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The origin of recently established red fox populations in the United States: translocations or natural range expansions?

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Red foxes (*Vulpes vulpes*) are native to boreal and western montane portions of North America but their origins are unknown in many lowland areas of the United States. Red foxes were historically absent from much of the East Coast at the time of European settlement and did not become common until the mid-1800s. Some early naturalists described an apparent southward expansion of native foxes that coincided with anthropogenic habitat changes in the region. Alternatively, red foxes introduced from Europe during Colonial times may have become established in the east and subsequently expanded their range westward. The red fox also was absent historically from most lowland areas of the western United States. Extant populations of red foxes in those areas are considered to have arisen from intentional introductions from the east (and by extension are putatively European), escapes or releases from fur farms, or range expansions by native populations. To test these hypotheses we compared mitochondrial DNA sequences (cytochrome *b* and D-loop) from 110 individuals from 6 recently established populations to 327 native (primarily historical) individuals from Eurasia, Alaska, Canada, the northeastern United States, and montane areas in the western contiguous United States, and to 38 individuals from fur farms. We found no Eurasian haplotypes in North America, but found native haplotypes in recently established populations in the southeastern United States and in parts of the western United States. Red foxes from the southeastern United States were closely related to native populations in eastern Canada and the northeastern United States, suggesting that they originated from natural range expansions, not from translocation of European lineages, as was widely believed prior to this study. Similarly, recently established populations in the Great Basin and in western Oregon originated primarily from native populations in western montane regions, but also contained a few nonnative North American haplotypes. In contrast, populations in western Washington and southern California contained nonnative, highly admixed stock that clearly resulted from intracontinental translocations. Several common haplotypes in these populations originated in regions where fur-farm stocks originated. Although European red foxes translocated to the eastern United States during Colonial times may have contributed genetically to extant populations in that region, our findings suggest that most of the matrilineal ancestry of eastern red foxes originated in North America.

Key words: fur farm, mitochondrial DNA, museum samples, phylogeography, red fox, translocation, *Vulpes vulpes*

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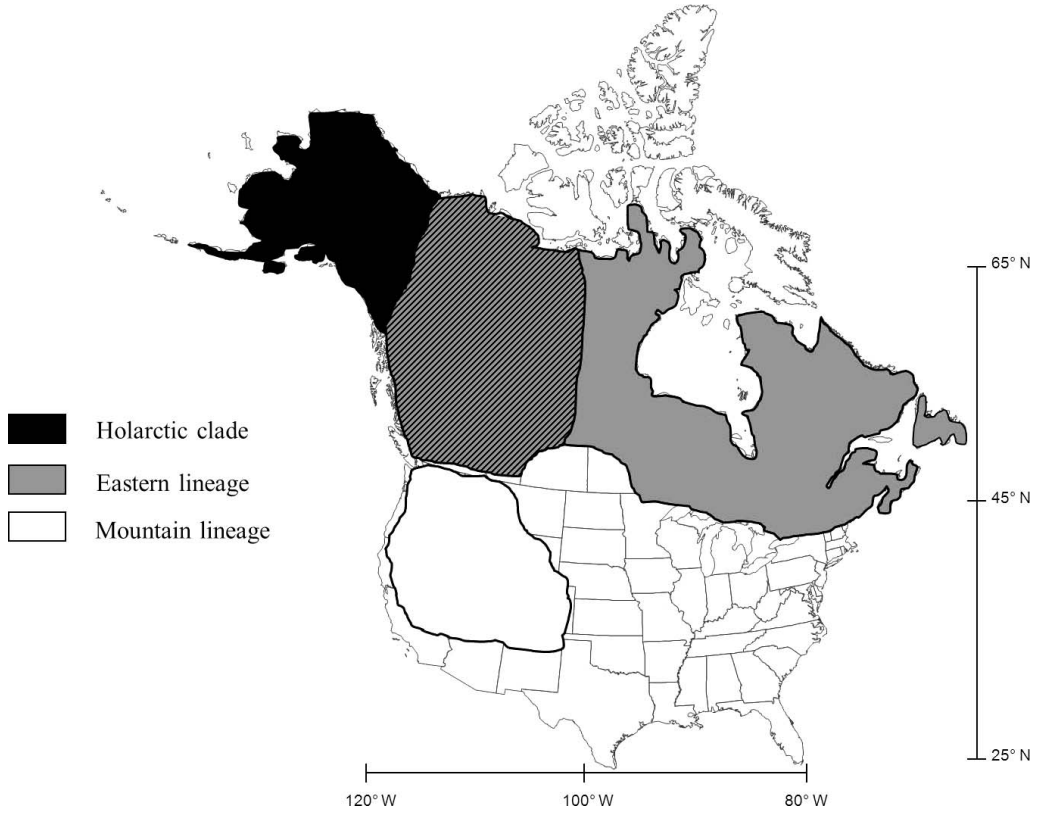


Fig. 1.—Approximate geographic distribution of North American red fox mitochondrial DNA lineages prior to European settlement modified from Aubry et al. (2009). The Eastern and Mountain lineages together comprise the Nearctic clade, which is restricted to North America. The Nearctic clade contains 3 subclades: Eastern, Mountain, and Widespread. The Mountain subclade makes up the majority of haplotypes within the Mountain lineage, whereas the Eastern subclade makes up the majority in the Eastern lineage; remaining haplotypes in both regions belong to the Widespread subclade. The Holarctic clade is distributed from Europe through Asia to Alaska and western Canada. The Holarctic and Eastern lineages overlap in western Canada, which is represented with gray and black diagonal lines. The area depicted for the Mountain subclade represents the distribution of native montane populations.

The red fox (*Vulpes vulpes*) is the world's most widely distributed terrestrial carnivore (Larivière and Pasitschniak-Arts 1996); its range has increased substantially in modern times due to expansion of native populations associated with habitat alterations (Lloyd 1980; Nowak 1991) and anthropogenic translocations (Long 2003). Whether origins of a particular population are natural or anthropogenic often is obscured by morphological similarity of even anciently diverged red fox lineages. For example, it remains unclear and contentious whether red foxes from the eastern United States originated from in situ range expansion from the north or intercontinental translocation of European foxes, which diverged from common ancestry 400,000 years ago and were once considered distinct species (Aubry et al. 2009; Churcher 1959; Kamler and Ballard 2002). Identifying the origins of red fox populations is important to conservation efforts aimed at endangered native populations and protection of endangered prey populations impacted by nonnative red foxes. Given the cryptic differences among native and nonnative populations, genetic tools are essential for understanding phylogeographic histories (Larsen et al. 2005; Sønstebø et al. 2008). Here, we focus on North American populations, particularly those established in the lowland areas of the contiguous United States.

Prior to European settlement, native populations of the red fox in North America comprised 3 evolutionarily divergent lineages that occurred primarily in the boreal forests of Canada and Alaska and the subalpine parklands and alpine meadows of montane regions in the western contiguous United States (Fig. 1; Aubry et al. 2009, but see Sacks et al. 2010). During the last or Wisconsin ice age, the Mountain and Eastern lineages (see Aubry et al. 2009) became isolated south of the ice sheets in the contiguous United States in forested refugia of the Rocky Mountains, Cascade Range, and Sierra Nevada (hereafter, the western mountains) and in the eastern contiguous United States (hereafter, the East). These 2 lineages, which currently dominate red fox populations in the western mountains and in eastern Canada, together comprise the Nearctic clade. The 3rd phylogenetically distinct lineage, the Holarctic clade, was isolated in unglaciated portions of Alaska and the Yukon during the last glaciation, and is the dominant lineage in Alaska and western Canada. The Nearctic and Holarctic clades diverged about 400,000 years ago and represent 2 separate colonization events by the red fox across the Bering Land Bridge from Eurasia during Pleistocene glaciations (Aubry et al. 2009).

