

GENETIC STRUCTURE OF SENSITIVE AND ENDANGERED NORTHWESTERN BADGER POPULATIONS (*TAXIDEA TAXUS TAXUS* AND *T. T. JEFFERSONII*)

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American badgers (*Taxidea taxus*) are semifossorial carnivores present in many arid regions of central and western North America. Negative demographic trends have prompted recent discussion concerning their conservation status in the northwestern portion of their range. As such, further information regarding the metapopulation structure of this species and factors affecting dispersal is needed. To provide a preliminary assessment of genetic structure and variation, badgers from Alberta and British Columbia, Canada, and Montana were sampled and genotyped at 12 microsatellite loci, including individuals from 2 subspecific designations: *T. t. taxus* and *T. t. jeffersonii*. Relatively high levels of genetic variation were observed (average expected heterozygosity [H_E] = 77%). Gene flow between prairie populations of *T. t. taxus* did not seem to be restricted, nor did there seem to be a restriction of gene flow for populations within mountain ranges for *T. t. jeffersonii*. In contrast, minimal gene flow was observed between populations separated by mountain ranges. Our results support the current geographic delineation of the northwestern subspecies, *T. t. taxus* and *T. t. jeffersonii*, and have implications for their conservation by identifying genetically distinct units that may have independent population dynamics.

Key words: American badger, conservation genetics, genetic structure, mustelid, population fragmentation, *Taxidea taxus*

American badgers (*Taxidea taxus*) are solitary, semifossorial mustelids that are found throughout much of central and western North America. Badgers are known to inhabit regions ranging from below sea level to elevations >3,600 m. They prefer treeless areas but can sometimes be found in savannah and forest regions (Lindzey 1982). Four subspecies have been recognized on the basis of differences in skull size and pelage color (Long 1972): *T. t. berlandieri*, found in the southern United States; *T. t. jacksoni*, found in the north-central United States and southern Ontario in Canada; *T. t. taxus*, found in the Great Plains ecosystem ranging from the United States into the prairie provinces of Canada; and *T. t. jeffersonii*, found in western United States and southern British Columbia (Fig. 1).

Several ecological characteristics of badgers likely affect the levels of genetic variation within, and genetic structure between, their populations. Badgers can occur at densities up

to 6 individuals/km² (exceptionally high for a medium-sized carnivore) and the home ranges of males can overlap those of several females during the breeding season (Goodrich and Buskirk 1998; Messick and Hornocker 1981). Litters of 1–5 kits generally disperse by the age of 3–4 months (Lindzey 1982; Pattie and Fisher 1999). In the East Kootenay region of British Columbia, however, badgers were observed to disperse as late as 12 months of age (N. J. Newhouse, pers. comm.). Dispersing young females may move >52 km, whereas males may move >110 km (Messick and Hornocker 1981). These life history characteristics of relatively high densities and considerable dispersal potential might be expected to reduce genetic structure between populations. High densities may maintain high effective population sizes, such that the populations experience little genetic drift, as is thought to be the case for coyote populations (Roy et al. 1994). Similarly, movements of individuals between populations, such as long-distance dispersal events by juveniles, may genetically homogenize populations, as observed in northern North American wolverines and lynx populations (Kyle and Strobeck 2001, 2002; Schwartz et al. 2002).

Badgers have experienced negative demographic trends throughout their northern range (Adams et al., in press;

