

Elevational isolation of red fox populations in the Greater Yellowstone Ecosystem

Bradley J. Swanson^{1,*}, Robert T. Fuhrmann² & Robert L. Crabtree³

¹Department of Biological Sciences, Central Michigan University, Mount Pleasant, MI 48859, USA;

²Ecology Department, Montana State University, Bozeman, MT 59717, USA; ³Yellowstone Ecological Research Center, 7500 Jarmen Circle, Suite 2, Bozeman, MT 59715, USA (* Corresponding author: E-mail: brad.swanson@cmich.edu)

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Abstract

Foxes in the Greater Yellowstone Ecosystem are reported to show high frequencies of blonde and gray coat colors. A survey of park sighting records showed that the frequency of the novel coat colors significantly increases at elevations greater than 2300 m, suggesting some form of elevational isolation. We evaluated the degree of genetic separation between the high-elevation foxes (> 2300 m) and contiguous populations of foxes at mid-elevations (1600–2300 m). Low-elevation (< 1600 m) foxes from North Dakota, > 1000 km straight line distance from our populations, were used as a control group. We genotyped 15 high-elevation, 15 mid-elevation, and 10 low-elevation foxes at 10 microsatellite loci each. Heterozygosity was significantly lower in both the high-elevation and mid-elevation populations compared to the low-elevation foxes. The genetic differentiation was significantly greater between the high-elevation and mid-elevation foxes than between the mid-elevation and low-elevation foxes. Similarly, estimates of R_{ST} and F_{ST} suggest less gene flow occurs between the contiguous high- and mid-elevation fox populations than between the mid- and low-elevation fox populations separated by > 1000 km. The assignment test further supports this hypothesis. Although further work is needed, we suggest that the high-elevation foxes are remnant populations from the Wisconsin glaciation and should be managed as a unique population.

Introduction

The red fox in North America is almost continuously distributed across the continent as six subspecies. *Vulpes vulpes fulva* and *V. v. abietorum* are the two most widely distributed subspecies, covering almost the entire southern and northern half of the continent, respectively (Figure 1). Three recognized subspecies of red fox are found in mountainous areas of the western United States, *V. v. cascadenis* in the Cascades, *V. v. necator* in the Sierras, and *V. v. macroura* throughout the Rocky Mountain region (Figure 1; Merriam 1900). Prior to European colonization, it appears

that red fox in North America occurred only in forested regions of what is now Canada and the montane and subalpine forest zones of western US mountain ranges.

In the Cascade Mountain range, Aubry (1983) suggests that only foxes found in the “subalpine meadows and parkland habitats” are actually *V. v. cascadenis* and that these populations are isolated from the low-elevation populations found below a belt of coniferous trees, in the surrounding scrub and farmland. Aubry (1983) concluded that the larger sized low-elevation foxes are descendants of the European red fox (*V. v. fulva*) that were introduced during colonial times, while the

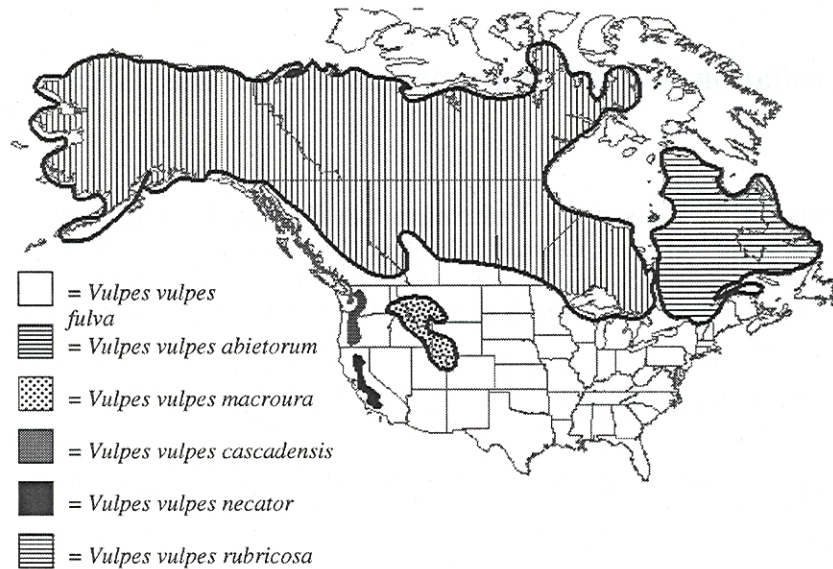


Figure 1. Geographical distribution of red fox subspecies in North America (modified from Aubrey 1983).

