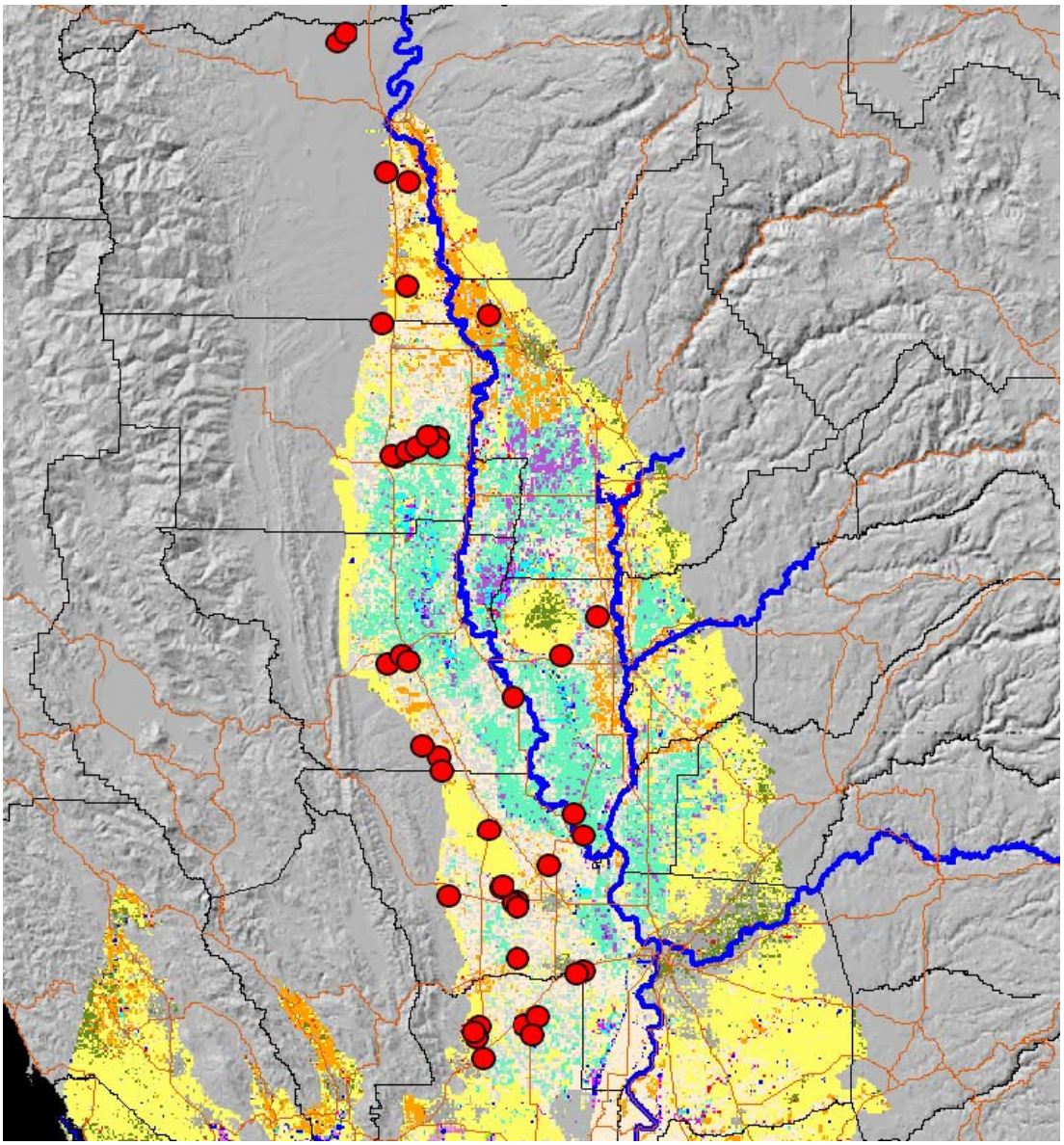
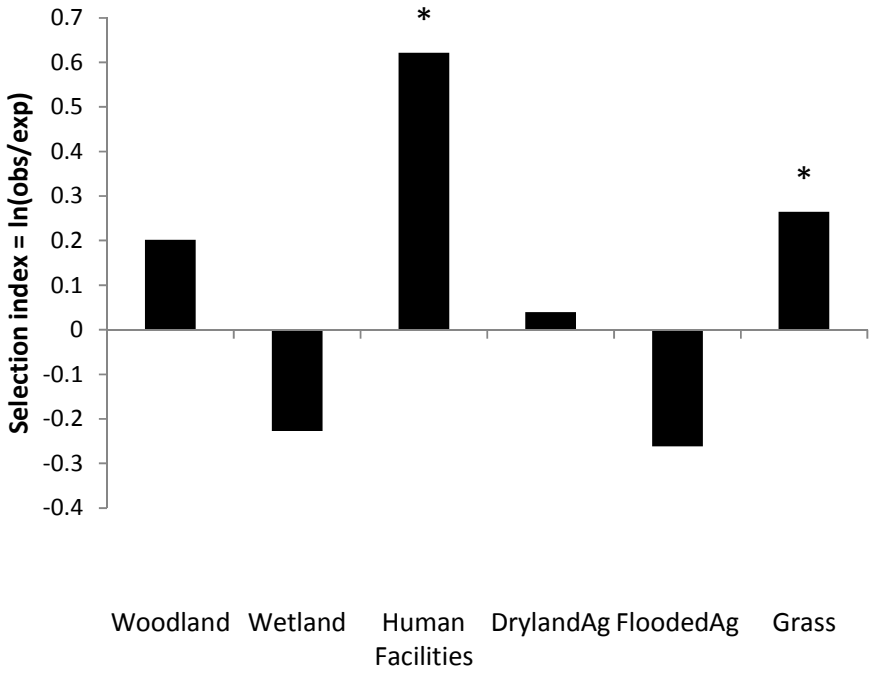