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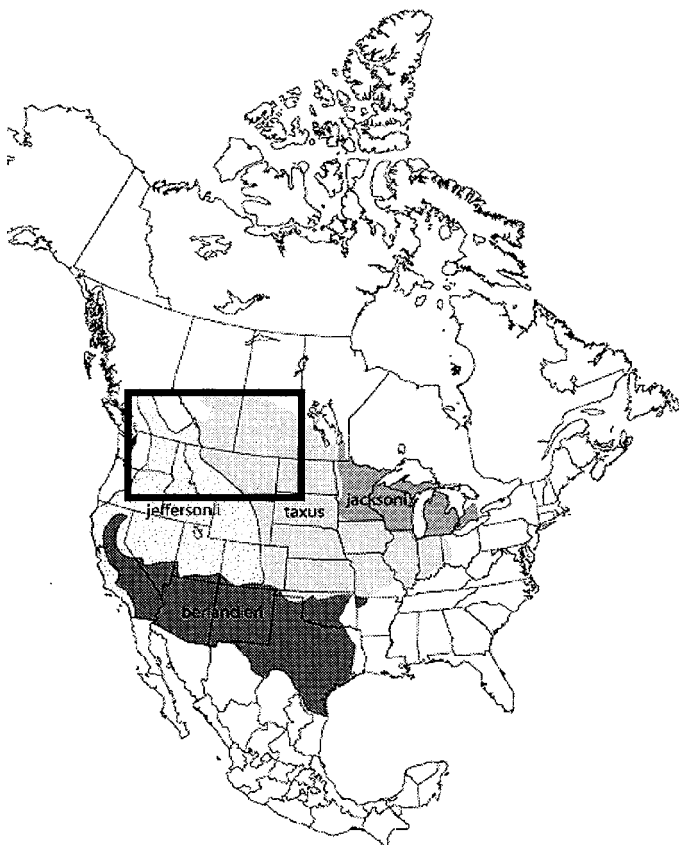
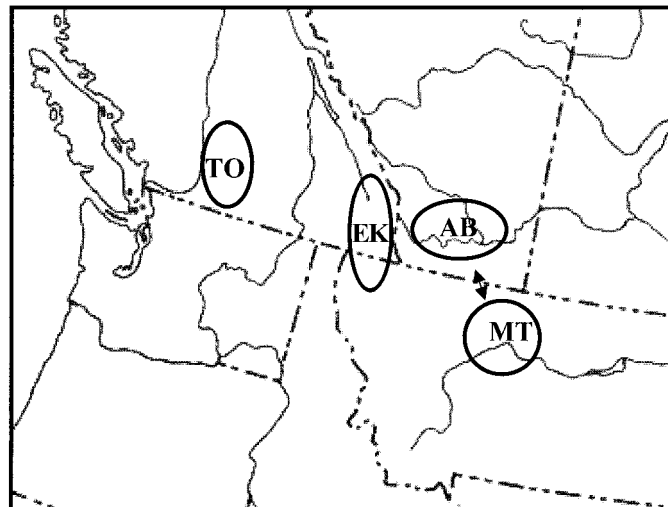


FIG. 1.—North American range of badgers showing subspecific distributions. Area within rectangular insert is enlarged in Fig. 2 and indicates study area.

Newhouse and Kinley 2000), and it is suspected that this may be the case across their entire distribution. These trends have been linked to declines in the distribution and suitability of habitat resulting from agriculture, urban development, and forest ingrowth. Loss of prey species, fur harvesting, and unsustainable mortality from motor vehicles are other likely contributors to this trend (Apps et al. 2002; Newhouse and Kinley 2000; Scobie 2002). Furthermore, badgers have a history of persecution, and are often perceived by humans as a pest species, for which they are shot or poisoned (Rahme et al. 1995). In Canada, both *T. t. jacksoni* in Ontario and *T. t. jeffersonii* in British Columbia are recognized as endangered (COSEWIC 2000), with as few as 200 and 600 animals remaining, respectively. Further, *T. t. taxus* is recognized as a sensitive species in Alberta (Scobie 2002). Given these observed negative demographic trends, populations may have become fragmented from one another and genetic variation may be lost from these populations. Such populations are thought to be more susceptible to local extirpation (Bijlsma et al. 2000; Brook et al. 2002; Keller and Waller 2002).

Genetic data, because they help to contribute to a thorough understanding of species ecology, are essential to the development of effective conservation programs. The goal of this study is to provide a preliminary overview of the genetic variation and structure of badgers from the northwestern part of



Scale ←→ 130 km

FIG. 2.—Map of sampled locations. Populations are represented by the following abbreviations: TO = Thompson–Okanagan; EK = East Kootenay (includes samples from northwestern Montana); AB = Alberta; and MT = north-central Montana. Arrow represents region of high gene flow between the AB and MT populations.

their range. The identification of discrete populations and their genetic interrelationships will provide additional information for conservation planning and a framework for proposed reintroduction programs that may want to identify appropriate genetic stocks for relocation.