smaller montane fox descended from Canadian populations (*V. v. abietorum*) pushed south during the Wisconsin glaciation. *V. v. abietorum* then migrated up elevationally following glacial retreat (Merriam 1900; Bailey 1936; Aubry 1983). Following introduction and range expansion of the European red fox, climate prevented the European red fox from occupying the higher elevations, while the montane fox is competitively, as well as climatically, excluded from the lower elevations (Merriam 1900; Bailey 1930; Aubry 1983).

Little work has been done on the other two high elevation subspecies (but see Fuhrmann 1998), despite two distinct coat-color phenotypes, blonde and gray, being described in populations of *V. v. macroura* in the Greater Yellowstone Ecosystem (Norris 1881; Bailey 1930; Brodrick 1954). These two phenotypes, along with the traditional color morphs (red, cross, black/silver), have been commonly found in the park since at least the late 1800s (Bailey 1930; Brodrick 1954, unpublished park records) with Norris (1881) listing the frequency of the color morphs seen in Yellowstone as red > gray > black > cross. Despite the rankings given by Norris (1881), Merriam (1900) makes no mention of alternative phenotypes despite clearly describing similar phenotypes in *V. v. cascadenis* and foxes of the northern plains. Merriam (1900) and current taxonomy (Kamler and Ballard 2002) consider all foxes in the Greater Yellowstone

Ecosystem to be *V. v. macroura*, however, the presence of the different pelage phenotypes suggest that further investigation is needed.

Kamler and Ballard (2002) suggest that all low elevation foxes in the western United States are descendants of introduced European red fox and point out that different management strategies are required if this is the case; low elevation red foxes can be considered as an introduced species. If foxes found below subalpine regions are nonnative, and climate and competitive abilities keep the two populations isolated to some degree, we should see genetic population structure based upon elevation producing a unique multilocus genetic signature for each population and significant genetic distances between the populations.

We utilize color-morph distribution, and microsatellite DNA to investigate the possibility that red fox in the Greater Yellowstone Ecosystem are isolated in a fashion similar to that found in the Cascades. Specifically, we examine the question of the extent to which gene flow occurs between the high (>2300 m) and mid-elevation (1600–2300 m) populations of red fox in the Greater Yellowstone Ecosystem, compare this to low-elevation (>1000 m) foxes >1000 km distant in North Dakota, and suggest possible explanations for the observed distribution of coat colors.

Methods

We live trapped red fox at various elevations, using padded offset leg-hold traps in addition to Have-A-Heart, and plywood box traps. Animals were either tranquilized with a mixture of ketamine and xylazine or restrained. Once the animal was immobilized each fox was ear tagged with the tissue punch being preserved for DNA analysis. Tissues were preserved by freezing in liquid nitrogen while in the field prior to transfer to a -80°C freezer. Additional samples came from opportunistically obtained road killed foxes. All fox samples were obtained from within a 60×30 km east-west transect (Figure 2). This area represents two types of habitat, a series of high elevation montaine habitats surrounded by a sea of low elevation habitat. Although the two sampling methods only provided us with 30 animals total, fox populations were depressed during this period of time due to large coyote populations (Crabtree and Sheldon 1999). We also sampled foxes from North Dakota to provide an estimate of the amount of genetic similarity expected between fox populations which cannot be experiencing genetic exchange. North Dakota tissue samples were collected from road-killed fox found by driving along Route 38 (north-south) and Interstate 94 (east-west) in Cass County (7535 km²), eastern North Dakota, over a three-

