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WHEN REINTRODUCTIONS ARE AUGMENTATIONS: THE GENETIC LEGACY OF FISHERS (*MARTES PENNANTI*) IN MONTANA

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Fishers (*Martes pennanti*) were purportedly extirpated from Montana by 1930 and extant populations are assumed to be descended from translocated fishers. To determine the lineage of fisher populations, we sequenced 2 regions of the mitochondrial DNA genome from 207 tissue samples from British Columbia, Minnesota, Wisconsin, and Montana. In northwestern Montana, fishers share haplotypes with samples from the upper Midwest and British Columbia; in west-central Montana, we detected haplotypes found in British Columbia samples, but also detected a control region and cytochrome-*b* haplotype not found in source populations. Based on the unique haplotypes found in west-central Montana, we propose that individuals with these haplotypes are descended from a relic population. Fishers in northwestern Montana are likely descended from fishers from the Midwest and British Columbia.

Key words: augmentation, control region, *Cytb*, fisher, genetics, mitochondrial DNA, reintroduction, translocation, *Martes pennanti*, Montana.

Wildlife managers often try to recover species that have been eliminated or reduced in portions of their range. Translocations, the intentional movement of individuals from one area to another, can be used to reestablish extirpated populations (reintroductions) or to add individuals to existing populations (augmentations). Although translocations are frequently used to recover populations, the evaluation of these methods and their success has lagged behind implementation (Breitenmoser et al. 2001).

Translocations are a relatively easy and direct approach to population recovery, but the genetic impacts of translocations are seldom examined. Given the small size of most reintroductions, concerns regarding inbreeding effects are warranted. Conversely, when augmenting an existing population, the negative impacts of introgressing genes from distant populations (outbreeding depression—Boitani 2001; Tallmon et al. 2004) are of concern.

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Fishers (*Martes pennanti*) are medium-sized mustelids that hunt in woody debris, thick brush, and forests (Buskirk and Powell 1994). They are opportunistic predators that forage on small mammals, birds, snowshoe hares (*Lepus americanus*), carrion, and porcupines (*Erethizon dorsatum*). In the western United States, fishers are found in low to middle elevation moist coniferous forests with high structural complexity (Banci 1989; Heinemeyer and Jones 1994; Jones 1991; Powell and Zielinski 1994; Zielinski et al. 2004). Foresters consider fishers beneficial because porcupines (*E. dorsatum*), which damage trees, are a preferred prey item (Davis 1997).

Historically, fisher pelts have been valuable (Hamilton and Cook 1955); in fact, fishers once brought some of the highest returns of all North American furbearers (Lewis and Aubry 1997; Seton 1927). Trapping, in concert with extensive habitat losses, led to widespread extirpation of fishers in the United States by 1930 (Douglas and Strickland 1987; Powell 1993). In Montana, Weckworth and Wright (1968) were unable to find records of fishers trapped or observed between 1930 and 1959. They concluded that fishers were extirpated from the state by 1930.

Three petitions were filed in the last decade that sought to list West Coast fisher populations as ''threatened'' under the

United States Endangered Species Act (Beckwitt in litt.; Carlton 1994; Greenwald et al. 2000). In 2004, the United States Fish and Wildlife Service found that listing fishers as threatened in California, Oregon, and Washington was ''warranted, but precluded'' due to higher-priority actions (United States Fish and Wildlife Service 2004). Their decision was based on recent scientific data documenting the limited range and isolation of fishers in the Coast Range, Cascades, and Sierra Nevada (Aubry and Lewis 2003; Drew et al. 2003; Wisely et al. 2004). Little is known about the status of fishers in the Rocky Mountains, as there is little published information on fishers in this region (Heinemeyer and Jones 1994; Powell and Zielinski 1994).

Because fishers are valued as a biological control, furbearer, and native carnivore, many translocation efforts have been undertaken to restore fisher populations nationwide (Berg 1982). Translocations in the northeast and upper Midwestern United States resulted in viable, expanding populations (Irvine et al. 1962; Kohn et al. 1993; Williams et al. 2000), but translocations on the west coast have been less successful (Aubry and Lewis 2003).

