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GENETIC DIVERSITY AND STRUCTURE OF THE FISHER (*MARTES PENNANTI*) IN A PENINSULAR AND PERIPHERAL METAPOPULATION

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Evolutionary processes can be strongly affected by landscape features. In vagile carnivores that disperse widely, however, genetic structure has been found to be minimal. Using microsatellite DNA primers developed for other mustelids, we found that populations of a vagile forest carnivore, the fisher (*Martes pennanti*), exhibit high genetic structure (F_{ST}=0.45, *SE*=0.07) and limited gene flow (*Nm* < 1) within a >1,600 km narrow strip of forested habitat; that genetic diversity decreases from core to periphery; and that populations do not show an equilibrium pattern of isolation by distance. Genetic structure was greater at the periphery than at the core of the distribution and our data fit a 1-dimensional model of stepping stone range expansion. Multiple lines of paleontological and genetic evidence suggest that the fisher recently (<5,000 years ago) expanded into the mountain forests of the Pacific coast. The reduced dimensionality of the distribution of the fisher in western coastal forests appears to have contributed to the high levels of structure and decreasing diversity from north to south. These effects were likely exacerbated by human caused changes to the environment. The low genetic diversity and high genetic structure of populations in the southern Sierra Nevada suggest that populations in this part of the geographic range are vulnerable to extinction.

Key words: dimensionality, fisher, genetic diversity, *Martes pennati*. microsatellite DNA, peninsula, periphery, stepping-stone

Rates and patterns of evolution at the population level are affected by position in and shape of the geographic range (Briggs 1996). Populations at the periphery of a distribution tend to be more fragmented and have lower and more variable population densities (Brown et al. 1995) with lower migration rates and less gene flow (Hoffman and Blows 1994: Lawton 1993) than populations at the core of a species' distribution. These population dynamics result in reduced genetic diversity and increased population structure (Li and Adams 1989; Maharadatunkamsi et al. 2000). For boreal carnivores, this core periphery pattern of increasing population structure and decreasing genetic diversity is particularly striking. Wolverines (*Gulo gulo* Kyle and Strobeck 2001), Canada lynx (*Lynx canadensis* Schwartz et al. 2003), and brown bears (*Ursus arctos*—Paetkau et al. 1998) all exhibit a correlation between latitude and genetic diversity that has been attributed, in part, to increased habitat fragmentation at the southern periphery of boreal forest habitat.

In addition to the relative position of a population in a species' distribution, local geography and dimensionality affect the pattern of migration and isolation of a population. For terrestrial mammals, biologists typically model genetic structure with migration occurring in a 2-dimensional (1-D) pattern. However, in certain circumstances, a 1-dimensional (1-D) model of migration might be more appropriate. Kimura and Weiss (1964) modeled the 1-D stepping stone system and predicted that reduced dimensionality increased population genetic structure, due to a reduced number of pathways for genetic exchange in a linear (compared to a grid like) arrangement of populations. Data simulations confirm that patterns of isolation by distance arc more apparent in 1-D than in 1-D systems even when migration rates are greater in the 1-D system (Slatkin 1993).

Here, we examine the cumulative effects of relative position in and dimensionality of a species distribution on population genetic structure and diversity in the fisher (*Martes pennanti*).

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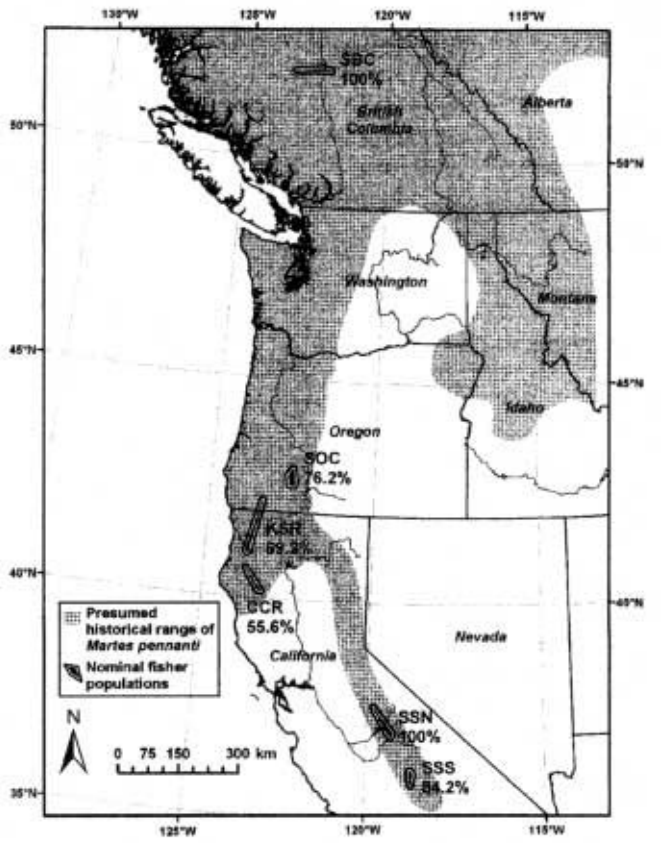