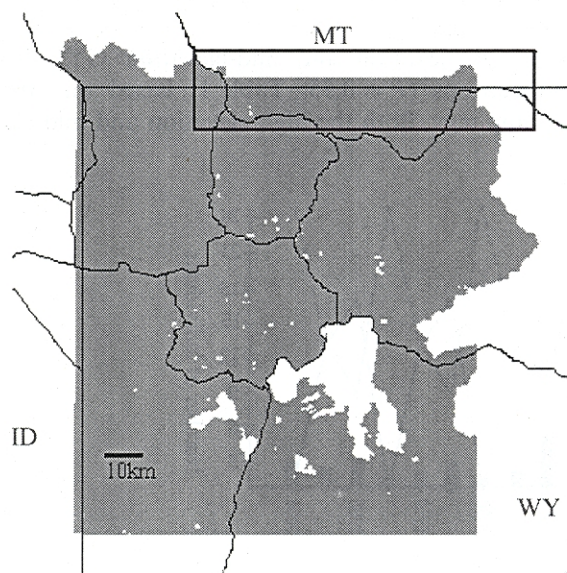


Figure 2. Map of Yellowstone National Park and approximate boundaries (thick dark line) of this study. Paved roads through the park are indicated by the thin dark lines and lakes as white.

day period from August 10–12, 1997. Median fox dispersal distances are 21.3 km for males and 3.1 km for females (Storm 1972), thus it is unlikely that any dispersal occurs between Cass County North Dakota and the Greater Yellowstone Ecosystem (shortest straight line distance 1075 km).

DNA extraction followed a traditional phenol/chloroform method. We utilized 13 canid primers *cx.x.20*, *cx.x.109*, *cx.x.123*, *cx.x.147*, *cx.x.155*, *cx.x.172*, *cx.x.204*, *cx.x.213*, *cx.x.246*, *cx.x.250*, *cx.x.251*, *cx.x.442*, and *cx.x.671* (Ostrander et al. 1993, 1995, Mellersh et al. 1997) for microsatellite analysis. Genomic DNA was amplified via PCR containing $0.16 \mu\text{M}$ of each primer, $120 \mu\text{M}$ dNTPs, 2 mM MgCl_2 , 0.5 U of *Taq* DNA polymerase, and 1X PCR buffer (10 mM Tris buffer, pH 8.8, 0.1% Triton X-100, 50 mM KCl, and 0.16 mg/ml BSA). PCR reactions were run at 20 μl in an Eppendorf MasterGradient thermal cycler (Brinkman Inc. Westbury, NY 11590-020). Cycling time consisted of 1 min at 94°C , three cycles of 30 s at 94°C , 20 s at $52\text{--}54^{\circ}\text{C}$, and 5 s at 72°C , followed by 33 cycles of 15 s at 94°C , 20 s at 54°C , and 1 s at 72°C . A final extension period of 30 min at 72°C preceded ramping down to 4°C . PCR products were resolved on a 310 DNA Sequencer and analyzed using GENESCAN and GENOTYPER software (Applied Biosystems, Foster City, CA).

We tested for Hardy-Weinberg equilibrium using a Markov chain randomization as implemented in GENEPOP for each locus and population following a global Fisher's exact test. Bonferroni adjustments were made for all appropriate tests following the method of Rice (1989). Linkage disequilibrium was examined between all pairs of loci with the randomization test in GENEPOP (Raymond and Rousset 1995).

Prior to interpopulation analysis we tested for genetic differences between populations using GENEPOP's randomization methods (Raymond and Rousset 1995) for each locus and combined over loci using Fisher's method (Sokal and Rohlf 1995). The partitioning of genetic variance due to population structure was estimated using both F_{ST} and R_{ST} as estimated from GENEPOP (Raymond and Rousset 1995).