During the past 300 years, humans have dramatically altered many habitats in the contiguous United States and

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implemented both inter- and intracontinental translocations of red foxes (Aubry 1984; Bailey 1936b; Lewis et al. 1999; Nowak 1991; Whitlow and Hall 1933). Consequently, it has been unclear (and biologists have long debated) whether recently established red fox populations in North America originated from natural range expansions or anthropogenic translocations (Aubry 1983, 1984; Churcher 1959; Grinnell et al. 1937; Kamler and Ballard 2002; MacPherson 1965; Newberry 1857). The emergence of red fox populations in new locations of North America occurred during 2 distinct time periods: those that appeared in the eastern United States during the Colonial era (approximately 1650–1800), and those that appeared in various parts of the western contiguous United States (hereafter, the West) during the 20th century (Aubry 1984; Kamler and Ballard 2003; Lewis et al. 1999; Seton 1929).

Red foxes were reportedly absent from much of the East during Colonial times, and did not become common in that region until the mid-1800s (Churcher 1959; Rhoads 1903). Some early naturalists described an apparent southward range expansion by populations of native red foxes that had been restricted previously to the northeastern United States and southeastern Canada. They hypothesized that this shift in the red fox's southern range boundary was driven by the conversion of hardwood forests to farmlands by European settlers, and resulting changes in competitive interactions with the gray fox (*Urocyon cinereoargenteus*—Audubon and Bachman 1849; Baird 1857; Newberry 1857). In particular, Audubon and Bachman (1849) described the serial emergence and increase of red foxes from southern New York and possibly northern Pennsylvania southward into Virginia, North Carolina, South Carolina, and, by 1840, northern Georgia, along the Appalachian Mountains. Newberry (1857) described a similar trend from eastern Canada southward into the Midwest. On the other hand, red foxes imported from Europe during the mid-1700s for hunting purposes provided another potential source of colonists to the changing landscape of the Eastern Seaboard, leading other naturalists to surmise that the ''east American Red-fox is probably a mongrel …'' (Rhodes 1903:145) or as Seton (1929:475) later put it, that the European red fox ''has mixed with the native Red fox and the offspring spread and increased through the forest region as it was opened up … .''

Churcher's (1959) morphometric study of North American and Eurasian red foxes provided the 1st empirical evidence for evaluating the extent to which European ancestry might influence eastern red fox populations. Churcher (1959) found that certain dental and cranial characteristics varied clinally from Europe through North America, via Beringia, and that European red foxes were most distinct from those in eastern North America (i.e., that they represented opposite ends of a morphological continuum), indicating that eastern red fox populations were derived primarily from native North American ancestry. Nonetheless, some contemporary researchers have presumed that modern red fox populations in the east are primarily European in origin (Kamler and Ballard 2002).

During the 20th century, red fox populations arose in several areas in the West where they were absent historically. With the exception of an ecologically distinct subspecies endemic to the Sacramento Valley of California (Sacks et al. 2010), red foxes native to the West were thought to have been restricted to the subalpine parklands and alpine meadows of the western mountain ranges (Aubry 1983, 1984; Grinnell et al. 1937). Populations of unknown origin began appearing outside these ecologically restricted areas during the 1900s (Aubry 1983, 1984; Fichter and Williams 1967; Kamler and Ballard 2002; Lewis et al. 1999; Verts and Carraway 1998). Most recently established populations of the red fox in the West were hypothesized to have originated from translocations from the East or from the escape or release of fur-farm animals that were presumably imported primarily from Prince Edward Island, Canada, or southern Alaska (Aubry 1983, 1984; Balcom 1916; Laut 1921; Lewis et al. 1999; Petersen 1914; Westwood 1989). However, others hypothesized that the recent (after 1940) colonization of previously unoccupied habitats in southern Idaho (Fichter and Williams 1967) and in the Willamette Valley in Oregon (Verts and Carraway 1998) could partly or fully reflect natural range expansions by native populations or increases in density by previously undetected native populations. In the Central Valley of California, where the native Sacramento Valley red fox (*V. v. patwin*) is contiguous with a population of nonnative red foxes, the 2 populations interbreed within a narrow hybrid zone, suggesting the possibility of admixture in other locations as well (Sacks et al. 2011).

Based on their extensive review of the topic, Kamler and Ballard (2002) hypothesized that post-Colonial range expansions resulted primarily from the dispersal of introduced European red foxes throughout the East, whereas range expansions that occurred during the 20th century resulted from the gradual expansion westward of these putatively nonnative red foxes. They further hypothesized that European red foxes have expanded into the native red fox range and ''likely replaced native red foxes throughout all northern boreal regions … .'' Thus, they proposed that, with the exception of montane populations in the West, most North American red foxes are of European ancestry.

Because of strong phylogenetic differences among native North American and Eurasian red fox populations (Aubry et al. 2009), sequence data from mitochondrial DNA (mtDNA) can be used to test these hypotheses. We used mtDNA analyses to investigate the ancestry of populations of red foxes in the contiguous United States that apparently became established after European settlement. In particular, we tested the following hypotheses: red foxes in the eastern United States are of European descent or stem from native populations in northern Appalachia or southeastern Canada; and red fox populations in lowland areas of the western United States stem from fur farms, a wave of expansion from the east, or range expansion by nearby native populations.

Materials and Methods

Sample collection.—We investigated the origins of red foxes in 6 geographical units (hereafter referred to as

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populations) in the contiguous United States. Populations 1 and 2 occupy areas south of the range of native red foxes in North America (Fig. 1) and did not appear in those areas until after European settlement: (1) Southeastern United States (Arkansas, Georgia, Indiana, North Carolina, Oklahoma, Texas, and West Virginia; $n = 18$) and (2) Central United States (Iowa, Kansas, Minnesota, North Dakota, and South Dakota; $n = 13$). We considered these populations as distinct because they have marked differences in body size, and are classified as separate subspecies (Bailey 1936b; Hall and Kelson 1959; Merriam 1900). The remaining 4 populations were more recently established (<100 years ago) in the West: (3) Western Washington (lowland areas in Washington west of the Cascade Range; $n = 23$), (4) Western Oregon (lowland areas in Oregon west of the Cascade Range; $n = 13$), (5) Great Basin (lowland areas in Oregon and Washington east of the Cascade Range, in Idaho south of the Snake River plain, and in Nevada; $n = 28$); and (6) Southern California (lowland areas south of the American River in California; $n = 21$). We also included 38 samples from red fox fur farms in the United States, Canada, Norway, and Russia.

Most of our samples were nasal turbinate bones ($n = 66$), skin snips ($n = 7$), or frozen tissues ($n = 20$) obtained from museum specimens collected from 1885 to 1991 (Appendix I). Several modern samples were from frozen or dried tissue ($n = 25$) or buccal swabs ($n = 4$). Additionally, we used 8 previously extracted DNA samples from Norwegian farmed red foxes provided by D. I. Våge (Norwegian University of Life Sciences), and sequences from 24 domesticated Russian silver foxes known to have originated from fur farms (Statham et al. 2011).

To reference native North American populations, we used previously published cytochrome-*b* and D-loop haplotypes from Alaska ($n = 69$), Canada ($n = 72$), and the western mountains ($n = 94$), which were primarily museum specimens collected in the late 1800s and early 1900s, augmented with modern samples proven to reflect continuous ancestry (Aubry et al. 2009; Sacks et al. 2010). We included 7 additional samples from the northeastern United States and southeastern Canada in the native data set from eastern Canada because all were from the historical range of native red foxes, most were collected during the 1800s prior to the advent of fur farming, and all have native North American haplotypes. To reference European populations, we used cytochrome-*b* haplotypes collected from wild populations throughout continental Europe ($n = 47$) and Britain ($n = 10$—Aubry et al. 2009; C. Edwards and C. Soulsbury, in litt.; Frati et al. 1998), and 8 D-loop haplotypes from continental Europe (Aubry et al. 2009). To reference Asian populations, we used cytochrome-*b* and D-loop haplotypes from China, Mongolia, and eastern Siberia ($n = 21$—Aubry et al. 2009). Insufficient numbers of published European D-loop haplotypes homologous to our 342-base pair (bp) fragment (see below) were available for inclusion in formal analyses; however, we compared our sequences to overlapping portions of European ($n = 74$—Valiere et al. 2003) and Asian ($n = 88$—Inoue et al. 2007) D-loop haplotypes available in GenBank.