MATERIALS AND METHODS

Sample collection.—Samples consisted of pelt clippings from fur houses, hair samples and plugs of ear tissue from radiotagged badgers, hairs from bait stations with barbed wire from which hairs were collected, and road-killed animals. All animal capture and immobilization protocols are outlined as per Apps et al. (2002).

Two badger subspecies were collected in this study, *T. t. taxus* and *T. t. jeffersonii* (see Fig. 1 for distribution of North American badger subspecies). From the subspecies *T. t. taxus*, we sampled 33 badgers from south-central Alberta (Calgary, Strathmore, Cayley, and Redcliff) and 30 from north-central Montana. From the subspecies *T. t. jeffersonii*, we sampled 8 badgers from northwestern Montana, 36 from the East Kootenay region of British Columbia (Invermere, Sparwood, Cranbook, and Fernie), and 26 from the Thompson and Okanagan regions of British Columbia (Fig. 2; see Appendix I for approximate coordinates of sampled localities). Note that the subspecies *T. t. taxus* is geographically separated from the subspecies *T. t. jeffersonii* by the Rocky Mountain range. Furthermore, the *T. t. jeffersonii* sampled from northwestern Montana and the East Kootenay regions are themselves geographically separated from the other populations of *T. t. jeffersonii* sampled from the Thompson and Okanagan regions of British Columbia by several interior mountain ranges including the Selkirk and Purcell ranges.

Laboratory methods.—DNA was extracted with a DNAeasy Tissue Extraction Kit (QIAGEN Inc., Mississauga, Ontario, Canada). Twelve polymorphic microsatellites were amplified by using primers developed in badgers (Tt-1, Tt-2, Tt-3, and Tt-4—Davis and Strobeck 1998), martens (MA-1 and MA-15—Davis and Strobeck 1998), wolverines (Ggu 234—Duffy et al. 1998; GG-443 and GG-465—

TABLE 1.—Genetic variation of northwestern badger populations as measured by average number of alleles (A), average expected heterozygosity (H_E), average observed heterozygosity (H_O), and number of individuals sampled in this study (n).

	n	A	H_E	H_O
Alberta	33	11	0.816	0.764
Central Montana	30	10.7	0.798	0.775
East Kootenay	44	10.4	0.792	0.822
Thompson–Okanagan	26	7.4	0.666	0.667
Average		9.9	0.768	0.757

Walker et al. 2001), ermine (Mer082—Flemming et al. 1999), and mink (Mvis072—Flemming et al. 1999; Mvi87—O'Connell et al. 1996). Amplification conditions are given in Davis and Strobeck (1998). DNA fragments were visualized by using an ABI Prism 377 DNA sequencer (PE Applied Biosystems Inc., Foster City, California) and analyzed with the programs GeneScan Analysis 2.02 and Genotyper 2.0 (PE Applied Biosystems Inc., Foster City, California).

Tests of disequilibrium.—Departures from Hardy–Weinberg equilibrium were tested for each of the 12 loci in Genepop 3.1d (Raymond and Rousset 1995) by using a Markov chain method following the algorithm of Guo and Thompson (1992). Genepop also was used to evaluate genotypic disequilibria among loci.

Heterogeneity of sampled regions.—Population heterogeneity was assessed by using the program STRUCTURE (Pritchard et al. 2000), which uses a Bayesian clustering method. This program infers the number of population clusters among the individuals genotyped without relying on a priori location information. STRUCTURE was run by using genotypes formatted with the program MSA (Dieringer and Schlötterer 2003).

Genetic variation.—Relative genetic variation in each population was assessed by using mean number of alleles, unbiased expected heterozygosity (H_E —Nei and Roychoudhury 1974) and observed heterozygosity (H_O).