Fishers from 2 distinct subspecies, *Martes pennanti columbiana* and *Martes pennanti pennanti*, were introduced from British Columbia, Canada, and the Midwest (Minnesota and Wisconsin; Fig. 1) to Montana (Heinemeyer 1993; Roy 1991; Williams 1963a). Translocations placed 78 British Columbia fishers into western Montana and Idaho between 1959 and 1963 and another 110 fishers from Minnesota and Wisconsin into the Cabinet Range in northwestern Montana between 1989 and 1991 (Table 1; Fig. 1).

Although translocation success was never documented, current fisher occurrence in Montana has been interpreted as evidence of success. The lineage of existing populations is, however, unknown; Montana fishers could be descended from residual native populations, from the Midwestern and/or the British Columbia translocations, or a combination of relic and translocated individuals. Here we apply genetic techniques to investigate the origin of fisher populations in Montana.

Materials and Methods

Tissue collection.—We collected and sequenced 207 tissue samples (primarily muscle from trapper-harvested carcasses) to compare the genetic composition of Montana fishers to samples from British Columbia (*M. p. columbiana*), Minnesota (*M. p. pennanti*), and Wisconsin (*M. p. pennanti*). Eighty-five fishers trapped in Montana between 1993 and 2005 were included in our analyses. Montana samples are from 2 distinct regions, northwest and west-central Montana. We defined northwestern Montana as lands west of the Flathead River and north of the Clark Fork River; west-central Montana was defined as the area south of the Clark Fork River or east of the Flathead River and west of the Continental Divide (Fig. 1).

Reference samples from British Columbia, Minnesota, and Wisconsin were collected in many of the same localities that produced fishers for the translocations (Heinemeyer 1993; Roy 1991; Vinkey 2003). Midwestern samples ($n = 30$) came from animals harvested in Minnesota ($n = 11$) and Wisconsin ($n = 11$) during the winter of 2002, as well as from 8 marked fishers captured in the Midwest that were released in northwestern Montana (Heinemeyer 1993; Roy 1991). British Columbia samples ($n = 92$) were gathered from animals trapped in 2003 and 2004; over half (54) of the British Columbia samples were taken from the same region as source animals for the 1959–1963 translocations (Appendix I). The American Society of Mammalogists guidelines on animal care and use were followed for all live mammals that were handled (Animal Care and Use Committee 1998).

Mitochondrial DNA sequencing and analysis.—Mitochondrial DNA was extracted from tissues following standard protocols (DNeasy Tissue Kit, QIAGEN Incorporated, Hilder, Germany). Using polymerase chain reaction (PCR), we amplified 301 base pairs (bp) of the control region using species-specific primers MP-F′ and MP-R′ (Drew et al. 2003) and 428 bp of cytochrome *b* (*Cytb*) using primers CanidL1 and H15149 (Kocher et al. 1989; Paxinos et al. 1997). For the control region, our protocol followed Drew et al. (2003), except PCR reactions were run in a total volume of 50 μl with 2.5 mM $MgCl_2$ and 1.5 U Taq polymerase (Applied Biosystems, Foster City, California). For *Cytb* we used the following protocols: PCR reactions were run in a total of 50 μl containing 50–100 ng DNA, 1× reaction buffer (Applied Biosystems), 2.5 mM $MgCl_2$, 200 μM each dNTP, 1 μM each primer, and 1 U Taq polymerase (Applied Biosystems). The PCR program was an initial 94°C/5 min, followed by 34 cycles of 94°C/1 min, 50°C/1 min, and 72°C/1 min 30s, concluding with 72°C/5 min.

For both regions, PCR products were purified using the QIAquick PCR Purification Kit (QIAGEN) and directly sequenced using the Thermo Sequenase Cycle Sequencing Kit (USB, Cleveland, Ohio) and a Li-Cor 4200 DNA imager with Li-Cor Eseq sequencing software (Li-Cor Biotechnology, Lincoln, Nebraska). Sequence editing and alignment was completed with AlignIR (Li-Cor). To calibrate our control-region sequences with Drew et al. (2003) we sequenced 10 samples whose haplotypes had been previously published (Drew et al. 2003).