FIG. 1.—Sampling locations for the fisher in the Pacific states and British Columbia included 6 nominal populations: southern British Columbia (SBC, $n = 15$); southern Oregon Cascades (SOC, $n = 21$); Klamath-Siskiyou region (KSR, $n = 25$); California Coast Range (CCR, $n = 18$); Southern Sierra-north (SSN, $n = 14$); and southern Sierra-south (SSS, $n = 19$). The map details the presumed pre-settlement distribution, nominal populations (indicated by polygons), and classification success in Bayesian assignment tests; high values denote genetic distinctness of a population.

The core of the geographic range of the fisher spans the boreal forests of Canada (Gibilisco 1994). Along the Pacific coast of the contiguous United States and southern Canada, the distribution of this species is confined to a >1,600 km long peninsula of forest surrounded by habitat unsuitable to the fisher. In several places this narrow strip of habitat is only a few tens of km wide, yet it extends from southern British Columbia to the Sierra Nevada of southern California (Fig. 1). Paleontological evidence suggests that forests along the Pacific coast were colonized recently by fishers during the Holocene and that populations are <5,000 years old (Graham and Graham 1994). Even more recently, parts of this distributional peninsula have been rendered vacant during historical times, presumably by human caused factors. Fishers have apparently been extirpated in the northern Sierra Nevada of California (Zielinski et al. 1995), in most areas of Oregon (Aubry and Lewis 2003), and throughout Washington (Lewis and Stinson 1998).

Our objectives in this study were to use microsatellite genotypes to (1) test for losses in genetic diversity and for increases in genetic structure from the base to the tip of the Pacific coast distributional peninsula as predicted by the coreperiphery hypothesis of genetic diversity; (2) compare the magnitude of genetic structure of the 1-D stepping stone model of geographic distribution of fishers on the Pacific coast to the 2-D geographic distribution that occurs in the core of the species range; (3) determine if genetic data support the paleontological hypothesis of recent range expansion by fishers down the Pacific coast from British Columbia; and (4) investigate the geographic origin of a population of fishers in southwestern Oregon believed to have been translocated from 2 genetically distinct source populations (Drew et al. 2003). We use the resulting data to assess the vulnerability of fisher populations along the Pacific coast to extirpation.

Materials and Methods

Sampling locations.—We obtained tissue samples for molecular analyses from multiple, independent ecological studies of the fisher in the Pacific coast region. Most of the tissue samples used in our analyses were collected from livetrapped animals; several were collected from carcasses, and 2 were taken from frozen specimens at the Museum of Vertebrate Zoology. Berkeley, California (MVZ 185230 and MVZ 196716). All tissues were collected between 1993 and 2001. We analyzed 112 samples from 6 nominal populations in California, Oregon, and British Columbia (Fig. 1), after excluding known full sibling juveniles or the offspring of sampled females. Population assignment of individuals a priori was based on geographic proximity and ecological provinces. Of the 6 populations, all but southern Oregon Cascades were native populations; the reintroduced Oregon population comprises the descendents of translocations primarily from British Columbia and secondarily from Minnesota (Aubry and Lewis 2003: Drew et al. 2003).

Laboratory protocols.—For each extraction, we used 15-30 hairs or 20-30 µg of ear tissue. DNA was extracted from hairs and ear tissue using a standard phenol-chloroform extraction technique. We amplified DNA by polymerase chain reaction (PCR), using 8 pairs of microsatellite primers: Mer04l, Mer095, Mvis002, Mvis020, Mvis072 (Fleming et al. 1999). Mal, Ma19 (Davis and Strobeek 1998), and Mvi87 (O'Connell et al. 1996). All loci were dinucleotide repeat segments with a minimum of 11 consecutive repeats in the species for which they were developed. Amplifications were performed in 10 µl volumes containing 1 µl of DNA, 2 nmol deoxynucleotides (Sigma Aldrich, St. Louis, Missouri), 1,000 ng/µl bovine serum albumin (Sigma Aldrich, St. Louis, Missouri), 0.5-1.4 pmol each primer (Invitrogen, Carlsbad, California), 0.8-1.0 M betaine (SigmaAldrich, St. Louis, Missouri), and 0.6 units of Tag polymerase (SigmaAldrich, St. Louis, Missouri). Included in the PCR reaction was 0.5 pmol of a fluorescent 3rd primer (Li-Cor Inc., Lincoln, Nebraska) complementary to a 19 base pair extension on the 5' end of the forward primer. We amplified samples in a Peltier thermal cycler (PTC-200, M. J. Research Inc., Watertown, Massachusetts), and visualized samples electrophoretically using a 7% polyacrylamide gel in a Li-Cor Gene Readir 4200 automated sequencer (Li-Cor Inc., Lincoln, Nebraska). Genotypes, characterized as base pair length, were resolved with GenelmagIR software, V. 3.0.