Laboratory procedures.—We extracted DNA from historical samples (turbinates and skin snips) at Kansas State University following a phenol–chloroform extraction procedure described in Wisely et al. (2004) in a designated ancient DNA laboratory. We followed rigorous protocols to control for contamination of historical samples with modern DNA or polymerase chain reaction products (Aubry et al. 2009). We extracted tissue samples and buccal swabs using a DNeasy Blood and Tissue kit (Qiagen, Inc., Valencia, California) in separate modern DNA laboratories as described previously (Perrine et al. 2007; Sacks et al. 2010).

We amplified the 5′ portion of the cytochrome-*b* gene and the D-loop, and purified and sequenced polymerase chain reaction products as described previously (Aubry et al. 2009; Perrine et al. 2007; Sacks et al. 2010). We used Chromas version 1.45 (Technelysium Pty. Ltd., Helensvale, Australia), and Sequencher version 4.2 (Gene Codes, Inc., Ann Arbor, Michigan) to visualize chromatograms, and MegaAlign (DNASTAR, USA, Madison, Wisconsin) to align sequences.

Data analyses.—We based our analyses on a 354-bp portion of the cytochrome-*b* gene, and a 342-bp portion (including insertions and deletions) of the D-loop (Aubry et al. 2009; Perrine et al. 2007; Sacks et al. 2010). We translated the cytochrome-*b* sequences into amino acid sequences to ensure that they encoded for a continuous polypeptide.

Introduced populations often show genetic signatures of admixture, founder effects, and recent population expansion (Kidd et al. 2009; Kolbe et al. 2004; Norén et al. 2005; Senn and Pemberton 2009). Therefore, we used contrasting patterns of haplotype and nucleotide diversity to detect these signatures in recently established red fox populations. We estimated haplotype diversity (h) and nucleotide diversity (π—Nei 1987) using Arlequin 3.5 (Excoffier and Lischer 2010). We used 3 neutrality statistics to detect signatures of past demographic events on population growth or stability using Arlequin 3.5 and DnaSP version 5 (Rozas et al. 2003). Tajima's (1989) D statistic compares the number of nucleotide differences between sequences in a sample (π) and the number of differences between segregating sites (θ). Fu and Li's (1993) D^* is based on the difference between the number of single-occurring mutations in a population and the total number of mutations. Fu and Li's (1993) F^* is based on the difference between the average number of nucleotide differences between pairs of sequences and the number of singleton mutations. For a stable and randomly mating population, all 3 statistics are expected to be 0; negative values indicate an excess of low-frequency polymorphisms, suggesting population expansion, whereas positive values indicate an excess of intermediate frequency polymorphisms (Zhu et al. 2007), suggesting secondary contact between 2 or more distinct lineages (Fredsted et al. 2007). We calculated these statistics for the D-loop, which has greater variability than cytochrome *b*, and is assumed to be neutrally evolving. We used DnaSP version 5 to calculate Strobeck's (1987) S, an index of admixture, which is characteristic of populations originating from multiple sources. We also used the data from the fur-farm samples to screen for

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the same and similar haplotypes in putative nonnative populations. Where these occurred in such populations, but not in adjacent native reference populations, they were considered to be indicative of fur-farm ancestry.

We described relationships among haplotypes using a median-joining network (Bandelt et al. 1999) within Network 4.2.0.1 (www.fluxus-engineering.com). We estimated the extent of geographic divisions among populations using Φ_{ST} (Nei and Li 1979) in Arlequin 3.5. This statistic takes into account the divergence between haplotype sequences. We determined statistical significance ($\alpha = 0.05$) based on 1,000 permutations, then corrected for multiple tests using the sequential Bonferroni method (Rice 1989). We displayed resulting cytochrome-*b* and D-loop Φ_{ST} values as a clustering tree, using a neighbor-joining algorithm in the program PHYLIP 3.67 (Felsenstein 1989).

We determined the degree of support for different hypothesized origins of recently established populations using analysis of molecular variance (AMOVA—Excoffier et al. 1992) in Arlequin 3.1. We used the following groups of reference populations in these analyses based on the results presented in Aubry et al. (2009): (1) Eurasia (Europe and Asia), (2) Northwestern North America (Alaska and western Canada), (3) Southeastern Canada (central Canada, eastern Canada, and northeastern United States), and (4) Western Mountains (Washington Cascade Range, Oregon Cascade Range, Sierra Nevada, and Rocky Mountains), and (5) fur-farm samples. We then systematically combined samples from each recently established study population with those from Eurasia, fur farms, and the geographically closest North American reference group, and calculated the resulting degree of support (the proportion of variation contained among groups, Φ_{CT}). Because the cytochrome-*b* marker evolves more slowly than the D-loop, we used cytochrome *b* primarily to test hypotheses about Eurasian origins and the D-loop primarily to test hypotheses about North American origins, although we conducted intracontinental analyses using both markers. We performed a Mantel test for isolation by distance (in Arlequin) to help differentiate between continuous spread versus independent introductions among recently established populations.

Results

We obtained complete cytochrome-*b* sequences (354 bp) from 141 of 154 samples, and partial sequences (1 of 2 cytochrome-*b* fragments, 221 or 145 bp) from 3 additional samples. We used only complete cytochrome-*b* sequences in statistical analyses, and used partial sequences only to indicate clade affiliation (Fig. 2). We identified 13 distinct cytochrome-*b* haplotypes, 1 of which was novel (Table 1). We obtained complete D-loop sequences (342 bp) from 136 samples, resulting in 23 distinct haplotypes, 5 of which were novel (Table 2). We assigned novel cytochrome-*b* and D-loop haplotypes to previously identified clades (Aubry et al. 2009; Sacks et al. 2010) based on their positioning in the relevant haplotype network. All novel sequences were deposited in EMBL/GenBank/DDBJ nucleotide database (accession numbers HM590004–HM590011). We found no European haplotypes or haplotypes that clustered with European haplotypes anywhere in North America.

All fur-farm samples from the United States and Canada ($n = 6$) had haplotypes belonging to the Eastern subclade, as did the majority of all fur-farm samples (81.6%). All Russian fur-farm samples were North American in origin, with Eastern subclade haplotypes predominating. The Norwegian fur-farm samples ($n = 8$) were more variable, including 3 with a Eurasian haplotype and 5 with Nearctic clade haplotypes, indicating intercontinental translocation from North America to European fur farms. Of these 5 Nearctic clade haplotypes, 3 were from the Eastern subclade, which predominates in southeastern Canada and the northeastern United States, and 2 were from the Widespread subclade, which occurs at low prevalence in many native North American populations (Tables 1 and 2; Fig. 2a).

Neighbor-joining clustering trees based on Φ_{ST} values (Appendix II) indicated that many populations were substantially impacted by human translocations. The native reference populations occurred at the tips of the clustering trees, indicating they were most differentiated (Fig. 3). In general, these populations had a limited number of closely related haplotypes and lower nucleotide diversities than other populations. The Southeastern United States, Great Basin, and Western Oregon populations also had lower nucleotide diversities and clustered with neighboring native populations near the tips of trees. The Western Oregon population had significant negative values for 2 neutrality statistics (Tajima's *D*, and Fu and Li's *D**), consistent with population expansion (Table 3).