Pairwise F_{ST} and genetic distance measures.—Nei's standard genetic distance (D_S —Nei 1972) was calculated by using programs designed by John Brzustowski (<http://www.biology.ualberta.ca/jbrzusto/Doh/php>, last accessed 20 April 2004). Pairwise F_{ST} estimates were obtained from Genepop 3.1d (Raymond and Rousset 1995; as per Weir and Cockerham 1984). The association between geographic and genetic distance values was tested by using a 2-way Mantel test (Mantel 1967; <http://www.fas.umontreal.ca/BIOL/legendre/>, last accessed 20 April 2004). A 3-way Mantel test (as per Smouse et al. 1986) also was used to test for the presence or absence of a barrier to gene flow (represented as a matrix of ones and zeros for the presence or absence of a barrier) while controlling for distance. Geographic distance was measured by taking the approximate centroid of each of the sampled regions.

Assignment test.—Two types of assignment tests were used to evaluate levels of gene flow and migration between regions; Doh (Paetkau et al. 1995—<http://www.biology.ualberta.ca/jbrzusto/Doh/php>, last accessed 20 April 2004), determines the log-likelihood that a genotype will occur in the population from which it was sampled and in all other populations tested. Individuals are then assigned to the population where their genotype has the highest likelihood of occurring (see Waser and Strobeck 1998). The other program used was STRUCTURE (Pritchard et al. 2000). Once this Bayesian clustering method has been used to infer the number of population clusters among the individuals genotyped, the program can be used to determine the probability of each individual genotype occurring in each of the clusters.

TABLE 2.—Genetic distance (Nei's standard genetic distance, D_S , above diagonal) and pairwise F_{ST} (as per Weir and Cockerham 1984; below diagonal) of northwestern badger populations.

	Central		East	
	Alberta	Montana	Kootenay	Thompson–Okanagan
Alberta	—	0.082	0.217	0.501
Central Montana	0.002	—	0.190	0.448
East Kootenay	0.036	0.031	—	0.333
Thompson–Okanagan	0.119	0.118	0.096	—

RESULTS

Tests of disequilibrium.—After accounting for sample-wise error (Dunn–Sidak method—Sokal and Rohlf 1995), several departures from Hardy–Weinberg equilibrium were observed. Loci Mvi87 and MA-15 violated Hardy–Weinberg equilibrium in all populations because of heterozygote deficiencies and were therefore removed from further analyses. Locus Tt3 also was shown to be heterozygote deficient in Alberta, and GG443 deviated from Hardy–Weinberg equilibrium in Alberta and the East Kootenay population. Because these deviations from Hardy–Weinberg equilibrium for Tt3 and GG443 were not found in the majority of the populations sampled, they were retained for further analyses.

Genotypic disequilibrium was observed for 4 pairs of loci: Tt4 with GG443 and Tt4 with GG465 in central Montana, and Mer083 with GG443 and MA1 with Ggu443 in the East Kootenay population. Because genotypic disequilibria were not observed for these loci in any other population, it is unlikely that they are physically linked and were therefore retained for further analyses.

Heterogeneity of sampled regions.—By using the program STRUCTURE (Pritchard et al. 2000), the number of clusters yielding the highest log-likelihood value based on the genotype data provided was $K = 4$ (with a burn-in of 10,000 and 1,000,000 replicates). Based on the geographic location of the majority of samples in each identified cluster, 4 separate populations were identified: Alberta, north-central Montana, northwestern Montana combined with the East Kootenay region of eastern British Columbia (henceforth referred to as the East Kootenay population), and the Thompson and Okanagan regions of British Columbia (Thompson–Okanagan; see Fig. 1).

Genetic variation.—Average expected heterozygosity (H_E) among the sampled regions was 77% (Table 1). Thompson–Okanagan (67%) was the only population with a significantly lower level of genetic variation (pairwise comparisons; Wilcoxon's signed-ranks test, $\alpha = 0.05$ —Sokal and Rohlf 1995).