Evaluation of nominal populations.—We evaluated genetic support for the distinctness of our preliminary nominal populations using a Bayesian assignment procedure (Comuet et al. 1999) that classified

each animal according to the nominal population its genotype most closely resembled. We evaluated Hardy-Weinberg equilibrium for each population using an exact probability test generated by a Markov chain analysis in GENEPOP 3.3 software (Raymond and Rousset 1995). Linkage disequilibrium was tested by the genotypic equilibrium test in GENEPOP 3.3. All tests were adjusted for multiple comparisons using a sequential Bonferroni correction (Rice 1989).

Characterisation of genetic diversity and structure.—We characterized genetic diversity in each population using Nei's (1978) unbiased heterozygosity (H_E) calculated using Tools for Population Genetic Analyses (TFPGA) 1.3 (Miller, M. P. 1997. TFPGA version 1.3: A Windows program for the analysis of allozyme and molecular population genetic data. http://bioweb.usu.edu/mpmbio/, last updated 1 February 2000. Downloaded 1 October 2002.). We calculated allelic richness (*A*, compensating for sample size effects) using F-Stat (Goudet 1995). We used the computer program Populations (O. Langella, 2002. Populations, a free population genetic software. http:// www.pge.cnrs-gif.fr/bioinfo.populations, last updated 5 December 2002. Downloaded 15 May 2003.) to calculate chord distance (*D*c—Cavalli-Sforva and Edwards 1967) and build a neighbor joining tree that was bootstrapped 10,000 times. We examined phylogenetic tree topology using TREEVIEW software (Page 1996). We examined patterns of genetic diversity from the base of the distributional peninsula (southern British Columbia) southward using 2 approaches. Using only native populations (excluding southern Oregon Cascades), we tested whether the southernmost populations (southern Sierra north and south) differed in genetic diversity (based on *A* and H_E) from fishers at the base of the peninsula using a paired, 1-sample t test. We then tested for continuous variation in genetic diversity along the distributional peninsula using linear regression analysis and the 2 measures of genetic diversity.

We estimated population subdivision with pairwise F_{ST} calculated with F-Stat (Weir and Cockerham 1984) for comparison with previously published estimates of genetic differentiation in fisher and with ρ_{ST} using GENEPOP 3.3 (Roussel 1996) which assumes a stepwise mutation model. We compared pairwise estimates of population subdivision with a Mantel test (Mantel 1967; Sokal and Rohlf 1995). We estimated gene flow as $M = {}^{1/4}[(1/\rho_{ST}) - 1]$ (Slatkin 1993) using our estimates of ρ_{ST} for the calculation. We estimated the effective number of migrants (*Nm*) using 2 approaches. We initially estimated the effective number of migrants per generation using the multilocus, private allele method of Barton and Slatkin (1986) and Slatkin (1985). We also used a coalescent model to estimate Nm and $\theta = 4N\mu$ (Beerli and Felsenstein 2001) using the software program MIGRATE (Beerli, P. 1997 2(103. MIGRATE: documentation and program of LAMARC. Version 1.6.9. Distributed over the Internet, http://evolution.genetics.washington.edu/lamarc.html, last updated 10 April 2002. Downloaded: 16 June 2003.). In an initial run of the program we used estimates of F_{ST} to calculate starting values of Nm and θ. Resulting values from the initial run were used as starting values for 3 subsequent runs. We used default search parameters for every run; all runs (except for the initial one) gave similar results. For maximum likelihood estimation we selected a full migration model to estimate Nm and θ.

We modeled isolation by distance using both equilibrium and nonequilibrium approaches. Because available evidence indicates that fishers colonized the Pacific coast recently, it was unlikely that populations were in drift migration equilibrium. Initially we tested for isolation by distance with ρ_{ST} using a Mantel test. We also analyzed isolation by distance by computing regression coefficients for the log-log regression of *M* on geographic distance; this analysis is more sensitive to patterns of isolation by distance in systems that are not in equilibrium (Slatkin 1993). Finally, we used Good's model of stepwise range expansion (Slatkin 1993) to test the hypothesis that fishers recently colonized the Pacific coast from north to south in a slepwise fashion. This analytical method also assumes nonequilibrium; a regression coefficient is calculated from the log-log regression of *M* onto the geographic distance from the source population of the expansion to each of the other populations. Pairwise values of *M* are not independent (Slatkin 1993), so regression slopes and correlation coefficients are provided for descriptive purposes only.