We used the program DOH (<http://biology.ualberta.ca/jbrzusto/Doh.php>) to determine the most likely population of origin for each fox (Paetkau et al. 1995; Waser and Strobeck 1998).

and used the option to leave the individual being assigned out of the population when estimating allele frequencies to reduce bias. Allele frequencies were adjusted to avoid zero frequencies in any population following the method of Titterton (1981) as implemented by DOH. Foxes were assigned to the population where their genotype was significantly more likely to have occurred based on the randomization test in DOH. Significance of the number of misassignments was determined using the resampling test found in DOH by determining how often the given number of misassignments would have occurred by chance if the populations were completely isolated.

Results

Analysis of Yellowstone National Park records suggests that the novel phenotypes occur most frequently at higher elevations (Figure 3). The sighting frequency of the novel phenotypes increases dramatically at elevations greater than 2300 m (Figure 3), the approximate boundary of subalpine habitat (Fritz 1984), however, the red phenotypes are still commonly reported above the subalpine boundary. There is a significant difference ($t = -9.15$, $P < 0.0001$) in the average elevation of sightings for traditional phenotypes (avg. = 1876 ± 174.4 m) and other phenotypes (avg. = 2346 ± 351.3 m). Because the frequency of novel coat-color increases at the approximate boundary of the subalpine habitat this elevation was used as the dividing point between the mon-

tane population (foxes at elevations ≥ 2300 m) and mid-elevation foxes (individuals found from 1600–2300 m) for the genetic analysis. All of the foxes in the low-elevation (North Dakota) and mid-elevation samples expressed the traditional red phenotype. The high-elevation samples contained 9 traditional red phenotype foxes, 2 blonde phenotypes, and 4 gray phenotypes.

Three loci (*cxx.20*, *cxx.109*, and *cxx.250*) showed significant departure from Hardy-Weinberg equilibrium using the Markov chain randomization described by Gou & Thompson (1992). Each of these three loci had 1–2 samples that would not amplify despite the same individuals amplifying at all other loci. Using CERVUS (Marshall et al. 1998) these three loci were found to have a high frequency of null alleles ($> 20\%$) and were removed from further analyses. We found no significant linkage disequilibrium between any of the loci based on the randomization test of GENEPOP (Raymond and Rousset 1995). No loci showed significant F_{IS} values and there were no observable patterns to the F_{IS} estimates in any of the populations (allele frequency tables are available at <http://www.cst.cmich.edu/users/swans1bj/previous.html>). No significant differences were found between the allelic diversity of either the high- or mid-elevation GYE fox populations compared to the low-elevation North Dakota population ($P = 0.31$, $P = 0.26$, respectively; Table 1), or between the heterozygosity of the high-elevation and mid-elevation GYE fox populations ($P = 0.35$; Table 1) based on 1000 resamplings. Both the high-elevation and mid-ele-

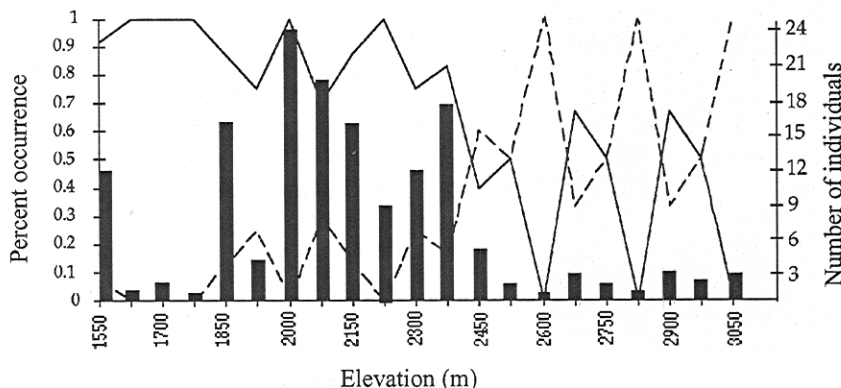


Figure 3. Distribution of novel (yellow and gray, dashed line) and normal (red, cross, black, solid line; right hand side y-axis) coat colors of foxes in Yellowstone National Park based on park sighting records (1890–1995) and the number of records at each elevation (black bars; left hand side y-axis).