Data analysis.—We examined the spatial distribution of haplotypes by plotting each Montana sample and its associated haplotype on a map that also displayed release sites of fisher translocations. Samples were assigned to 1 of 4 groups based on their place of origin: British Columbia, the Midwest (Minnesota and Wisconsin), northwestern Montana, and west-central Montana. We grouped the Minnesota and Wisconsin samples into 1 category because they had a common origin: the Wisconsin populations were founded from Minnesota fishers introduced between 1956 and 1967 (Williams et al. 1999).

Montana samples were grouped into northwest and west-central Montana because we had a priori knowledge of their different translocation histories, source populations, and local geography. A major river (the Clark Fork), a major interstate highway (Interstate 90), a mountain range, and over 200 km lie between sampling regions, making gene flow between the 2 regions unlikely.

All quantitative analyses were based on control-region haplotypes. To illustrate the relationships among control-region haplotypes and show the relative frequency of haplotypes, we created a minimum spanning network. We tested whether the sample groups were statistically similar using contingency tables; all χ^2 values were Yates-corrected (Zar 1999). We estimated population subdivision by estimating pairwise Φst using program Arlequin version 2.00 (Michalakis and Excoffier 1996; Excoffier et al. 1992), and displayed these estimates using a neighbor-joining tree (MEGA Version 2.1; Kumar et al. 2001). Finally, where determining the likelihood of failing to detect a haplotype was important, we conducted power analyses using the binomial distribution: $(1 - p)^n$ where p = haplotype frequency and n = sample size.