We included nonnative southern Oregon Cascades in the isolation by distance analysis by adjusting the geographic distance and latitude to reflect the primary source location (southern British Columbia) of translocated animals. Analysis of mtDNA revealed that most (8 of 9) haplotypes in southern Oregon Cascades were shared with southern British Columbia, and neighbor joining trees placed the 2 populations near one another (Drew et al. 2003). For all other populations, geographic distances were measured from the geometric center of the minimum convex polygon formed by sampling locations for individuals from each population using ARCVIEW 3.2 software (ESRI, Redlands, California). Distances between population centers were also calculated using ARCVIEW 3.2.

Results

Population assignment.—The success rate of a priori assignments of individuals into populations was >50% for all populations and reached values as high as 100% (Fig. 1). Not surprisingly, the lowest classification success (and highest cross-classification) was for the 2 populations with the shortest geographic distance between them (California Coast Range and Klamath Siskiyou region). We retained the initial population designations for all subsequent analyses. Of the 48 locus-population permutations, 37 had polymorphic genotype distributions that allowed testing of Hardy-Weinberg equilibrium (the other 11 permutations were untestable because some loci were monomorphic within some populations). For 5 populations, all loci were in equilibrium. Two loci exhibited significant departures from equilibrium at southern British Columbia (Mvis072 and Mal); both were heterozygote deficiencies. A global test of Hardy-Weinberg equilibrium found significant departures from equilibrium ($P < 0.001$). For all pairs of loci (with populations disaggregated or aggregated), we found no linkage disequilibrium. We therefore considered each locus-specific genotype to be independent for statistical purposes.

Genetic diversity.—Allelic richness (*A*) within populations averaged 2.0, and was highest in southern British Columbia and southern Oregon Cascades ($A = 2.6$) and lowest in southern Sierra north ($A = 1.4$; Table 1). Mean unbiased heterozygosity (mean of population means) was 0.28, with the highest value in southern Oregon Cascades (H_E=0.42) and the lowest in southern Sierra north ($H_E = 0.16$). Allelic richness was significantly greater at the northern end of the distributional peninsula (southern British Columbia) than at the southern tip (southern Sierra south, $t = -2.4$, $d.f. = 7$, $P = 0.02$). Allelic richness was positively related to latitude in a linear fashion (regression $F = 19.7$, $d.f. = 4$, $P = 0.02$: Fig. 2). Similarly, heterozygosity was lower in native southern populations than in southern British Columbia (1-sample $t = -7.0$, $n = 4$, $P = 0.006$), and showed progressive decreases

TABLE 1.—Expected heterozygosity (H_E) and allelic richness (A) of fisher populations in a distributional peninsula from British Columbia to the southern end of the Sierra Nevada. Populations are arranged from north to south. We present the total sample size summed for all populations and mean H_E and A averaged for all populations.

Nominal populations	Origin	n	H_E	A
Southern British Columbia	Native	15	0.37	2.6
Southern Oregon Cascades	Reintroduced	21	0.42	2.6
Klamath-Siskiyou Region	Native	25	0.26	1.8
California Coast Range	Native	18	0.24	1.8
Southern Sierra–north	Native	14	0.16	1.4
Southern Sierra–south	Native	19	0.20	1.7
Total, $\bar{X}$		112	0.28	2.0

with decreases in latitude (regression $F = 37.1$, $df = 4$, P = 0.009; Fig. 2). Five unique alleles were found in southern British Columbia, 2 unique alleles were found at southern Oregon Cascades, and no unique alleles were found south of Oregon.

Genetic structure.—For the 6 nominal populations, overall $F_{ST} = 0.42$ (SE = 0.07), with the largest pairwise F_{ST} (0.60) between California Coast Range and southern Sierra south, and the smallest (0.11) between California Coast Range and Klamath Siskiyou region (Table 2). Considering only native populations, $F_{ST} = 0.45$ (SE = 0.09), which was consistent with a mean migration rate of 0.31 migrants/generation between all population pairs. To compare our results with those reported from fishers in the core of their range (Kyle et al. 2001), we recalculated F_{ST} using only the 5 loci that both studies had in common. Global F_{ST} was 0.53 ± 0.09; bootstrapping over loci resulted in a 95% confidence interval from 0.35 to 0.67. Pairwise estimates of ρ_{ST} revealed a similar pattern of genetic differentiation among Pacific coast populations (Table 2). Care must be taken when interpreting the absolute value of these estimators of genetic structure, however, as they assume that populations are in drift migration equilibrium, which is likely not the case with fishers along the Pacific coast.