Our hypothesis-driven AMOVA, using both cytochrome-*b* and D-loop data sets, gave highest support to grouping the Southeastern United States population with native populations in eastern and central Canada; grouping the Great Basin and Western Oregon populations with native populations in the western mountains; and grouping Southern California, Western Washington, and Central United States populations with the fur-farm population (Table 4). In contrast, we consistently found the lowest support for any grouping of the recently established United States populations with those from Europe and Asia. In addition, a Mantel test of genetic versus geographic distance among the putative nonnative populations was nonsignificant (cytochrome *b*: $r < 0.01$, $P = 0.48$; D-loop: $r = 0.1$, $P = 0.20$), in contrast to what would be expected if they resulted from an expansion from the East.

The Central United States, Western Washington, and Southern California populations had many features in common. All occurred toward the center of the neighbor-joining clustering trees (Fig. 3) and were closer to one another in genetic distance (Φ_{ST}; Appendix II), despite being widely separated geographically. All 3 of these populations and the fur-farm samples contained a substantial number of haplotypes from ≥ 2 clades or subclades (Fig. 2b), and many of the same haplotypes occurred in ≥ 2 of these populations (Fig. 4), suggesting a common source. These 3 populations also had much higher levels of nucleotide diversity than all other

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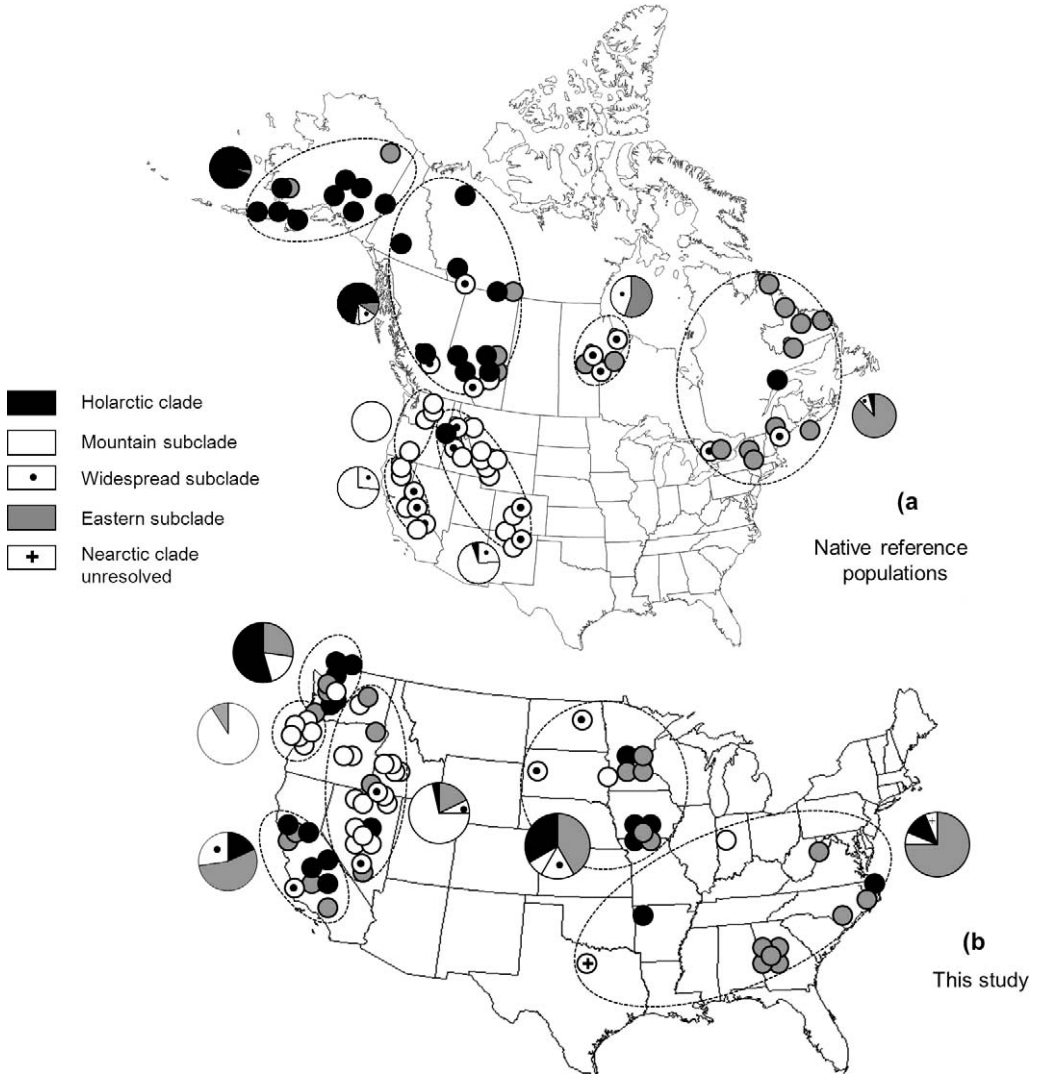


Fig. 2.—Geographic distribution of red fox mitochondrial DNA haplotypes among a) native reference populations (Aubry et al. 2009; Sacks et al. 2010; this study), and b) recently established populations (this study). Dotted lines encompass the populations analyzed, and shading indicates the clade or subclade.

populations (Table 3). The Western Washington and Southern California populations had significant signatures of admixture (Strobeck's *S*). We also found significant positive values for 2 neutrality statistics (Fu and Li's *D**, and Fu and Li's *F**) in the Western Washington population, consistent with admixture among lineages.

Discussion

European colonization of the eastern United States resulted in major anthropogenic changes to the landscape, including habitat conversion and introductions of nonnative animals and plants (Cronin 1983). By the 1700s, much of the east had been transformed by European-style agriculture, which greatly changed the character of the landscape and resulted in the extirpation of wolves (*Canis*) and the introduction of European red foxes in that region (Seton 1929). Since that time, there have been numerous translocations of red foxes within North America (Aubry 1983, 1984; Lewis et al. 1999). If all translocations had been successful, modern populations would likely reflect a complex admixture with intractable origins. However, introduced animals often fail to become established, especially where a competitively dominant native population is present (Norén et al. 2005; Rhymer and Simberloff 1996; Sacks et al. 2011). We investigated the origins of 2 spatially and temporally distinct range expansions by the red fox in the contiguous United States: one in the East that began about 300 years ago, and another in the West that occurred during the 20th century. Both of these range expansions could have resulted from human-mediated introductions in North America that began with an intercontinental translocation of red foxes from Europe to North America, followed by multiple intracontinental translocations associated primarily with fur farming. However, both of these expansion events also coincided with major anthropogenic landscape and faunal changes, including reductions in other canid populations, which could have facilitated natural range expansions by native red fox populations. Our findings indicate that natural

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Table 1.—Occurrence of 13 cytochrome-*b* haplotypes[a] among recently established red fox populations in the contiguous United States and a sample of red foxes from fur farms based on 354 base pairs from 141 individuals. The clade to which haplotypes belong is indicated.

		Nearctic clade										Holarctic clade		
Population	*n*	A	A3	C	E	E2	F	F3	F4	K	O	G	N	U4
Southeastern United States	16	1	1	—	—	1	5	5	1	—	—	2	—	—
Central United States	11	1	—	—	—	—	5	—	—	—	1	3	1	—
Great Basin	27	19	—	1	—	—	5	—	—	—	1	1	—	—
Western Washington	20	1	—	—	—	—	6	—	—	—	3	10	—	—
Western Oregon	11	10	—	—	—	—	1	—	—	—	—	—	—	—
Southern California	18	—	—	—	1	—	7	—	—	6	—	2	2	—
Fur-farm samples	38	1	—	—	10	—	21	—	—	2	—	1	—	3
Total	141	33	1	1	11	1	50	5	1	8	5	19	3	3

[a] Haplotypes A, C, E, F, G, K, N, and O are as reported by Perrine et al. (2007); A3, E2, F3, and U4 are as reported in Aubry et al. (2009); and F4 is from this study.

range expansions by native populations have had a greater influence on the current distribution of red foxes in North America than previously believed (e.g., Kamler and Ballard 2002).