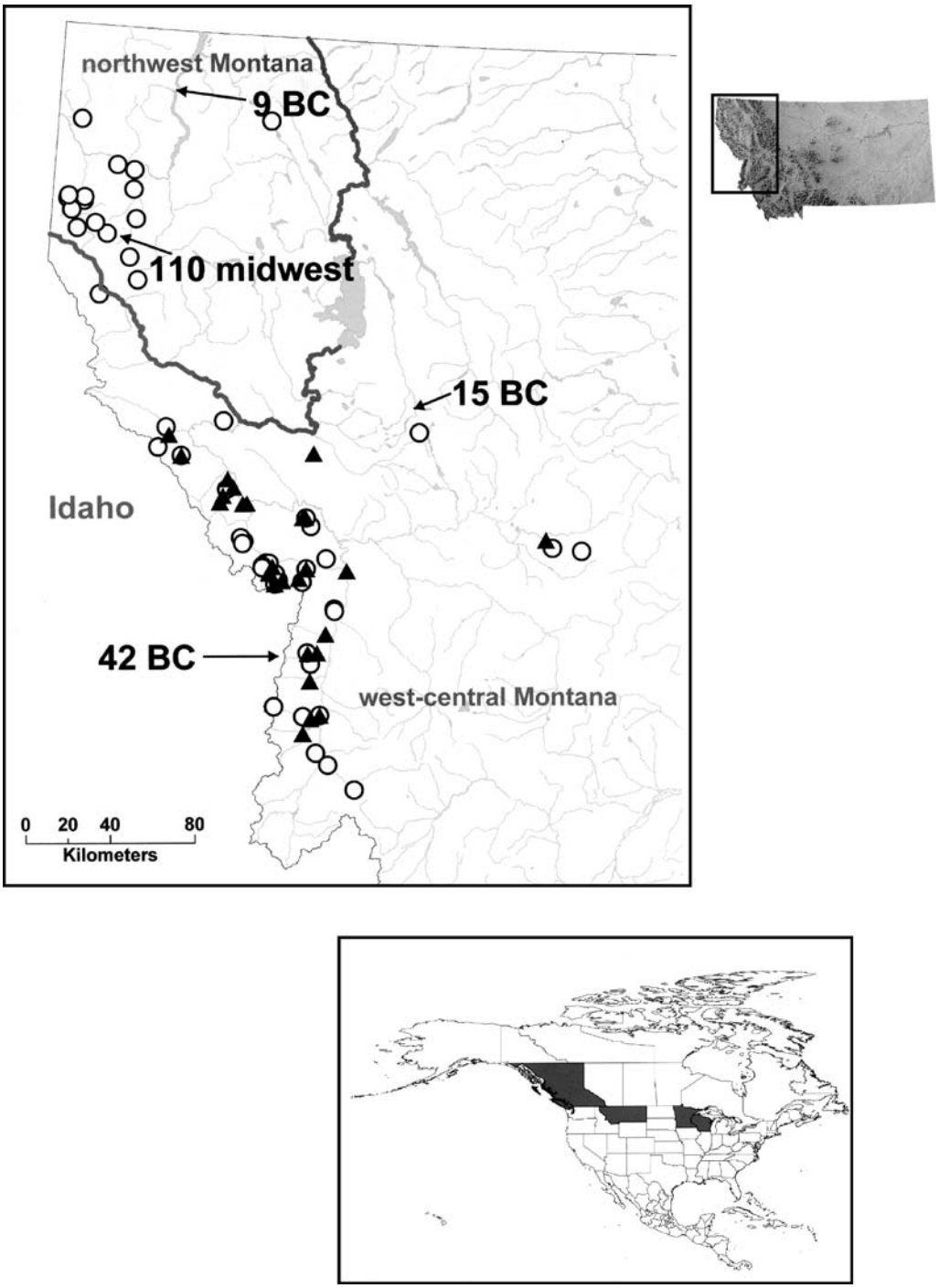

Fig. 1.—Distribution of control-region haplotypes in Montana. Arrows indicate introduction sites, and associated text indicates number and origin of *Martes pennanti* released. ▲ = Haplotype 12; ○ = other haplotypes. Shaded areas on inset map of North America indicate Midwestern states (Minnesota and Wisconsin) and the Canadian province (British Columbia) from which source population samples were obtained (see Appendix I for details); Montana is also shown shaded.

Results

Control region.—The most notable result was that haplotype 12 was only found in west-central Montana (Fig. 1; Table 2). The samples from west-central Montana did not contain haplotypes 1, 5, 9, 10, and 11, which were found in the samples from the Midwest and from northwestern Montana. The northwestern Montana samples did not contain haplotypes 7, 9, and 11, which were common in the British Columbia samples (Table 2).

Gene diversity, the probability that 2 randomly selected haplotypes in a sample are different (Nei 1987), was 0.631 (standard deviation ±0.051) in the Midwestern samples, 0.800 (±0.106) in those from British Columbia, 0.660 (±0.102) in northwestern Montana samples, and 0.656 (±0.026) in west-

TABLE 1.—Fisher translocations into western Montana and west-central Idaho. See Fig. 1 for mapped locations of introductions. Male fishers are abbreviated as M and females as F.

Dates of release	Release location[a]	Source population	Number and sex (M,F,unknown)
1959	Purcell Range, Montana	British Columbia	9 (4,5,0)
1959–1960	Swan Range, Montana	British Columbia	15 (8,7,0)
1960	Pintler Range, Montana	British Columbia	12 (4,8,0)
1962–1963	Clearwater Range, Idaho	British Columbia	42 (10,12,20)
1989–1991	Cabinet Range, Montana	Midwest	110 (47,63,0)

[a] Note: The Purcell and Cabinet ranges are in northwestern Montana; the Pintler and Swan ranges are in west-central Montana. The Clearwater Range is just west of west-central Montana in Idaho.

central Montana samples. Most adjacent haplotypes differed by a single bp change, usually a transition (Fig. 2).

The 4 sample groups were significantly different ($\chi^2 = 328.82$, $P < 0.001$), as were the Midwest and northwest Montana samples ($\chi^2 = 11.71$, $P = 0.008$) and the British Columbia and west-central Montana samples ($\chi^2 = 82.01$, $P < 0.001$). Comparing the northwestern Montana samples to those from the Midwest, the largest contribution to the χ^2 value was the high proportion of haplotype 6, common in British Columbia (Fig. 3a). By far the largest difference between the samples from British Columbia and those from west-central Montana was the presence of haplotype 12 in west-central Montana (Fig. 3b). Using Φst, the least substructure was detected between samples from west-central Montana and British Columbia ($\Phi st = 0.161$) and between those from northwestern Montana and the Midwest ($\Phi st = 0.173$), whereas the greatest substructure was between samples from west-central Montana and the Midwest ($\Phi st = 0.355$; Fig. 4).