Confirming high levels of genetic differentiation and population isolation was the low estimated effective number of migrants between populations. Estimates of M calculated from fix, ranged from 2.6 (between California Coast Range and Klamath Siskiyou region) to 0.2 (between California Coast Range and southern Sierra south) with a mean and SE of 0.75 0.18. Using the private allele method, we estimated Nnr to be 0.95; using the maximum likelihood approach, all estimates of Nm were < 1 migrant per generation with the highest estimates of migration occurring between southern British Columbia and southern Oregon Cascades (1 migrant approximately every 2 generations; Table 3). Most estimates were substantially lower than migration between the 2 northernmost populations: from <1 migrant per 1,000 generations to 1 migrant every 3 generations. Estimates of migration were significantly different from a stepping stone model and migration rates were asymmetric among populations that were only 1 step away (likelihood ratio test = 421, $d.f = 30$, $P < 0.001$). Assuming constant mutation rates among populations, effective population size

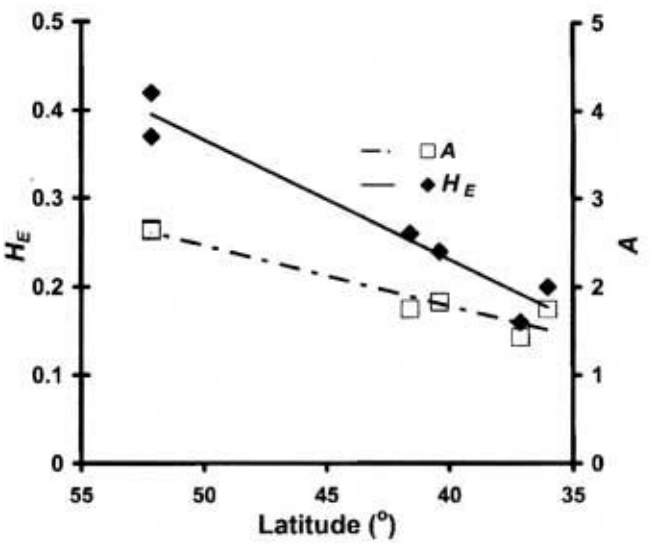

FIG. 2.—Regression of two measures of genetic diversity (H_E, expected heterozygosity and A, allelic richness) on latitude for 5 native populations and 1 translocated population of the fisher within the Pacific distributional peninsula. For the translocated population (southern Oregon Cascades), we used geographic distance from the presumed source population (southern British Columbia). Regressions for both measures are significant at $P = 0.01$.

was significantly different among populations; populations in the north were larger than populations in the south (Table 3). Population branches of the neighbor joining tree formed the following 3 groups: southern British Columbia and southern Oregon Cascades, California Coast Range and Klamath Siskiyou region, and southern Sierras north and south with varying degrees of support (Fig. 3).

Isolation by distance. Using the parameter psi, which assumes that populations are in drift migration equilibrium, we found no significant association with geographic distance (Mantel test, $P = 0.16$). The regression coefficient (r^2) for the log-log regression of M and geographic distance was 0.27 ± 0.26 ($\bar{X}$ ± SE) with a slope of -0.19 ± 0.08. Using Good's model of range expansion the log log regression of M and the distance from the source produced an $r^2 = 0.63 \pm 0.36$ with a slope of -0.12 ± 0.05; excluding southern British Columbia and southern Oregon Cascades and considering KlamathSiskiyou region the source for the 3 populations south of it, $r^2 = 0.99 \pm 0.09$ with a slope of -1.3 ± 0.07 (Fig. 4).

DISCUSSION

Genetic patterns from core to periphery. Our measures of genetic diversity were lower than those reported in the core of the fisher's range by Kyle et al. (2001); our estimates of heterozygosity were less than half of those within the core. The mean number of alleles/locus they reported for southern British Columbia ($A = 3.9$) compares with our value of 3.0 (uncorrected for sample size) for a nearby area using similar microsatelfte loci. Interestingly, the allelic diversity of fishers in southern British Columbia was the lowest of the 13 sites

Table 2.—Two measures of genetic distance between nominal populations of the fisher in the Pacific states and provinces. Upper diagonal values are F_{ST} with significant ($P < 0.005$) pairwise differences (exact test of sample differentiation) indicated by asterisks. Lower diagonal values are ρ_{ST}. We found a significant correlation between F_{ST} and ρ_{ST} using a Mantel test ($P = 0.02$).