During the mid-1700s, settlers introduced European red foxes to multiple locations on the East Coast of the United States (Rhoads 1903; Seton 1929). Consequently, red fox populations in that area have been presumed to be either European in origin (Kamler and Ballard 2002), or a mixture of European and North American lineages (Seton 1929). Despite historical translocations from Europe, all of the modern red fox populations we sampled in North America were derived from matrilines that are native to North America. We found no European haplotypes, or any that clustered with European haplotypes, among North American red foxes in this study or in previous ones (Aubry et al. 2009; Perrine et al. 2007; Sacks et al. 2010). Furthermore, the Southeastern United States population clustered closely with those in eastern Canada, which are native to North America (Aubry et al. 2009). We cannot differentiate whether individual haplotypes in the East originated via natural range expansion or fur farms given the shared ancestry of these 2 sources (and both influences might be present). However, because red foxes predated the fur-farm industry in this region, they must have originated either from a natural expansion or from introductions from Europe. Given the large number of red foxes we sampled throughout Eurasia ($n = 247$) and North America ($n = 353$), the absence of European haplotypes in North America demonstrates that introduced European red foxes have not displaced native North American red foxes in any major portion of the continent.

An important caveat of our findings is that they only reflect matrilineal ancestry and, therefore, do not rule out the possibility that some degree of nuclear introgression (selective or random) has occurred. Moreover, our sample size in the east was too small to conclude that matrilineal European ancestry is absent from that region. Future sampling may yet reveal mitochondrial traces of European introductions in lowland portions of the Eastern Seaboard, particularly those with a long tradition of red fox hunting (e.g., Virginia). However, morphological patterns, which reflect the nuclear genome, are concordant with our mtDNA findings (Churcher 1959). If native red foxes exclude nonnative ones in the East, as has been observed in other areas (Norén et al. 2009; Sacks et al. 2011), then the Appalachian region, which was apparently colonized by native red foxes in the 18th and

Table 2.—Occurrence of 23 D-loop haplotypes[a] among recently established red fox populations[b] in the contiguous United States and a sample of red foxes from fur farms based on 342 base pairs from 136 individuals. The clade and subclade to which haplotypes belong is indicated.

		Nearctic clade																		Holarctic clade					
		Mountains subclade					Widespread subclade				Eastern subclade									Alaskan subclade				Eurasian subclade	
Population	*n*	19	24	26	43	87	36	37	63	65	9	12	17	76	79	81	85	86	88	7	38	61	73	57	
ES	15	—	—	—	—	1	—	—	—	—	3	—	—	8	—	1	—	—	—	—	2	—	—	—	
CS	7	—	—	—	—	—	1	1	—	—	2	2	—	—	—	—	—	—	—	—	—	1	—	—	
GB	26	17	1	—	2	—	—	—	—	1	2	—	2	—	—	—	—	—	—	—	1	—	—	—	
WA	22	1	—	3	—	—	—	—	—	—	6	—	—	—	—	—	—	—	—	—	12	—	—	—	
ORW	11	10	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	
CA	17	—	—	—	—	—	6	—	—	—	2	5	—	—	—	—	—	—	—	1	3	—	—	—	
FF	38	—	—	—	—	—	2	—	1	—	7	1	13	—	1	—	2	4	3	—	—	—	1	3	
Total	136	28	1	3	2	1	9	1	1	1	23	8	15	8	1	1	2	4	3	1	18	1	1	3	

[a] Haplotypes 7, 9, 12, 17, 19, 24, 34, 36, 37, 38, 43, 57, 61, 63, 73, and 79 are as reported by Aubry et al. (2009); 65 is as reported by Sacks et al. (2010); 85 and 86 are as reported in Statham et al. (2011); and 26, 76, 81, 87, and 88 are from this study.

[b] CA = Southern California, CS = Central United States, ES = Southeastern United States, GB = Great Basin, ORW = Western Oregon, WA = Western Washington, FF = fur-farm samples.

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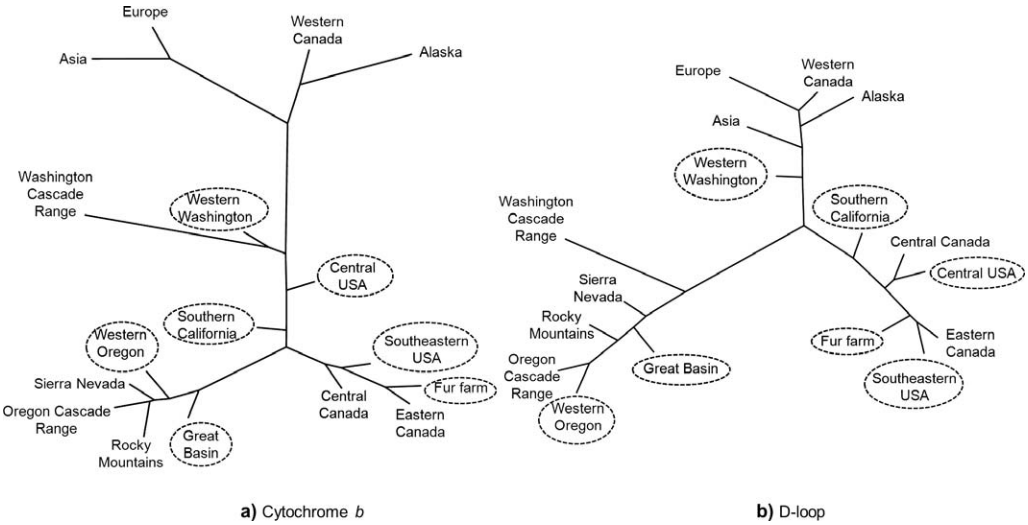


Fig. 3.—Unrooted neighbor-joining clustering tree based on pairwise Φ_{ST} values between 17 sampling localities (Appendix II). The lengths of the lines are proportional to the degree of genetic distance among sampling localities. a) Based on a 354-base pair (bp) segment of the cytochrome-*b* gene from 453 red foxes. b) Based on a 342-bp segment of the D-loop from 350 red foxes.

19th centuries (Audubon and Bachman 1849), could pose a barrier to the westward movement of nonnative foxes from coastal regions. Regardless of these caveats, and barring the unlikely possibility of systematic selection against European mitochondrial haplotypes in North America, it seems clear from our findings in this study and others of North American red fox mtDNA (Aubry et al. 2009; Perrine et al. 2007; Sacks et al. 2010, 2011) that contemporary North American red fox populations reflect primarily native ancestry. These findings clearly refute the conclusions of Kamler and Ballard (2002) that contemporary North American red foxes in lowland areas of the Pacific coastal states and throughout most of the historical range of native red foxes are of European ancestry.