Pairwise F_{ST} and genetic distance measures.—Pairwise F_{ST} ranged from very low (0.002) between Alberta and central Montana, to moderate (0.096–0.119) between Thompson–Okanagan and all other regions sampled (Table 2). D_S ranged from 0.082 to 0.501 (Table 2) and paralleled findings from F_{ST} estimates (2-way Mantel test: $r = 0.98$, $P = 0.04$). Neither F_{ST} nor D_S values were significantly correlated with geographic distance ($r = 0.239$, $P = 0.32$ and $r = 0.247$, $P = 0.37$, respectively). By using a 3-way Mantel test (as per Smouse

TABLE 3.—Genotype assignments of northwestern badger populations by 2 methods: Doh (Paetkau et al. 1995) and STRUCTURE with K = 4 (Pritchard et al. 2000). Leftmost column represents sample location, and top row represents where badgers were assigned by the 2 methods. Values within cells represent the number of individuals assigned by the 2 genotype assignment methods.

	n	Alberta		Central Montana		East Kootenay		Thompson–Okanagan	
		Doh	STRUCTURE	Doh	STRUCTURE	Doh	STRUCTURE	Doh	STRUCTURE
Alberta	33	19	15	12	16	2	2	0	0
Central Montana	30	10	14	17	14	3	2	0	0
East Kootenay	44	4	6	2	1	37	34	1	3
Thompson–Okanagan	26	1	0	0	1	0	0	25	25

et al. 1986), the presence or absence of a potential barrier to gene flow, in this case mountain ranges, was tested. When controlling for pairwise geographic distance with this test, F_{ST} and D_S values were found to correlate relatively strongly to the presence or absence of mountain ranges between them ($r = 0.725$, $P = 0.08$ and $r = 0.706$, $P = 0.08$, respectively), although not quite significantly.

Assignment test.—Results from Doh and STRUCTURE (Table 3; with K = 4) assignment tests were largely concordant (with some exceptions; see Table 4). A large number of cross-assignments were observed between the populations of *T. t. taxus* from Alberta and central Montana, but few individuals were cross-assigned from either of these prairie populations of *T. t. taxus* to the population of *T. t. jeffersonii* from East Kootenay. Furthermore, no individuals of *T. t. taxus* were cross-assigned to the Thompson–Okanagan population (Tables 3 and 4). A small number of East Kootenay badgers were assigned to populations of *T. t. taxus* and the Thompson–Okanagan population. Only 1 individual from the Thompson–

Okanagan population was cross-assigned to any other region; both methods place this individual in a population of *T. t. taxus* (Table 4; see “Discussion”).

DISCUSSION

Taxidea t. taxus.—Populations from southern Alberta and north-central Montana had relatively high levels of genetic variation (Table 1; $H_E = 82\%$ and 80% , respectively). Furthermore, gene flow between them was high, as reflected by low estimates of standard genetic distance (D_S) and pairwise F_{ST} (Table 2) and the high number of cross-assignments observed (Table 3). This is consistent with substantial dispersal abilities of juvenile badgers (Messick and Hornocker 1981) and the absence of strong barriers to dispersal in these regions (i.e., contiguous suitable habitat, no mountain ranges, and relatively low road densities). Several individual *T. t. taxus* were cross-assigned to the East Kootenay population (Tables 3 and 4), suggesting that, although the Rocky Mountains between these regions may have reduced gene flow, they do not act as

TABLE 4.—Cross-assigned individuals (individuals statistically assigned to a geographic location other than the location from which they were sampled) from northwestern badger populations. Individuals were grouped into 4 clusters and analyzed by 2 different assignment test programs, Doh and STRUCTURE. For STRUCTURE, the results are reported as P values based on K = 4. For Doh, the assignments are reported as approximate log-likelihood ratios and are based on separating the samples into 4 populations. In the leftmost column, the prefix describes where each sample was obtained. The rightmost column, Agreement, denotes the agreement between the 2 methods of genotype assignment. Note that badgers cross-assigned between Alberta and central Montana prairie populations of *Taxidea taxus taxus* were excluded from this table.^a