We were particularly interested in haplotype 12, because it was the only haplotype unique to Montana. All releases in west-central Montana were fishers that originated in British Columbia (Fig. 1) and haplotype 12 was absent from our British Columbia sample. The trapping dates and locations of a number of control-region haplotype 12 samples (7 fishers trapped within 3 years of the last introduction in 1991 at distances up to 200 km south of the release sites) make it likely that control-region haplotype 12 was present in west-central Montana before the introduction of Midwestern fishers to northwestern Montana.

TABLE 2.—Results of genetic analysis of the mitochondrial DNA control-region for 207 samples combined with 47 additional samples reported by Drew et al. (2003). MN = Minnesota, WI = Wisconsin, BC = British Columbia, Canada, NW MT = northwest Montana, and WC MT = west-central Montana.

Haplotype	MN, WI	MN[a]	NW MT	WC MT	BC	BC[b]	Totals
1	13		10		1	1	25
4			1	13	16	3	33
5	7		1				8
6			4	24	19	13	60
7	1			1	23	5	30
9					18	8	26
10	9	16	2				27
11		1			15		16
12				29			29
Totals	30	17	18	67	92	30	254

[a] Minnesota samples reported by Drew et al. 2003.
[b] British Columbia samples reported by Drew et al. 2003.

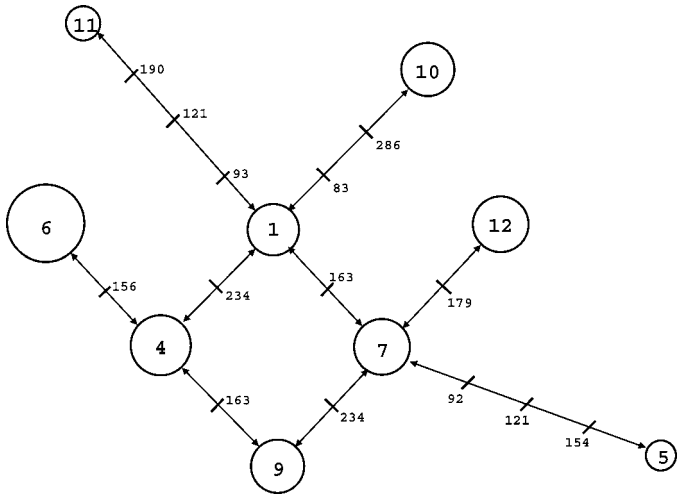

FIG. 2.—Minimum spanning network for 9 control-region haplotypes sampled in Midwestern (Minnesota and Wisconsin) and Western (British Columbia and Montana) populations of *Martes pennanti*. Circle size indicates relative frequency of a haplotype in our sample ($n = 254$). Sites that result in differences between haplotypes are shown; for example haplotype 7 differs from haplotype 12 by a single substitution at bp 179. Locations of all mutations are calibrated with Drew et al. (2003).

Combining our British Columbia samples with those from Drew et al. (2003), a total 122 samples from British Columbia were analyzed at the control region. Assuming that our samples and those of Drew et al. (2003) were randomly drawn from the population, if control-region haplotype 12 represented more than 2.4% of the British Columbia source population, we would have a better than 95% chance of detecting it. We did not detect haplotype 12 in British Columbia and can reasonably conclude that it is absent.

Cytochrome b.—Two haplotypes within the *Cytb* region were found, differing by a transversion at bp 117. Haplotype "A" was present in all locations; however, a novel haplotype, labeled "B" (Genbank accession number AY998986), was only found in samples from west-central Montana that also carried control-region haplotype 12. In fact, all samples with control-region haplotype 12 also had *Cytb* haplotype B, and vice versa. Forty-three percent (29/67) of the west-central Montana fishers that we sampled were of this type.