Table 1. Genetic diversity in each geographical region

Geographical region	Samples size	Allelic diversity	H_e
GYE High-elevation	15	4.8 ^a	0.577 ^a
GYE Mid-elevation	15	4.7 ^a	0.627 ^a
ND Low-elevation	10	6.5 ^b	0.769 ^b

H_e = expected heterozygosity. Values with similar superscripts are not significantly different based on 1000 resamplings. GYE – Greater Yellowstone Ecosystem, ND – North Dakota. Values with the same letters (a or b) are not significantly different ($P \geq 0.05$) based on 1000 resamplings, values with different letters are significantly different ($P \geq 0.05$) based on 1000 resamplings.

vation GYE foxes exhibited significantly less heterozygosity than the low-elevation North Dakota foxes ($P = 0.01$, $P = 0.026$, respectively; Table 1).

STRUCTURE indicated that there were most likely three populations (Figure 4) and we found significant interpopulation differentiation across all populations ($\chi^2_{df=20} = \infty$, $P = 0.00$) so each population was analyzed separately. Estimates of R_{st} and F_{st} were in agreement with each other; pairwise population comparisons showed a greater degree of subdivision between the contiguous high-elevation and mid-elevation foxes than between the allopatric mid-elevation and low-elevation North Dakota fox populations (Table 2). The estimated number of migrants between populations using the private allele method (Barton & Slatkin 1986) also agreed with the estimates of population subdivision; estimates of migration between the high-elevation foxes and mid-elevation foxes was less ($N_m = 1.09$) than that found between either the mid-elevation foxes and the low-elevation North Dakota foxes ($N_m = 1.55$) or the high-elevation foxes and the low-elevation North Dakota foxes ($N_m = 1.17$). Similarly, the assignment test correctly assigned the majority of foxes to their correct populations and failed to reject the null hypothesis that each group is a distinct population in Hardy-Weinberg equilibrium (all $P_s > 0.10$, Table 3). STRUCTURE clustered individuals into three populations with the same animals identified as

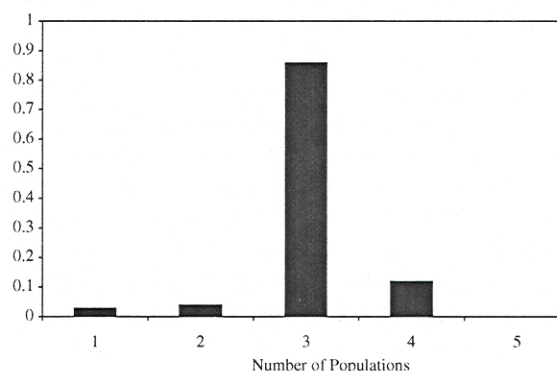


Figure 4. The probability of each number of populations existing in the data as calculated by the program STRUCTURE (Pritchard et al. 2000).

dispersers as in the assignment test (Figure 5). The one fox captured at mid-elevation but assigned to the high-elevation expressed the red phenotype; all three foxes captured at high-elevation but assigned to the mid-elevation expressed the red phenotype.

Discussion

Our results suggest that the fox populations in the Greater Yellowstone Ecosystem experience an unexpected degree of genetic isolation at different elevations, given their contiguous distribution. Mid-elevation foxes (animals caught between 1600

Table 2. Microsatellite estimates of population subdivision based on F_{ST} (below the diagonal) and R_{ST} (above diagonal) for each geographical region

Geographical region	GYE high elevation	GYE mid-elevation	North Dakota
GYE high-elevation		0.102	0.076
GYE mid-elevation	0.031		-0.017
ND low-elevation	0.064	0.023	

GYE – Greater Yellowstone Ecosystem; ND – North Dakota.