Nominal populations	Southern British Columbia	Southern Oregon Cascades	Klamath-Siskiyou Region	California Coast Range	Southern Sierra-north	Southern Sierra-south
Southern British Columbia	—	0.20*	0.39*	0.37*	0.35*	0.42*
Southern Oregon Cascades	0.13	—	0.43*	0.41*	0.37	0.38*
Klamath-Siskiyou Region	0.31	0.28	—	0.11*	0.56*	0.48*
California Coast Range	0.32	0.24	0.08	—	0.58*	0.60*
Southern Sierra–north	0.18	0.35	0.42	0.44	—	0.51*
Southern Sierra–south	0.29	0.45	0.47	0.54	0.24	—

studied by Kyle et al. (2001), and heterozygosity was lower than that of most other populations they studied. Considering the results from Kyle et al. (2001), Drew et al. (2003), and this study, it appears that genetic diversity declines from the center of the fisher's range toward its southwestern periphery (British Columbia), then decreases further along the Pacific distributional peninsula to its southern tip. These findings suggest that losses of genetic diversity in a peripheral distributional peninsula are additive to those from the center to the periphery of the fisher's core geographic range.

Measures of genetic structure for fishers within the Pacific coast distributional peninsula are among the highest reported for a mammalian carnivore. F_{ST} calculated using only loci from Kyle et al. (2001) was 0.35-0.67, between 2.5 and 4.8 times that reported for fishers in the core of their range (Kyle et al. 2001) and 10-20 times that reported for American martens (Kyle et al. 2000), wolverines (Kyle and Strobeck 2001), and Canada lynx (Schwartz et al. 2002).

Genetic structure, gene flow and dimensionality.—The geographic distribution of suitable habitat for fishers along the Pacific coast (Fig. 1) suggests a 1-D pattern of gene flow. Genetic data support this hypothesis; as predicted by Good's model of stepwise range expansion, we found a relationship between M and distance from the source population. This relationship was particularly strong for the 4 peninsular populations; the regression had a slope of -1.3, similar to the slope of -1.0 predicted for l-D systems rather than the slope of -0.5 predicted for 2-D systems (Slatkin and Maddison 1990). Although the likelihood ratio test did not support a stepping stone model of migration, *Nm* was more than twice as great between populations separated by 1 step (0.18 ± 0.07) as compared to populations separated by 2 or more steps (0.08 ± 0.02).

The ecology of fishers likely compounds the effects of a peninsular and peripheral distribution on genetic diversity. The fisher is regarded as a habitat specialist in the western United States (Buskirk and Powell 1994), occurring only at mid- to lower elevations in mature forests characterized by dense canopies and abundant large trees, snags, and logs (Powell and Zielinski 1994). Buskirk and Powell (1994) noted that fishers seem even more inclined than American martens to avoid areas lacking overhead cover. Such habitat barriers could contribute to the strong population genetic structure we observed. Habitat specificity explains similarly high genetic structure found in swift foxes, kit foxes (*Vulpes velox*—Mercure et al. 1993). and black footed ferrets (*Mustela nigripes*—Wisely et al. 2002). Habitat specificity might also contribute to the exceptionally low levels of gene flow (migrants per generation) estimated among populations.

Exemplifying this high degree of structure is the genetic differentiation between the 2 southern Sierra Nevada populations. These populations arc separated by <100 km of contiguous forest, yet $Nm = 0.02$, suggesting these populations exchange, on average, 1 migrant every 50 generations. The Kings River, which separates the 2 southern Sierra populations and has not frozen across its surface during historical times, could constitute a barrier to dispersal of previously unrecognized magnitude. Despite the piseivory implied by their common name, fishers do not readily swim, and large rivers can serve as formidable barriers to their movements. High levels of genetic

Table 3.—Estimates of the effective number of migrants per generation (Nm) and θ ($4N\mu$) for 6 populations of fishers from the Pacific coast using microsatellite data in the software program MIGRATE (see text for details).

Population	θ[a]	*Nm* (x = receiving population)					
		1, x	2, x	3, x	4, x	5, x	6, x
1: Southern British Columbia	0.25	—	0.55	0.15	0.06	0.07	0.04
2: Southern Oregon Cascades	0.24	0.61	—	0.13	0.04	0.33	0.18
3: Klamath-Siskiyou Region	0.11	0.02	0.04	—	0.15	0.08	<0.001
4: California Coast Range	0.12	0.03	0.04	0.04	—	0.02	0.01
5: Southern Sierra-north	0.09	<0.001	0.09	0.01	0.01	—	0.02
6: Southern Sierra-south	0.13	0.08	0.10	0.03	0.02	0.05	—

[a] H_0s are equal. Maximum likelihood log ratio = 120.8, $d.f. = 6$, $P < 0.001$.