DISCUSSION

One-hundred-nineteen fishers have been introduced to northwestern Montana, 9 in 1959 from British Columbia (Weckworth and Wright 1968) and 110 between 1989 and 1991 from Minnesota and Wisconsin (Heinemeyer 1993; Roy 1991). Not surprisingly, fisher populations in northwestern Montana are more similar to Midwestern source populations

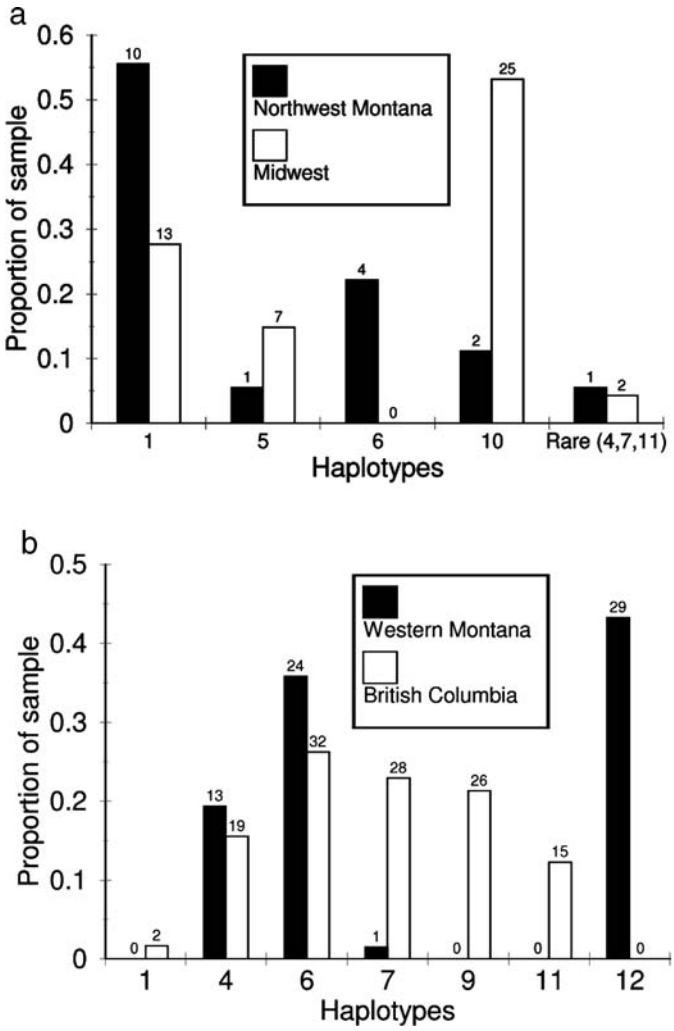

FIG. 3.—Haplotype proportions comparing a) northwestern Montana to the Midwest (Minnesota and Wisconsin) and b) British Columbia to west-central Montana. Rare haplotypes were grouped for contingency table analysis. Numbers above each bar indicate the number of samples comprising the proportion. Both comparisons were highly significant ($\chi^2 = 11.71$, $P = 0.008$; $\chi^2 = 82.01$, $P < 0.001$, respectively).

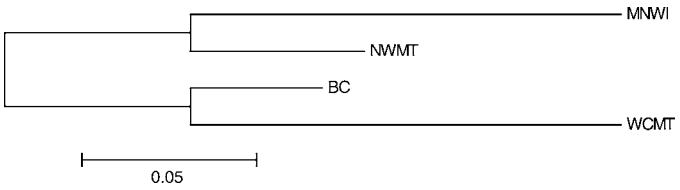

FIG. 4.—Neighbor-joining tree based on pairwise Φst and the geographical origin of *Martes pennanti* samples (BC = British Columbia, MNWI = Minnesota and Wisconsin, NWMT = northwestern Montana, and WCMT = west-central Montana).

than to the other analyzed populations (Fig. 4). Twenty-seven fishers from British Columbia were translocated to west-central Montana in 1959 and 1960 (Weckworth and Wright 1968) and 42 fishers from British Columbia were released nearby in Idaho in 1962 and 1963 (Williams 1963b; Table 1). West-central Montana populations are most similar to populations from British Columbia; however, there are significant differences between the 2 populations.

Importantly, almost half of the samples in west-central Montana have control-region haplotype 12, which is novel to this area and not found in any source population or documented elsewhere in North America (Drew et al. 2003). Additionally, all control-region samples that were haplotype 12 were *Cytb* haplotype B, which was also not found in samples from the other 3 populations analyzed. Due to the association between control-region 12 and *Cytb* B, it is difficult to interpret the evolutionary history that leads to haplotype 12 and *Cytb* B being found together. Conservatively, these haplotypes can be thought of as equivalent to a 2-step control-region mutation, though *Cytb* is 4 times more highly conserved than is the control region (Hosada et al. 1997).