The use of diagnostic nuclear markers will be needed to fully investigate the potential for traces of genetic introgression by introduced European red foxes into North American populations. However, several lines of evidence give reason to doubt that much of the genome will prove to be of European ancestry. For example, analyses of certain dental and cranial characteristics indicate greater divergence between European and eastern North American red foxes than between European and Alaskan red foxes (Churcher 1959). In addition, red foxes from the East are among the smallest in North America, and considerably smaller than those found in Sweden, England, and France (Cavallini 1995; Lloyd 1980; Merriam 1900), which were the 3 European sources of Colonial introductions to the United States (Long 2003). Moreover, Baird (1857) reported that red foxes from the southeastern and northeastern United States were similar morphologically, but differed substantially from European red foxes in muzzle length, pelage features, and other external characteristics. A series of climatic warming and cooling cycles occurred in North America during the Holocene (Dorf 1959), and fossils of the red fox have been found in the upper Midwest that date to the early and middle Holocene (10,000–4,000 years ago), and as far south as Georgia that date to the late Holocene (500–4,000 years ago [Faunmap Working Group 1996]). These records suggest that the southern range boundary of native red

Table 3.—Within-population statistics for 6 recently established red fox populations in the contiguous United States and a sample of red foxes from fur farms, based on mitochondrial cytochrome-*b* and D-loop data sets. Tajima's (1989) *D*, and Fu and Li's (1993) *D** and *F** are neutrality statistics, where departures from zero can indicate expansion (negative) or secondary contact between 2 or more lineages (positive). Significant Strobeck's (1987) *S*-values indicate admixture from multiple source populations. The neutrality statistics and Strobeck's *S*-values were only given for the D-loop data set.

Population	Cytochrome *b*				D-loop				Tajima's *D*	Fu and Li's *D**	Fu and Li's *F**	Strobeck's *S*
	n	No. haplotypes	*h*	π	*n*	No. haplotypes	*h*	π				
Southeastern United States	16	7	0.83	0.0068	15	4	0.47	0.0107	−0.86	−0.21	−0.51	0.14
Central United States	11	5	0.76	0.0083	7	5	0.90	0.0177	−0.49	−0.58	−0.65	0.68
Great Basin	27	5	0.48	0.0024	26	7	0.62	0.0131	−1.20	−1.02	−1.26	0.25
Western Washington	20	4	0.67	0.0080	22	4	0.64	0.0183	2.16	1.52**	1.87**	0.004**
Western Oregon	11	2	0.18	0.0005	11	2	0.17	0.0030	−1.85**	−2.32*	−2.50	0.34
Southern California	18	5	0.75	0.0088	17	5	0.79	0.0192	1.44	1.52	1.73	0.041*
Fur-farm samples	38	6	0.63	0.0056	38	11	0.82	0.0106	−0.69	0.58	0.19	0.55

* Significant at $P < 0.05$; ** significant at $P < 0.01$.

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Table 4.—Support values for grouping recently established red fox populations with reference native populations or fur-farm samples based on cytochrome-*b* and D-loop data sets using AMOVA (Excoffier et al. 1992). Reference population groupings are: (1) Eurasia (Europe and Asia), (2) Northwestern North America (Alaska and western Canada), (3) Southeastern Canada (central Canada, eastern Canada, and northeastern United States), and (4) the Western Mountains (Washington Cascade Range, Oregon Cascade Range, Sierra Nevada, and Rocky Mountains); and (5) fur-farm samples.

	European origins[a]			North American origins[a]		
Reference population	Eu only	Eu + FF	Eu + FF + Exp	FF only	Exp only	FF + Exp
Southeastern United States	1	1	1	5	3	3
Central United States	1	1	1	5	3	5
Western Oregon	1	5	4	5	4	4
Great Basin	1	5	4	5	4	4
Western Washington	1	5	5	5	4	5
Southern California	1	5	5	5	4	5
Cytochrome-*b* Φ_{CT}	0.23	0.37**	0.45**	0.51***	0.52***	0.53***
D-loop Φ_{CT}	—	—	—	0.30***	0.31***	0.40***

[a] Eu = Eurasia, FF = fur farm, Exp = range expansion from native populations.
* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

foxes in eastern North America may have shifted periodically in response to changing climatic conditions since the retreat of Wisconsin glaciers.

Although red foxes were historically absent or extremely rare in the central and western United States (with the exception of high-elevation areas in the western mountains and the Sacramento Valley of California), they became established in many lowland areas during the 1900s (Aubry 1983, 1984; Bailey 1936b; Sacks et al. 2010; Whitlow and Hall 1933). These recently established populations could have resulted from human translocations of fur-farm animals that subsequently escaped or were released (Aubry 1983, 1984; Lewis et al. 1999), continental-scale range expansions from the East (Kamler and Ballard 2002), natural range expansions by native montane populations (Bailey 1936a; Fichter and Williams 1967; Verts and Carraway 1998), or human translocations from native montane populations for fur farming.

In several putatively nonnative populations in the west and in the central United States, we found a few Eastern subclade haplotypes that were best explained by continental-scale translocations of fur-farmed foxes. Several haplotypes were common among our study populations but not necessarily common in the ancestral populations (i.e., consistent with origin from a common founder population). Although our sample size from the central United States was too low to rule out natural range expansions from the east, it is noteworthy

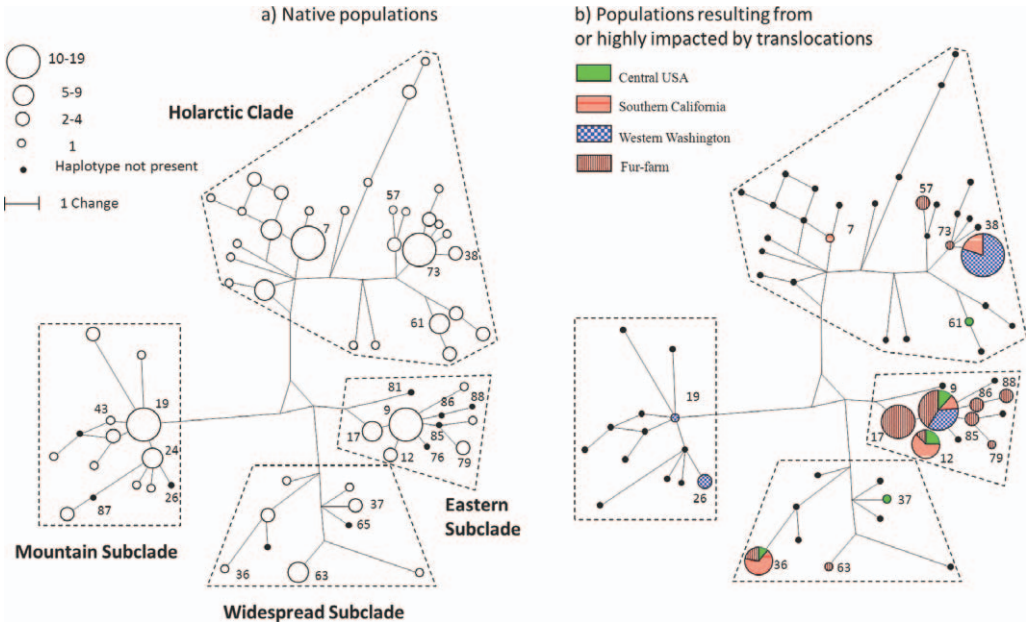


Fig. 4.—D-loop median joining network based on 342 base pairs with superimposed higher order clades and subclades as reported by Aubry et al. (2009). Branch lengths are proportional to the number of substitutions, and circle sizes are proportional to the number of individuals represented. Numbered haplotypes are those found in this study. Together, the Mountain, Eastern, and Widespread subclades comprise the Nearctic clade, which is restricted to North America. a) Network of haplotypes found in native populations (modified from Aubry et al. [2009]). b) Network of haplotypes present among populations resulting from or highly impacted by translocations.