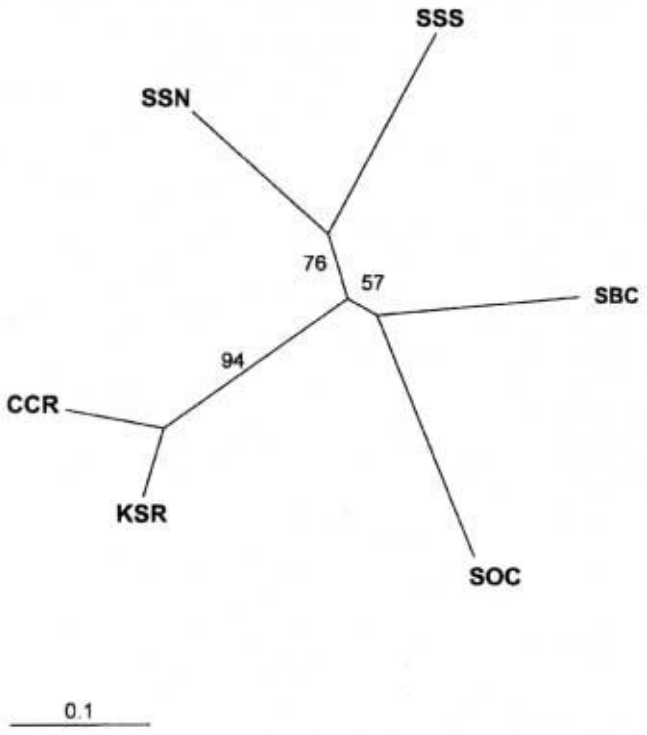

FIG. 3.—Unrooted tree phylogeny for 5 native and 1 reintroduced (southern Oregon Cascades) populations of the fisher in British Columbia, Oregon, and California, using D_C. Scale bar is in D_C units. See Figure 1 for definition of acronyms.

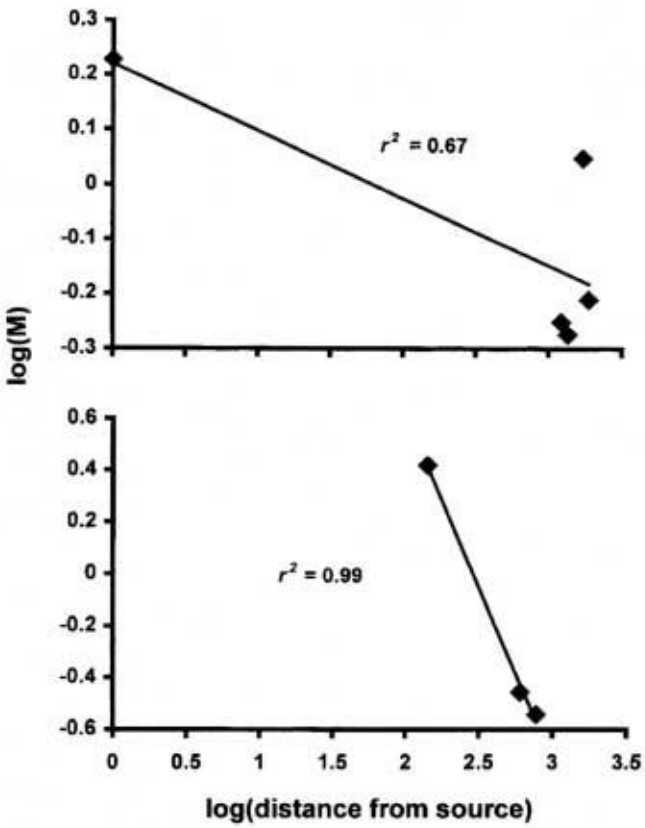

FIG. 4.—The log-log relationship between M (calculated as ¼ [(1/ρ_{ST}) − 1]) and the distance from the source population. The top graph assumes southern British Columbia to be the source with expansion south and has a slope of −0.12; the bottom graph assumes the Klamath-Siskiyou region to be the source of the southerly expansion and has a slope of −1.3.

structure between adjacent populations of fishers have previously been reported from British Columbia (C. J. Kyle, in litt.), and genetic structure is evident throughout the northern half of its distribution (Kyle et al. 2001).

Genetic diversity, paleontology, and patterns of coloniza tion. We hypothesize that fishers colonized the Sierra Nevada in a stepping stone fashion from the north to the south in the last 5,000 years, based on several lines of evidence. We detected a pattern of isolation by distance that was consistent with recent range expansion. According to Good's model of stepwise range expansion, the negative log-log relationship between M and distance from source population indicated that fishers expanded from British Columbia down the Pacific coast peninsula of forest. Because this model implies nonequilibrium between drift and migration (the pattern is obscured when migration occurs after range expansion), it suggests that fishers expanded down this peninsula recently with very little gene flow among populations after colonization. Our extremely low estimates of *Nm* further support the idea that there is little ongoing gene flow.