Although we cannot eliminate the possibility of control-region haplotype 12 being present in British Columbia introductions, based on our samples from the source populations, we can state that if present it is very rare. To argue that this haplotype is of British Columbian origin, one needs to argue 1) that a rare haplotype likely representing <2.5% of the population was included among a relatively small group of female fishers introduced into the area (a total of 37, including releases of fishers from west-central Montana and Idaho and assuming half of the 20 fishers of unknown sex were female; Table 1), 2) that this rare haplotype was not eliminated by genetic drift, and 3) its progeny came to dominate the local population.

The alternate, and more parsimonious, explanation is that fishers were not extirpated from west-central Montana, that the original population contained unique haplotypes, and that these have persisted. The 1st explanation, although possible, requires a series of unlikely events. Given that extirpation was never formally documented and that fishers in west-central Montana are associated with the largest wilderness complex in the conterminous United States, we feel that the persistence of a native refugium population is the more likely scenario. Wisely et al. (2004) found that fishers display a high degree of genetic structure over relatively short distances; thus the presence of unique haplotypes in native Montana populations is a reasonable expectation.

Unfortunately, despite inquiries to 51 North American mammal collections, we were unable to locate tissue samples from Montana before the 1st introductions in 1959, and thus we can not definitively identify native Montana haplotypes.

We conclude that fishers with haplotype 12 are likely descended from a maternal lineage unique to Montana and adjacent areas in Idaho, and therefore translocations of fishers into west-central Montana were augmentations and not reintroductions. Fishers may have been locally extirpated in Montana, but the Selway–Bitterroot Mountains of Montana and Idaho likely functioned as refuge for native fishers.

In northwestern Montana, the translocations resulted in the establishment of fisher populations with a preponderance of Midwestern haplotypes. The possibility exists that importation of individuals to this region was also an augmentation, but the observed haplotypes from northwestern Montana are

consistent with British Columbia and Midwestern source populations and lack haplotype 12. Differences between Midwestern and northwestern Montana fishers were largely due to the presence of a haplotype common in the British Columbia samples. Given that British Columbia fishers were introduced into northwestern Montana in 1959 (Table 1), we believe it likely that fishers from northwestern Montana are descended from both the 1959 and 1989–1991 reintroductions.

Our findings have important management implications for fishers in the inland northwest. Fishers in west-central Montana show evidence of a distinct native lineage unrelated to translocations in the region. Our research, like that of a number of other researchers (Drew et al. 2003; Kyle et al. 2001; Williams et al. 2000; Wisely et al. 2004), shows that widespread fisher introductions have left a genetic legacy throughout the species' range.

Translocations can be an effective tool in wildlife management (Griffith et al. 1989), but managers must be cognizant of the genetic consequences of moving individuals between populations. Haphazard translocations can lead to genetic swamping of locally adapted traits and reduced genetic variability from founder effects (Leberg 1990, Tallmon et al. 2004). Extirpation should be demonstrated, not just posited, before introducing genetically and geographically distinct organisms into an area. This example illustrates that it is essential to understand the genetic composition of existing populations before introducing animals from outside populations.

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APPENDIX I

Locality information for reference samples of fishers, Martes pennanti. Minnesota samples ($n = 11$) were from the counties of Lake of the Woods, Beltrami, Roseau, and Koochiching. Wisconsin samples ($n = 11$) came from Oneida County. Eight Midwestern samples came from the above counties, although exact locations were not specified. Of the British Columbia samples ($n = 92$), 41 were taken within 100 km of Williams Lake in south-central British Columbia (source population for the 1959–1963 translocations), 12 were from fishers caught within a 200-km straight-line distance from Williams Lake (Adams Lake, 1; Clinton, 3; Chilko Lake, 4; unspecified south Cariboo or north Thompson, 4); 7 samples were from distances greater than 200 km but still from the west side of the Rocky Mountain continental divide (Prince George, 1; Burns Lake, 3; Smithers, 1; Anahim Lake, 2); the remaining samples came from fishers caught >200 km away from Williams Lake and on the east side of the Rocky Mountains (Chetwynd, 21; Dawson Creek, 4; Fort Saint John, 4). The origin of 4 British Columbia samples was unknown.