Fig 7. Distribution of native Sacramento Valley red fox dens relative to 17 vegetation classes defined according to 1997 Landsat imagery (CDFG 1997; http://www.dfg.ca.gov/biogeodata/gis/clearinghouse.asp). County lines are shown in black, waterways in blue, and major roads in orange.

A



B

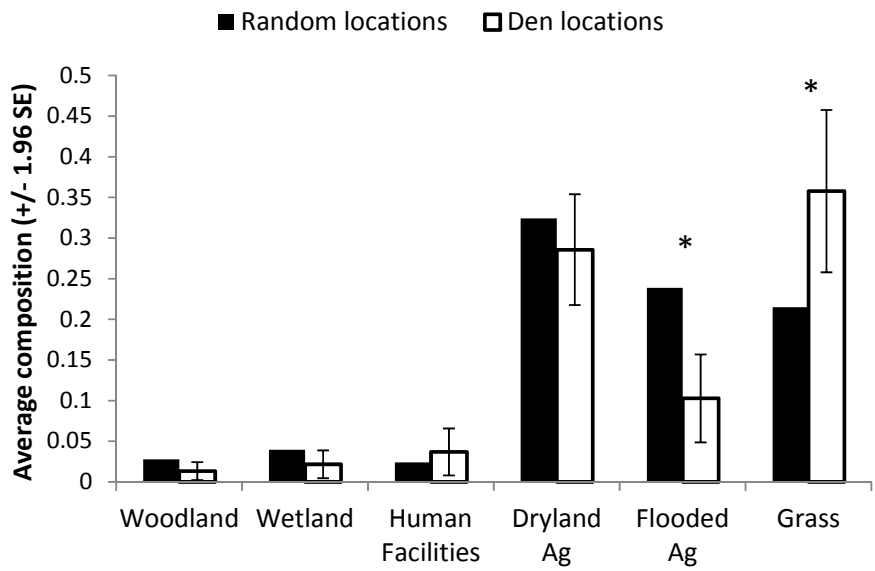


Fig. 8. Habitat composition of 1-km^2 areas surrounding 41 native den sites vs. 3,224 random sites in the Sacramento Valley. (A) habitat selection indexes, with positive values indicating higher-than-random frequency and negative values indicating lower-than-random frequency in den locations; (B) Average composition around den sites versus random sites. * indicates $P < 0.05$.