Badger no.	Locality assigned to	STRUCTURE (P)				Locality assigned to	Doh (log-likelihood ratio)				Agreement ^b
		AB	MT	EK	TO		AB	MT	EK	TO	
AB-1	EK	0.02	0.09	0.83	0.07	EK	10 ⁻²⁰	10 ⁻²⁴	10 ⁻¹⁹	10 ⁻²⁴	+
AB-2	EK	0.28	0.11	0.59	0.01	EK	10 ⁻¹⁷	10 ⁻¹⁷	10 ⁻¹⁷	10 ⁻³¹	+
MT-1	EK	0.19	0.07	0.72	0.02	EK	10 ⁻¹⁴	10 ⁻¹⁵	10 ⁻¹³	10 ⁻²⁰	+
MT-2	EK	0.19	0.04	0.74	0.03	EK	10 ⁻¹⁷	10 ⁻¹⁶	10 ⁻¹⁵	10 ⁻²⁵	+
MT-3	MT	0.12	0.46	0.16	0.26	EK	10 ⁻¹⁷	10 ⁻¹⁷	10 ⁻¹⁷	10 ⁻¹⁹	–
EK-1	AB	0.63	0.18	0.11	0.06	MT	10 ⁻¹⁴	10 ⁻¹¹	10 ⁻¹¹	10 ⁻¹⁸	±
EK-2	AB	0.85	0.02	0.12	0.02	TO	10 ⁻²¹	10 ⁻¹⁹	10 ⁻¹⁵	10 ⁻³⁰	–
EK-3	AB	0.89	0.02	0.06	0.03	TO	10 ⁻¹⁹	10 ⁻²⁰	10 ⁻¹⁵	10 ⁻²¹	–
EK-4	AB	0.69	0.15	0.15	0.01	AB	10 ⁻¹³	10 ⁻¹⁴	10 ⁻¹⁴	10 ⁻²⁷	+
EK-5	AB	0.43	0.14	0.38	0.05	TO	10 ⁻¹³	10 ⁻¹⁴	10 ⁻¹³	10 ⁻²²	–
EK-6	AB	0.65	0.02	0.33	0.01	TO	10 ⁻²¹	10 ⁻¹⁷	10 ⁻¹⁶	10 ⁻³⁴	–
EK-7	MT	0.32	0.40	0.26	0.02	AB	10 ⁻¹⁶	10 ⁻¹⁶	10 ⁻¹⁶	10 ⁻²³	±
EK-8	TO	0.21	0.09	0.23	0.48	AB	10 ⁻¹⁶	10 ⁻¹⁹	10 ⁻²¹	10 ⁻¹⁹	–
EK-9	TO	0.03	0.01	0.06	0.90	TO	10 ⁻²²	10 ⁻¹⁸	10 ⁻¹⁷	10 ⁻¹⁶	+
EK-10	TO	0.07	0.20	0.09	0.65	AB	10 ⁻¹⁸	10 ⁻²¹	10 ⁻²⁰	10 ⁻²⁰	–
EK-11	EK	0.16	0.20	0.61	0.04	TO	10 ⁻¹⁹	10 ⁻¹⁶	10 ⁻¹⁸	10 ⁻²²	–
TO-1	MT	0.23	0.40	0.34	0.03	AB	10 ⁻¹³	10 ⁻¹⁴	10 ⁻¹³	10 ⁻²¹	±

^a Abbreviations: AB = Alberta; MT = central Montana; EK = East Kootenay; and TO = Thompson–Okanagan.
^b ± = there was agreement between the 2 methods that the assignment went to a population of *T. t. taxus*.

a complete barrier to genetic exchange between badger subspecies. Investigation of populations of *T. t. taxus* from other Canadian prairie provinces and north-central United States are needed to determine if high genetic variation and gene flow are maintained throughout the distribution of this subspecies.

Taxidea t. jeffersonii.—Genetic variation in the East Kootenay population was nearly as high as that observed for the 2 sampled populations of *T. t. taxus* (Table 1). This finding was unexpected given the relatively dramatic demographic declines reported in this region (Apps et al. 2002; Newhouse and Kinley 2000), which may suggest that these demographic declines have been relatively recent and that the level of genetic variation has yet to diminish. The level of genetic variation observed in the East Kootenay region also may be a reflection of low levels of gene flow into this area from *T. t. taxus*. These individuals would likely introduce new allelic variants and hence maintain a relatively high level of genetic variation in the East Kootenay population.