Table 3. Summary of assignment of individuals to geographical regions, indicating the number of animals assigned to each geographical region (columns) based on the region from which they were sampled (rows)

Geographical region	GYE high-elevation	GYE mid-elevation	North Dakota
GYE high-elevation	12	3	0
GYE mid-elevation	1	12	2
ND low-elevation	0	3	7

Values in the diagonal are animals assigned to their population of capture. GYE – Greater Yellowstone Ecosystem, ND – North Dakota

and 2300 m) in the Greater Yellowstone Ecosystem are genetically more similar to low-elevation foxes in eastern North Dakota than the mid-elevation foxes are to contiguous high-elevation foxes (> 2300 m), show increased partitioning of genetic variance based on F_{ST} and R_{ST} , and have fewer migrants between populations. The red fox populations in the GYE also exhibit lower heterozygosity and had fewer alleles compared to red fox populations in North Dakota suggesting the GYE foxes have smaller populations.

The fox subpopulations show a degree of division ($R_{st} = 0.14$) comparable to that found between an island and mainland population ($R_{st} = 0.15$) of red fox in Australia connected by a causeway for less than 15 years (Lade et al. 1996).

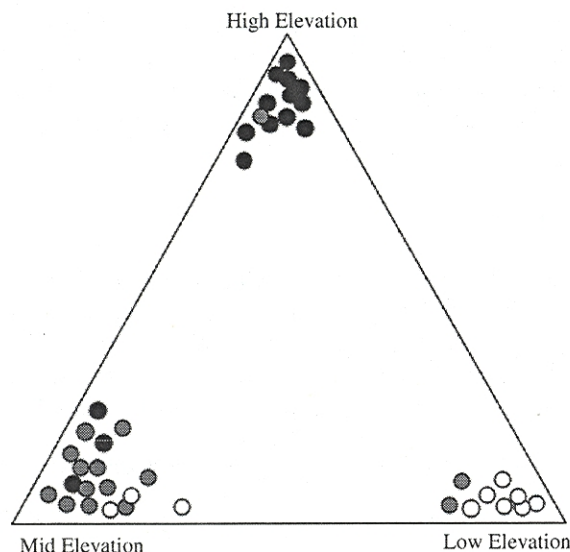


Figure 5. Cluster output from the program STRUCTURE for the most likely number of populations (3). Black circles represent individuals captured at high-elevations, gray circles indicated individuals captured at mid-elevations, and the white circles indicated individuals captured at low-elevations. The proximity to the corner of the triangle represents the probability of the animal belonging to that population.

Despite the fact that the estimated number of interpopulation migrants was greater than the 1 per generation that prevents fixation of alternate alleles it is low enough that differentiation between allele frequencies of the population should occur. Further, it is likely that the estimates of the amount of interpopulation dispersal are overestimates and more accurately represent phylogenetic effects given the $N_m = 1.55$ estimate between the North Dakota and mid-elevation Greater Yellowstone Ecosystem foxes; it is unlikely that any foxes regularly make the > 1000 km traverse. The results of the assignment test further support the conclusion that interpopulation dispersal between mid- and high-elevation populations of Greater Yellowstone Ecosystem foxes is low enough that they can be considered distinct populations.

An elevation trend exists in the frequency of occurrence of the novel phenotypes and the mid- and high-elevation Greater Yellowstone Ecosystem fox populations are genetically differentiated. While it is possible that these results are due to selection, latitudinal trends in the frequencies of the traditional color morphs failed to show evidence of selection (Swanson and Johnson 1996) and, the more parsimonious explanation of drift can explain the trends observed in the Yellowstone foxes. The observed distributional pattern could have been the result of a founder event during the Wisconsin glaciation reducing genetic variation (Nei et al. 1975; Nei 1977). Hewitt (1999) described how glacial retreat can result in cryptic population structure, hybrid zones and founder effects; Wisconsin glaciation founder events have produced a number of divergent populations in other vertebrates including fresh water fish (e.g. O'Reilly et al. 1993) and birds (e.g. Zink and Dittman 1993).