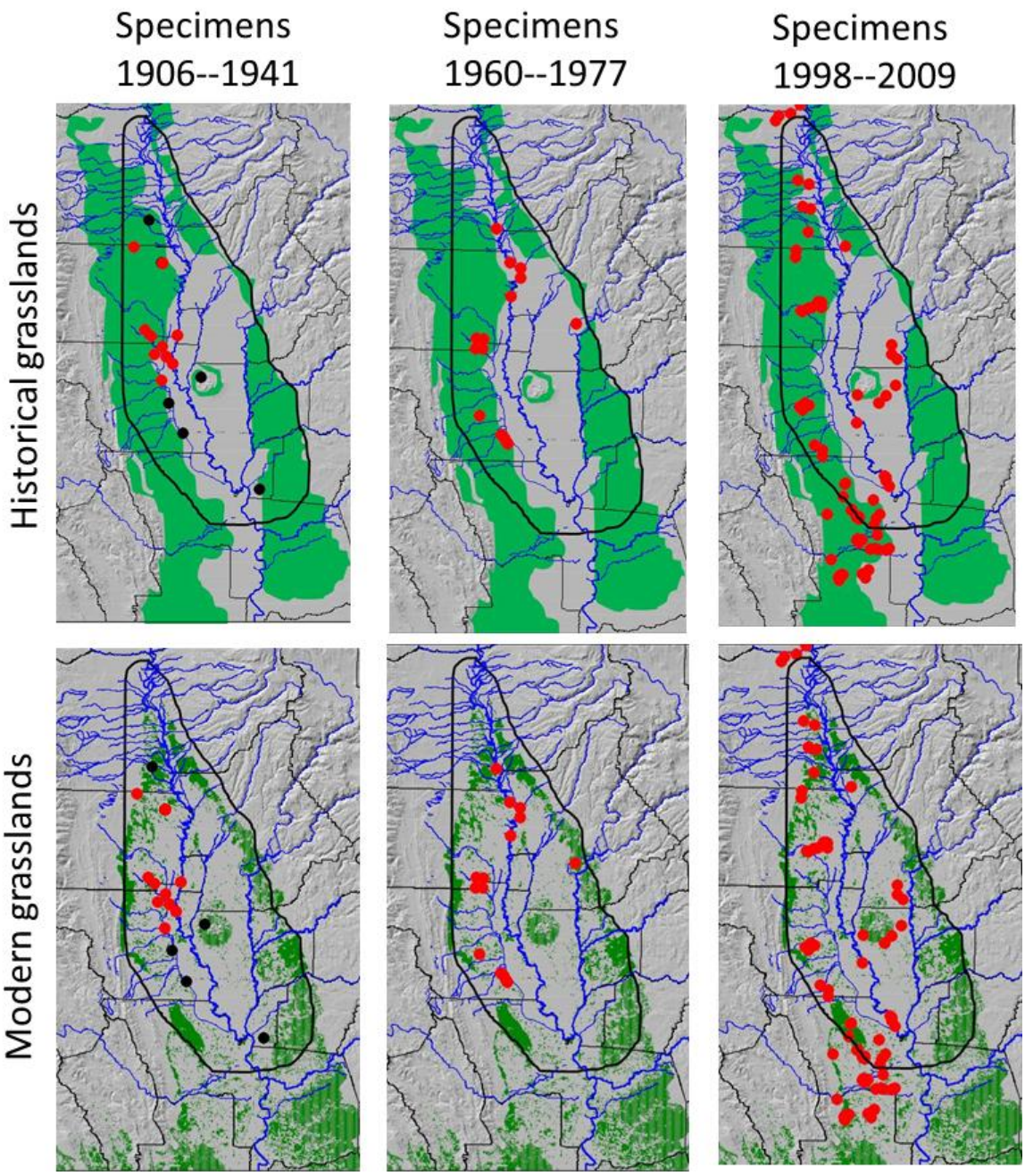


Figure 9. Locations of Sacramento Valley red fox specimen records verified genetically (red circles) or unverified reports by Grinnell et al. (1937) (black circles) during three time periods relative to the distribution of grasslands (green) before 1900 (top row, drawn from Nelson et al. 2003) and presently (bottom row, CDFG 1997). The black polygon represents Grinnell et al's (1937) estimation of the range. Records are from specimens collected in the present study and museum specimens listed in Perrine et al. (2007), Sacks et al. 2010, and Sacks et al., submitted. Nonnative and hybrid foxes from after 1960 were excluded.