Also indicative of range expansion was the observed geographic pattern of genetic diversity, which was defined by a progressive loss of diversity in fisher populations from the base to the tip of the Pacific distributional peninsula. Heterozygosity in southern British Columbia, the population considered to be in the core of the fisher's distribution, was nearly twice that of southern Sierra south, the population at the southern tip of the distributional peninsula. Likewise, allelic richness was 1.5 times greater in the population representing the core than in the most peripheral population. Stepwise expansion is colonization as a result of consecutive founder events at the leading edge of the expansion, thus we would expect to see a gradient of diversity along the path of expansion. This pattern is exemplified by the positive correlation between latitude (the directional vector of the expansion) and genetic diversity we found. Additionally, unique alleles occur only in southern British Columbia and southern Oregon Cascades; populations to the south only contain alleles that are shared with neighboring populations, which suggests that gene flow was largely unidirectional from north to south without genetic input from the east.

The hypothesis of a recent north to south colonization is further supported by paleontological and archeological evidence. Fishers appear to have colonized western North America relatively recently (i.e., during the late Holocene); the earliest records of fishers in the Pacific Northwest date from <5,000 years ago (Graham and Graham 1994). Despite the presence of other *Martes* species in western North America during the late Pleistocene and early to mid Holocene, there are

no records of fishers from that period. By the late Holocene, records of fishers on the Pacific coast are common. However, there is no evidence that fishers ever inhabited the Great Basin, which would have been the most likely dispersal route if fishers had colonized the Sierra Nevada from the cast (Graham and Graham 1994). Taphonomic bias is unlikely because there are records of other *Martes* species from the Great Basin during the late Holocene (Heaton 1990).

Genetic data support the paleontological evidence that the fisher evolved in eastern North America, expanded westward during the late Pleistocene, entering western North America (British Columbia) during the Holocene, and eventually colonizing the Sierra Nevada during the late Holocene (Graham and Graham 1994). In support of a rapid expansion westward, Kyle et al. (2001) found decreasing levels of heterozygosity and fewer alleles in western populations. In our study, we found an additional decrease in genetic diversity from British Columbia southward as populations colonized more southern teaches of boreal forest habitat.

A non native population.—Drew et al. (2003) concluded that the reintroduced southern Oregon Cascades population did not exhibit reduced genetic diversity associated with the founder event of translocation; this finding stands in contrast to a decrease in diversity associated with a translocation founder event described by Kyle et al. (2001). Indeed, southern Oregon Cascades had the highest H_E and shared the highest allelic diversity of the populations we studied. Two alleles at 2 loci were not found in any population except southern Oregon Cascades. We attribute the unique alleles, the relatively high heterozygosity, and the high allelic diversity to the admixing of genes from 2, and possibly 3, widely separated source locations. These include southern British Columbia, the source of 28 animals translocated from 1961-1980; Minnesota, the source of 13 animals translocated in 1981; and, possibly, resident native animals that were undetected at the time of the translocations. The likelihood that resident native animals admixed with translocated animals appears to be small, because Drew et al. (2003) found no mtDNA haplotypes in common between southern Oregon Cascades and neighboring native populations in northwestern California. The presence of microsatellite alleles unique to southern Oregon Cascades supports the findings of Drew et al. (2003) that this population is non native with a strong genetic affinity to fishers in southern British Columbia.

Conclusions. Patterns of genetic diversity and structure in fisher populations within the Pacific coast distributional peninsula are consistent with reduced dimensionality of the geographic range, and with the loss of genetic diversity along a distributional peninsula as fishers expanded south towards the periphery of their distribution. Paleontological and genetic evidence suggest that expansion likely occurred <5,000 years ago. The magnitude of genetic structure and lack of gene flow we found was unexpected given the relatively recent colonization of the peninsula and the fisher's large spatial requirements and longdispersal distances. For the fisher, home ranges are as large as 79 km^2 (Powell 1994) and dispersal distances as long as 100 km (York 1996). It appears, however, that even for some apparently vagile carnivores, intermediate distances might represent evolutionarily important barriers to movement that can facilitate rapid divergence. Human induced habitat fragmentation likely increased isolation of extant populations in recent times.

The relatively high level of genetic structuring among populations of fishers throughout their range has been amplified in the Pacific distributional peninsula. This genetic structure is the result of population isolation and limited gene flow. Reduced dimensionality, habitat specificity and habitat fragmentation are the likely causes. One effect of population isolation and reduced gene flow is vulnerability to extinction (Gilpin and Soule 1986). Erosion of remaining genetic diversity threatens these populations with inbreeding, inbreeding depression, and a reduced ability to adapt to changing environments (Allendorf and Leary 1986). Of equal concern is the demographic fate of these isolated populations. Populations in the south have a smaller effective population size than northern populations. Small population size coupled with low migration rates increase vulnerability to stochastic demographic events and environmental changes (Holsinger 2000). We have demonstrated isolation among populations with limited exchange, suggesting that populations on the Pacific coast have little demographic buffer from variation in the population growth rate. Immediate conservation action might be needed to limit further erosion of the unique genetic architecture found in this one dimensional metapopulation.

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