Red fox are thought to have been absent from the western portion of the United States, including the Greater Yellowstone Ecosystem (Macpherson

1964; Aubry 1983; Kamler and Ballard 2002), prior to the Wisconsin glaciation. During the glaciation, fox populations from Canada (*V. v. abietorum*) would have been forced south to the tundra habitat at the edge of the ice sheet (Butler 1945; Calhoun 1950; Macpherson 1964; Aubry 1983), the southern most advance reaching the Missouri River (Aubry 1983; Dyke and Prest 1987). With glacial retreat, the fox populations would have been forced to move northward with the tundra habitat, or up elevationally to the alpine environment (Butler 1945; Macpherson 1964). Red foxes that migrated elevationally into the subalpine environment would probably have originated as small isolated populations with unique genetic signatures (Hewitt 1999). Alternatively, during the glaciation, nunataks (isolated areas of ice free mountaintop habitat surrounded by glacial ice) may have harbored small populations of *V. v. abietorum* trapped during glacial advance. Each of these scenarios produce a founder effect and could result in populations with a high frequency of the novel color morphs, both of which can be produced by a single gene mutation (Adalstenison et al. 1987). Maintenance of the subdivision may follow a pattern similar to that of the mountain fox in the Cascades, with climate and competition preventing either population from extending its range. Aubry (1983) found the Cascade mountain fox (*V. v. cascadiensis*) to be smaller than *V. v. abietorum* in all morphological measurements. Fuhrmann (1998) failed to find significant morphological differences between high- and mid-elevation foxes in the Greater Yellowstone Ecosystem although he had small sample sizes.

Two novel color-morphs found in high elevation populations of the red fox in the Greater Yellowstone Ecosystem appear to be absent from conspecific populations at lower elevations (Figure 3). Analysis of distributional and genetic evidence indicates that red fox populations exhibit some genetic isolation along an elevational gradient, despite their continuous distribution. We suggest that two semi-isolated populations of fox exist in the Greater Yellowstone Ecosystem, a mid-elevation fox (1600–2300 m), possibly derived from introduced European stock and a high-elevation montane fox (>2300 m) that is descended from populations pushed south during the Wisconsin glaciation, and isolated following glacial retreat.

Conservation implications

Although few studies have investigated red fox in this region, and little is known about the life history or size of either population, the genetic and morphological distinction of these two fox populations suggests that they should be managed as unique entities. Currently there is no management plan for red fox in the Greater Yellowstone Ecosystem. The need for independent management and more studies is highlighted by Sierra-Nevada mountain fox (*V. v. necator*) which was declared threatened in 1980 despite healthy populations of low-land foxes (California Department of Fish and Game, pers. comm). The need for management considerations is further exacerbated by the impact of the reintroduced wolves in Yellowstone National Park. The wolves rapidly altered prey communities and vegetation (Smith et al. 2003) as well as the predator community, producing an 80% reduction in coyote population size in areas with wolf packs (Crabtree and Sheldon 1999). Wolves, in an apparent attempt to minimize interspecific competition have been observed killing coyotes, similarly, coyotes have been observed killing red fox (Crabtree and Sheldon 1999). While not investigated yet, the reduction in coyote populations is expected to bring about an increase in red fox populations due to competitive release. The majority of the coyote/red fox interactions take place below the subalpine region (R. Crabtree pers obs.), so it is likely that the mid-elevation population will benefit the most from competitive release as exhibited by an increase in population size. Although there currently appears to be little movement between mid- and high-elevation populations increased population size in the mid-elevation foxes may increase pressure on the unique high-elevation foxes. Given the small amount of gene flow between the high- and mid-elevation populations, future management plans should considered the two populations as effectively unique populations. Further, the fractured topography in the Greater Yellowstone Ecosystem suggests that isolation may exist between populations of high-elevation foxes presenting additional conservation difficulties.

Several lines of further investigation are suggested by this study. The lack of dispersal, as indexed by gene flow, between the populations is surprising. In contrast to the situation with the Cascade fox no gaps are found between the

mid-elevation and high-elevation populations. Behavioral studies are likely to shed light on the isolating mechanisms. In addition, sequence analysis to determine the phylogenetic relationship between the foxes in the Greater Yellowstone Ecosystem and other foxes is necessary as is a determination of the amount of gene flow across lower elevation regions.

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