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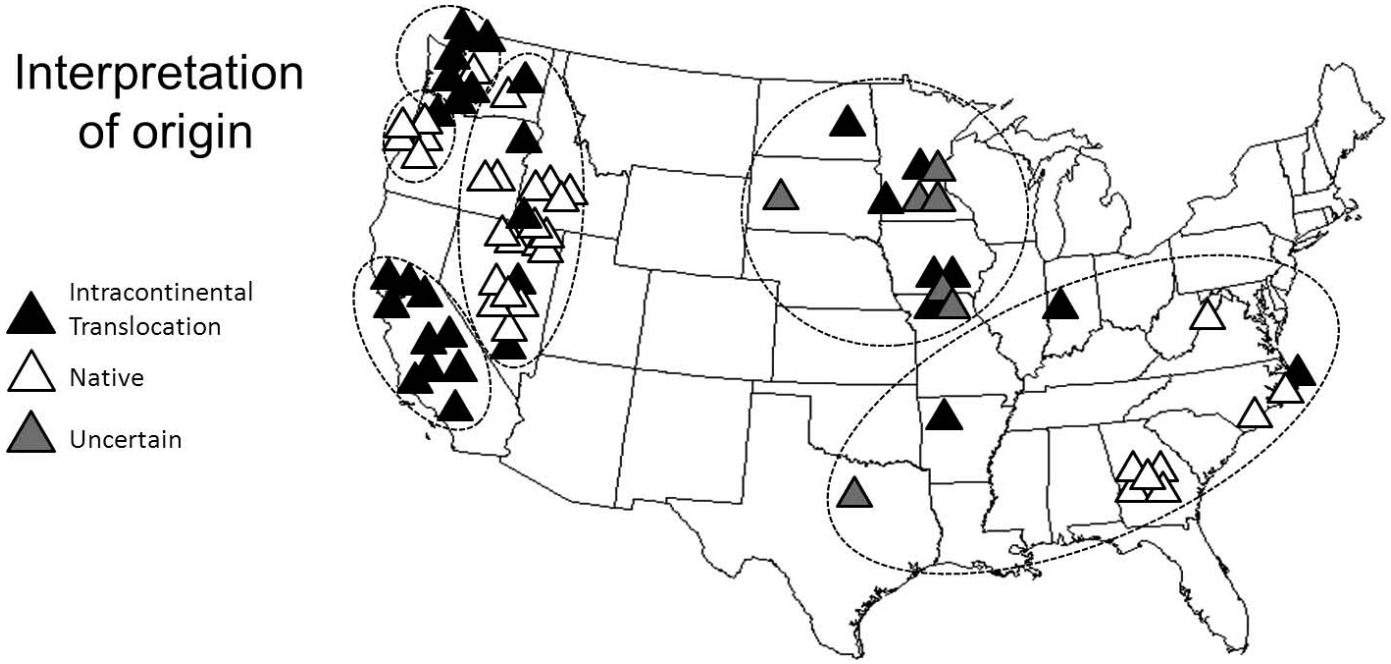


Fig. 5.—Interpretation of the origin of red fox samples analyzed in this study; black triangles indicate samples with haplotypes that reflect intracontinental translocations, white triangles indicate samples with haplotypes that occur primarily in native populations, and gray triangles indicate samples of uncertain origin (i.e., samples with haplotypes that have a widespread distribution or incomplete sequences). Dotted lines encompass the populations analyzed. We consider the following haplotypes to have a signature of translocation, by region: Southeastern United States: G-38; Central United States: G-38, G-61, G-? (x2), and ?-36; Great Basin: F-17, F-?, and G-38; Western Washington: A-19, F-9 (x8), G-38 (x12), and O-26 (x3); Western Oregon: F-9; and Southern California: E-9, F-9, F-12 (x3), F-? (x3), ?-12 (x2), G-38 (x2), ?-38, K-36 (x6), N-7, and N-?.

that some of the Eastern subclade haplotypes found here also occurred in other isolated western populations that clearly originated from translocations (see below). In contrast, native populations in the western mountains were distinct from the Central United States and Eastern United States populations, indicating that Rocky Mountain red foxes did not expand their range eastward to lower-elevation habitats in the Great Plains (Fig. 5). Thus, midelevation areas along the eastern edge of the Rocky Mountains may represent a natural contemporary barrier between populations of native western and eastern red foxes.

In the West, we found evidence that some of these recently established populations were derived from native montane populations, whereas others clearly originated from translocations. Our samples from western Oregon and the Great Basin exhibited low mitochondrial diversity, significant negative neutrality statistics (Western Oregon population), and a high prevalence of the basal Mountain subclade haplotype A-19 (see Aubry et al. 2009), consistent with origins from native populations in the western mountains. Our findings provide support for previous hypotheses about natural range expansions by montane red foxes in these regions (Fichter and Williams 1967; Verts and Carraway 1998), but do not exclude the possibility that the recent establishment of these populations was human-mediated, nor that introgression of particular nonnative alleles could have facilitated a broadening of their habitat niche, enabling them to expand to habitats that were unsuitable previously. The widespread occurrence of the basal A-19 haplotype throughout most of the montane reference populations limited our resolution, enabling us only to trace the ancestry of these animals to the western mountains; however, previous microsatellite analyses of our samples from lowland Idaho and Nevada demonstrated that they were closely related to adjacent native Rocky Mountain populations (Sacks et al. 2010). Moreover, there is evidence that remnant populations of montane red foxes may have occurred in Nevada in some of the areas where we have now confirmed the presence of native genotypes (Hall 1946; Sacks et al. 2010). In the intermountain west, winter snowfall may create connectivity among otherwise distinct habitats during the peak dispersal period, which could facilitate natural range expansions. However, neither of these scenarios could explain the occurrence of native montane haplotypes among red foxes in western Oregon—winter snowpacks do not form there and the red fox clearly did not occur in the Willamette Valley until the 1940s (Bailey 1936a; Verts and Carraway 1998). Microsatellite analysis will be needed to isolate the region from which this population originated and genome-wide scans or selective sweep-mapping will be needed to assess the possibility of introgression by adaptive nonnative alleles in this and other populations (e.g., Great Basin).

In contrast to the Western Oregon and Great Basin populations, we found clear evidence of nonnative origins for recently established Western Washington and Southern California populations. Red fox populations in these regions had high mitochondrial diversity, consistent with a well-

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documented history of fur farming. Additionally, both populations had significant Strobeck's *S*-values (indicating admixture), clustered with the geographically distant Central United States population in the neighbor-joining tree, and contained similar mixtures of phylogenetically divergent haplotypes. Translocations or fur farms have been documented in or adjacent to all of the Washington counties where we detected these haplotypes (Aubry 1984), and throughout southern California (Lewis et al. 1999).

Relatively few haplotypes were common to >1 of these populations, making them useful indicators of nonnative stock. Most of these haplotypes were from the Eastern subclade and native to populations in southeastern Canada and the northeastern United States (E-9, F-9, F-12, and F-17), or in native Holarctic-clade populations in Alaska and western Canada (G-38, G-73, and N-7). Of the 38 samples we sequenced from red fox fur farms, most belonged to the Eastern subclade ($n = 31$), including those from Norway and Russia. Thus, these haplotypes also will be useful when screening for nonnative ancestry in Eurasian populations. According to historical records, most of the original breeding stock for the fur-farming industry came from Prince Edward Island in southeastern Canada, and consisted predominantly of locally caught foxes supplemented with those imported from southern Alaska (Balcom 1916; Laut 1921). Fur farmers on Prince Edward Island primarily raised the silver–black color phase, which had the greatest economic value. Farmed foxes from Prince Edward Island were subsequently used to stock fur farms in many areas of North America and Eurasia (Petersen 1914; Westwood 1989). At the same time, red fox breeders independently farmed other strains in Ontario, Quebec, and Maine (Balcom 1916). Given that silver fox breeders could charge as much as $1,500 each in the mid-1920s (Eugene Guard 1924), it is possible that fur farmers obtained their breeding stock from wild populations having high frequencies of the silver–black color phase, such as those in Alberta or British Columbia, Canada, or the Cascade Range in Washington (Butler 1945; Cowan 1938), as was done in Alaska until at least 1927 (Anchorage Daily Times 1927). Indeed, the presence of haplotype O-26 in a translocated population likely originated in the Washington Cascades (Aubry et al. 2009).