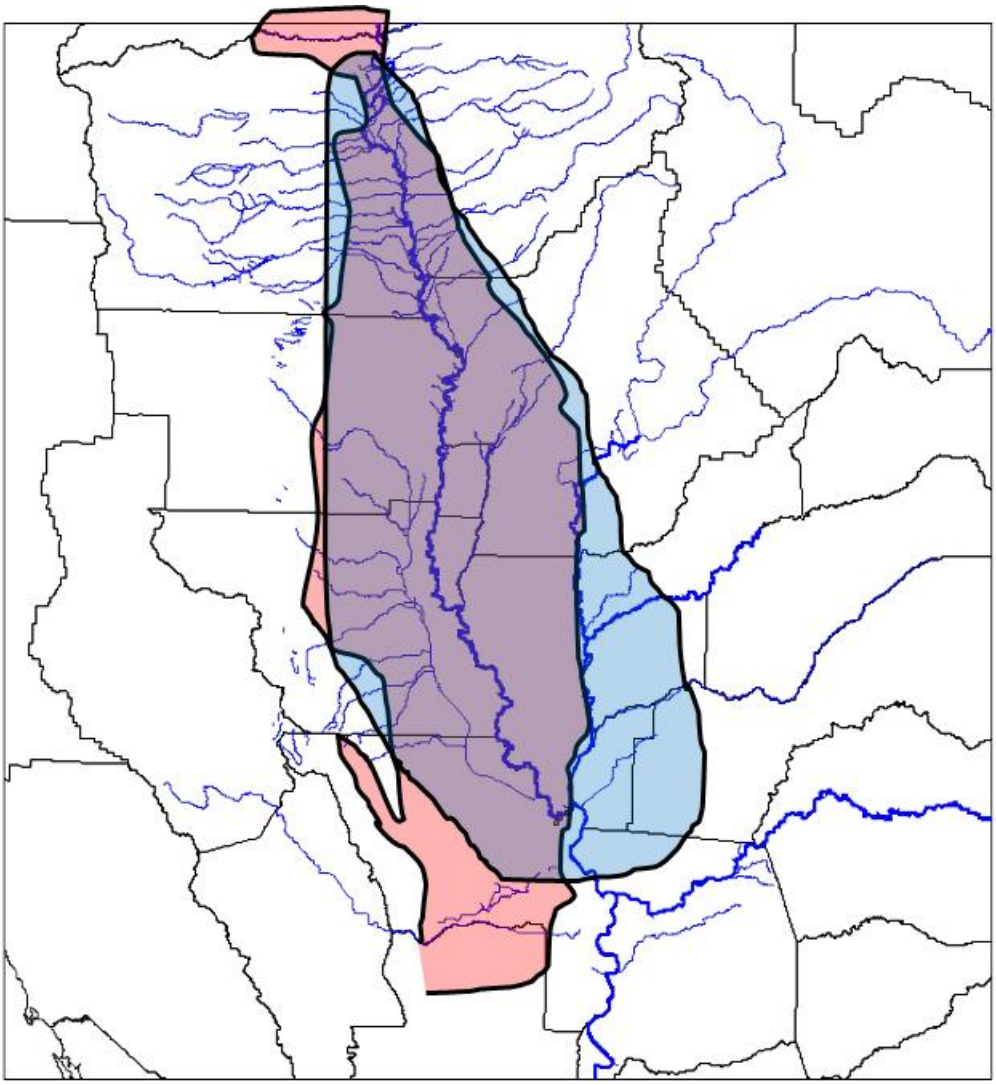


Figure 10. Present estimate of the historical and current range (presumed to be the same) of the native Sacramento Valley red fox (red) compared to that estimated by Grinnell et al. (1937) (blue). The overlap between estimates (purple) represents a minimum estimate of the historical range.