Gene flow did not appear to be impaired between the sampled regions of northwestern Montana and the East Kootenay region of British Columbia (Tables 2 and 3), nor was there any indication of substructure (as assessed by the program STRUCTURE) within these regions. This result was not unexpected given that few physical barriers to gene flow exist between these regions and the dispersal capabilities of this species. The finding suggesting that the badgers in northwestern Montana and the East Kootenay region of British Columbia exist as a single population should be considered preliminary, however, because only 8 individuals were sampled from northwestern Montana. Additional sampling from this region would help to more clearly determine the degree of genetic homogeneity between these areas.

Few individuals sampled from the East Kootenay population were cross-assigned to the 2 prairie populations of *T. t. taxus* (6 and 7 individuals cross-assigned by Doh and STRUCTURE software programs, respectively) and very few were cross-assigned to the Thompson–Okanagan population (1 and 3 cross-assigned by Doh and STRUCTURE, respectively; Tables 3 and 4). Hence, gene flow appears somewhat limited between the East Kootenay population and other regions sampled, which is further supported by moderately high pairwise D_S and F_{ST} values to this population (Table 2).

The level of genetic variation ($H_E = 67\%$) in the Thompson–Okanagan population was significantly lower than observed in all other sampled populations. Thompson–Okanagan badgers also were quite distinct from the other *T. t. jeffersonii* sampled in the East Kootenay population (Tables 2 and 3). In fact, the genetic distances between the Thompson–Okanagan and East Kootenay populations were larger than those observed between the East Kootenay and 2 prairie populations of *T. t. taxus*. The 1 individual that was cross-assigned from the Thompson–Okanagan population was assigned most strongly to the prairie populations of *T. t. taxus* (see Tables 3 and 4). This individual badger was thought to have originated from the Thompson–Okanagan population; however, some of the samples obtained from the region originally were acquired during suspected

poaching cases by conservation officers (O. Dyer, pers. comm.). This cross-assignment may be the result of a very distant dispersal event, or more likely, a sample that may have been taken from a region that the hunter did not want to disclose.

Decreased genetic variation, elevated genetic distances, and very few cross-assignments to other populations imply that Thompson–Okanagan badgers form an insular population. The insularity of this population is not surprising because habitat suitability in portions of the range of *T. t. jeffersonii* are much less contiguous than those elsewhere (Apps et al. 2002). Insular groups often have smaller effective sizes and their long-term viability may be compromised (Bijlsma et al. 2000; Brook et al. 2002; Keller and Waller 2002). Furthermore, badgers in the Thompson–Okanagan region, on the northern periphery of the species' range, may be more susceptible to stochastic events that may promote local extirpation (Hanski 1999).

Gene flow between subspecies.—Evidence for gene flow between populations of *T. t. taxus* in Alberta and central Montana and populations of *T. t. jeffersonii* in the East Kootenay region was provided by both assignment test methods (see Table 4). Some individuals appeared to have genotypes more similar to those found in populations of the other subspecies, and thus may have been migrants, or offspring of migrants, from one region to the other. These findings do indicate reduced levels of gene flow between populations of these 2 subspecies at the edges of their distributions and support the current geographic delineation of the subspecies *T. t. taxus* and *T. t. jeffersonii*. However, further tests of subspecies validity should be provided by mitochondrial DNA, which mutates more slowly than microsatellites and thus contains signatures of older genetic events.

Conservation implications.—Within the subspecies *T. t. taxus*, high levels of genetic variation were detected and there appear to be few barriers to gene flow despite the observation of negative demographic trends for this subspecies within Alberta (Scobie 2002). This suggests that demographic declines have been quite recent in Alberta, or that the number of badgers has not decreased to the point where negative population trends may be reflected in the genetic fingerprint of these populations.