Contrary to previous interpretations, we found no matrilineal descendants of European red foxes anywhere in North America. Although more intensive sampling in the East may yet uncover evidence of limited or localized European red fox ancestry, the clear lack of European haplotypes found thus far in the east, and in a relatively large sample of nonnative foxes derived largely from eastern stock, clearly indicates that North American red foxes have retained primarily North American ancestry. However, many populations in the contiguous United States bear a genetic signature of translocations from other North American locations. Lowland populations in western Washington, southern California, and the central United States represent an unnatural admixture of clades and subclades translocated from disparate parts of North America. In contrast, recently established populations in western Oregon and the Great Basin had little genetic diversity and were not significantly differentiated from most native montane populations. Thus, it is clear that these recently established populations were derived, at least in part, from montane populations. Despite an extensive history of red fox translocations into and throughout North America, nonnative lineages apparently have persisted only in regions where native red foxes were absent historically. A focused study of microsatellite and single nucleotide polymorphism diversity in the native Sacramento Valley and adjacent nonnative red fox population in California suggested that native foxes may be able to competitively exclude nonnative foxes, hybridizing only on the margins of the native range (Sacks et al. 2011). Similar studies would be useful for understanding the ecological dynamics between native and nonnative red foxes in the intermountain west.

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APPENDIX I

Accession numbers of museum specimens from which we acquired DNA for this study.

Fort Roosevelt Vertebrate Collection: FRC027, FRC061, FRC087; Museum of Vertebrate Zoology: MVZ175993, MVZ207041, MVZ208591, MVZ208595, MVZ222348, MVZ222369, MVZ222471, MVZ33635, MVZ33636, MVZ52099, MVZ52100, MVZ52101, MVZ52102, MVZ57149, MVZ57150, MVZ57151, MVZ57152, MVZ57153, MVZ84481, MVZ90621, MVZ90798, MVZ91097; National Museum of Natural History: USNM107765, USNM110812, USNM188069, USNM188070, USNM19969, USNM224077, USNM242343, USNM242921, USNM242922, USNM242924, USNM243681, USNM243682, USNM243683, USNM243745, USNM263367, USNM263368, USNM263369, USNM263372, USNM263373, USNM264977, USNM264979, USNMA03071, USNMA03707, USNMA03713, USNMA03714, USNMA21156, USNMA21157; University of Washington Burke Museum: UW20182, UW32526, UW32527, UW32530, UW32531, UW32532, UW32534, UW32540, UW32541, UW32543, UW32544, UW32545, UW32547, UW32563, UW32950, UW34306, UW41617, UW73061; Natural History Museum of Los Angeles County: LA2, LA5, LA85700, LA87624; Oregon State University Fisheries and Wildlife Mammal Collection: OSU1175, OSU5543, OSU8778, OSU8779, OSU9017; Santa Barbara Natural History Museum: SB-1, SB-2, SB-3, SB-4, SB-5, SB-6; Slater Museum of Natural History: UPS10841, UPS1252, UPS13382, UPS13383, UPS14885.

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Appendix II

Pairwise Φ_{ST} values between 10 native and 6 recently established red fox populations[a] in North America, and a sample of red foxes from fur farms. Values in boldface type on the diagonal indicate the number of sequences compared (cytochrome *b*/D-loop). Below the diagonal, values are based on the cytochrome-*b* data set, whereas above the diagonal, values are based on the D-loop data set. Asterisks indicate statistical significance ($P < 0.05$) based on sequential Bonferroni correction for multiple tests (Rice 1989).

	AK	AS	CA	CC	CS	EC	ES	EU	GB	ORW	ORC	RM	SN	WA	WAC	WC	FF
AK	**69/49**	0.25*	0.34*	0.52*	0.40*	0.53*	0.46*	0.24*	0.56*	0.61*	0.62*	0.57*	0.56*	0.21*	0.65*	0.17*	0.47*
AS	0.40*	**21/13**	0.28*	0.45*	0.33*	0.51*	0.41*	0.19	0.56*	0.63*	0.64*	0.58*	0.55*	0.22	0.70*	0.25*	0.42*
CA	0.59*	0.64*	**18/17**	0.14	−0.04	0.19*	0.12	0.38*	0.42*	0.47*	0.47*	0.46*	0.42*	0.19*	0.56*	0.29*	0.17*
CC	0.73*	0.82*	0.06	**6/9**	−0.02	0.13	0.14	0.56*	0.53*	0.64*	0.67*	0.56*	0.52*	0.33*	0.75*	0.41*	0.12*
CS	0.50*	0.60*	0.03	0.11	**11/7**	0.04	0.01	0.46*	0.45*	0.56*	0.57*	0.50*	0.45*	0.22	0.69*	0.34*	0.03
EC	0.73*	0.81*	0.20	0.07	0.20	**26/22**	0.00	0.65*	0.55*	0.65*	0.70*	0.59*	0.55*	0.37*	0.75*	0.49*	0.00
ES	0.68*	0.73*	0.11	0.02	0.09	0.07	**16/15**	0.56*	0.46*	0.58*	0.62*	0.53*	0.50*	0.26*	0.69*	0.40*	0.02
EU	0.42*	0.11*	0.55*	0.63*	0.48*	0.67*	0.61*	**57/8**	0.66*	0.75*	0.77*	0.65*	0.62*	0.21	0.80*	0.16	0.53*
GB	0.73*	0.83*	0.16*	0.04	0.23*	0.30*	0.21*	0.66*	**27/26**	−0.03	0.00	0.02	0.05	0.39*	0.27*	0.52*	0.46*
ORW	0.74*	0.86*	0.15	0.24	0.26*	0.37*	0.23*	0.64*	−0.04	**11/11**	−0.06	0.01	0.04	0.44*	0.42*	0.57*	0.53*
ORC	0.73*	0.85*	0.13	0.33	0.23	0.40*	0.23*	0.63*	−0.03	−0.05	**7/6**	−0.02	0.02	0.44*	0.50	0.58*	0.57*
RM	0.74*	0.84*	0.22*	0.22*	0.31*	0.43*	0.32*	0.67*	0.02	−0.02	−0.06	**30/30**	0.03	0.44*	0.20*	0.54*	0.52*
SN	0.75*	0.85*	0.25*	0.21*	0.34*	0.45*	0.35*	0.69*	0.02	−0.01	−0.05	0.00	**37/35**	0.42*	0.23*	0.52*	0.50*
WA	0.37*	0.50*	0.12	0.25*	−0.03	0.34*	0.22*	0.43*	0.33*	0.33	0.30*	0.37*	0.40*	**20/22**	0.52	0.06	0.32*
WAC	0.77*	0.87*	0.39*	0.64*	0.46*	0.61*	0.47*	0.69*	0.51*	0.71*	0.73*	0.51*	0.52*	0.46*	**15/16**	0.63*	0.64*
WC	0.16*	0.40*	0.34*	0.51*	0.19	0.55*	0.46*	0.38*	0.53*	0.53*	0.51*	0.54*	0.57*	0.07	0.62*	**43/28**	0.42*
FF	0.69*	0.73*	0.14*	0.04	0.15	−0.02	0.06	0.64*	0.23*	0.26*	0.28*	0.34*	0.36*	0.29*	0.49*	0.51*	**38/38**

[a] AK = Alaska, AS = Asia, CA = Southern California, CC = Central Canada, CS = Central United States, EC = Eastern Canada and Northeastern United States, ES = Southeastern United States, EU = Europe, GB = Great Basin, ORW = Western Oregon, ORC = Oregon Cascade Range, RM = Rocky Mountains, SN = Sierra Nevada, WA = Western Washington, WAC = Washington Cascade Range, WC = Western Canada, FF = fur-farm samples.