Relatively low levels of genetic variability and genetic exchange with other populations for Thompson–Okanagan suggest that this population is at considerable conservation risk because of its insularity and susceptibility to negative stochastic events. Hence, this region may be appropriate for concerted conservation efforts such as attempting to reestablish connectivity between other populations of *T. t. jeffersonii*. This may be a challenge, however, because limited numbers of this subspecies persist in Canada (Adams et al., in press; Newhouse and Kinley 2000). Examination of more southerly populations of *T. t. jeffersonii* within the same mountain range from the states of Washington and Oregon may identify populations that are genetically similar to those of the Thompson–Okanagan regions, and that may therefore be more appropriate genetic stocks for proposed reintroductions into southern British Columbia. Genes, like animals, can become locally adapted

(Carvalo 1993) and, therefore, genetic differentiation among regions should be a consideration when relocating animals.

Trends in other carnivores.—Genetic variation in badgers was high compared to that found by other studies of mustelids using microsatellites (*T. taxus*, H_E avg = 77%; *Martes americana*, H_E avg = 58–63%—Kyle et al. 2000; Kyle and Strobeck 2003; Small et al. 2003); *Martes pennanti*, H_E avg = 62%—Kyle et al. 2001; and *Gulo gulo*, H_E avg = 63%—Kyle and Strobeck 2001, 2002). Although it is not entirely clear why higher levels of genetic variation exist in badgers, historically higher effective population sizes in this species may be responsible.

It is difficult to make appropriate population genetic comparisons between badgers and other carnivores because few studies have been conducted on species that exist in similar geographic regions with similar life history characteristics. However, low levels of genetic structure and high genetic variation were observed in another prairie carnivore, the coyote (Roy et al. 1994), that are consistent with our results for *T. t. taxus*. The similarities observed between coyotes and prairie badgers are likely due to their similar dispersal capabilities, relatively continuous habitat, and high effective population sizes.

The insularity of the peripheral Thompson–Okanagan badger population provides an example similar to that observed for wolverines (*G. gulo*) from Idaho (Kyle and Strobeck 2001, 2002) and brown bears (*Ursus arctos*) from Yellowstone National Park in Wyoming (Paetkau et al. 1998). In all these cases, animals on the edge of their contiguous distribution are genetically fragmented from other populations and display lower levels of genetic variation.

In conclusion, it should be noted that we have sampled only a small part of the overall range of badgers in North America. Further studies are required to identify additional genetically distinct badger populations that may require conservation attention (e.g., the endangered subspecies *T. t. jacksoni* in Ontario). We also recommend additional studies using other molecular markers (mitochondrial DNA and the Y chromosome) to further test and refine the subspecific designations of this species, similar to the work by Small et al. (2003) revealing 2 distinct clades of martens in northwestern North America. Research with other types of markers, combined with the data from rapidly evolving nuclear DNA markers in this study, would help establish whether patterns of gene flow are recent or reflect long-standing population divisions. Fine-scale studies to assess the impact of roads on the movement of badgers also would be appropriate. For instance, use of techniques such as baited hair snags to detect real-time dispersal events of individuals from unique genetic identification of the hairs can help to clearly identify those factors that influence and limit dispersal events and influence the genetic structure and variation observed in this species.

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APPENDIX I

Localities and sample sizes.—Samples obtained from south-central Alberta were either from road-killed animals or fur houses, and reported as coming from near: Calgary ($n = 18$; 51°05'N, 115°34'W), Strathmore ($n = 8$; 51°30'N, 113°23'W), Cayley ($n = 2$; 50°27'N, 113°51'W), and Redcliff ($n = 5$; 50°05'N, 110°47'W). From north-central Montana, 30 badger samples were collected from fur houses that were reported to have been collected from the between the Havre and Lewiston regions of the state (approximately 48°05'N, 110°00'W). As part of an ongoing ecological study (see Apps et al. 2002), samples were taken from 8 northwestern Montana badgers (between approximately 48°08'N, 110°05'W and 48°05'N, 115°02'W). As part of this same study, 36 badgers were collected from within the East Kootenay region of British Columbia between the towns of Invermere (50°30'N, 116°02'W) and Fernie (49°54'N, 115°04'W). Finally, 26 badgers samples were obtained from the Thompson and Okanagan regions of British Columbia between the cities of Kamloops (50°07'N, 122°57'W) and Kelowna (49°54'N, 119°29'W; see Figs. 1 and 2).